



Spatiotemporal distribution of Arctic herbivores in spring: Potential for competition?

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ABSTRACT

Biotic interactions are important to the structure and dynamics of food webs and may affect the spatial and temporal distribution of species. In the Arctic, spring snow-cover limits food availability at a critical time for herbivores, potentially leading to resource competition. This study investigates the potential for competition over forage resources during spring in a high-Arctic herbivore community comprising the resident, endemic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and the migratory pink-footed goose (*Anser brachyrhynchus*) and barnacle goose (*Branta leucopsis*). First, we investigated herbivore behaviour that could indicate the potential for competition by conducting a field study, and second, we quantified the effects of snow-cover extent, vegetation type and presence of potential herbivore competitors on the spatiotemporal distributions of herbivores using camera-traps in one early and one late snow melt year. Only reindeer and geese appeared with sufficient sample sizes for analysis. The field study revealed that reindeer and geese foraged in the same areas, particularly moss tundra habitats. Although geese were regularly alerted by reindeer, no direct aggressive interactions were observed. The camera-trap study showed that neither of the herbivores significantly affected the spatiotemporal distribution of its potential competitor, but reindeer and goose distribution was instead driven by snow-cover extent and vegetation type. However, the shared space use by these species may lead to different types of interactions, such as facilitation or exploitative competition, which require further assessment, including dietary overlap studies, particularly in the context of climate change-induced shifts in snow melt timing and herbivore abundances.

1. Introduction

Species interactions are important drivers of the spatiotemporal distribution of populations and play a crucial role in the structure and dynamics of food webs (Barrio et al., 2016). Identifying drivers of species' spatial ecology is crucial for the understanding of

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community structure and habitat use, especially in relation to ongoing climate changes and increasing anthropogenic disturbance of wildlife habitats (Constable et al., 2022). Both abiotic conditions, like climate and other environmental factors, and biotic interactions impact the distribution of species on regional and local scales (Barbaro et al., 2019; Leach et al., 2016; Wisz et al., 2013). For example, facilitative interactions may be a cause of species co-occurrence, while resource competition often leads to spatial segregation because of interference or exploitative competition (Amarasekare, 2003; MacArthur, Levins, 1967). Competitive interactions, particularly in resource limited ecosystems, can arise between species with similar niches (Connor, Simberloff, 1979). Species may select different habitats, although they are ecologically similar, such as in the case of mountain hare (*Lepus timidus*) and arctic hare (*Lepus europaeus*) (Thulin, 2003) or forage in the same area but utilize different forage resources such as musk oxen (*Ovibos moschatus*), Arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus muta*) that have low dietary overlap, but similar area use (Schmidt et al., 2018). Habitat use and patterns in spatiotemporal distribution and co-occurrence can hence provide useful insights to understand the potential for interactions between species (Barrio et al., 2013).

Periods of limited access to resources may intensify resource competition (Seyer et al., 2020), which may in turn change species' spatial co-occurrence. In the Arctic, long winters and short growing seasons limit the availability of food resources. Both resident and migratory arctic herbivores rely on body reserves during the winter and in early spring, prior to the breeding season, their reserves are depleted (e.g., Klaassen et al., 2006; Mortensen et al., 1983; Reimers et al., 1982; Tombre et al., 1996). Therefore, snow-cover extent and spring snow melt, which modify spring forage availability in the Arctic, might cause increased potential for competition over forage resources at this critical time. The spring season is undergoing rapid climatic changes in the Arctic (Hanssen-Bauer et al., 2019; Isaksen et al., 2022), including variable onset of the growing season (Karlsen et al., 2022). Warmer temperatures may advance the onset of snow melt (Høye et al., 2007), while in contrast, predicted increases in precipitation (Bintanja, 2018) may also lead to prolonged snow-cover making food resources unavailable prior to the breeding season. Thus, understanding species interactions and co-occurrence, and how they are linked to the distribution and melting of snow in spring is important.

The high-Arctic Svalbard is a region where climate change is happening at a very rapid pace compared to other places on Earth (Isaksen et al., 2022). Here, the vertebrate herbivore guild consists of only two widespread resident, endemic species, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and two herbivorous migratory goose species, pink-footed goose (*Anser brachyrhynchus*) and barnacle goose (*Branta leucopsis*) (Descamps et al., 2017). Populations of most of these species have increased substantially over the last decades (i.e., from 1980's till today); the pink-footed goose population has five-folded (Heldbjerg et al., 2021), the barnacle goose population has eight-folded (Tombre et al., 2019) and the reindeer population has doubled (Le Moullec et al., 2019). The Svalbard rock ptarmigan appear in low numbers, but the population is increasing (Marolla et al., 2021). Despite differences in life-histories, the herbivores share several food plants (Bjørkvoll et al., 2009; Fox et al., 2006; Soininen et al., 2010; Unander, Mortensen et al., 1985) and habitats, of which moss tundra is an important stratum for foraging (Pedersen et al., 2017; Speed et al., 2009). In shared habitats, the potential for competitive interactions may be high (Barrio et al.,

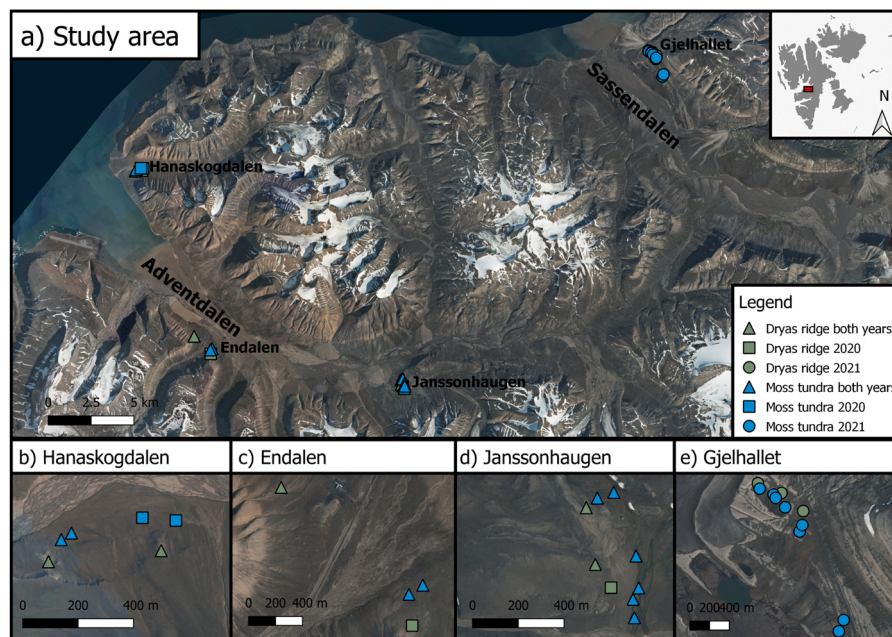


Fig. 1. General study area and location of camera-trap sites. Sites were distributed in two focal vegetation types defined by the study design: *Dryas* ridges (green colour) and moss tundra (blue colour). Symbols represent whether the site was sampled only in 2020 (squares), only in 2021 (circles) or in both years (triangles). *Upper panel (a)*: Placement of the study area within Svalbard. *Lower panels (b-e)*: Camera-trap sites within the four study locations. Each site covers an area of 30 × 30 m. Note that the scale is different in the smaller map panels. Orthophoto retrieved from the Norwegian Polar Institute (2022).

2013; but see Fox, Bergersen, 2005), particularly when snow-cover is extensive and limits access to forage and nesting areas (Anderson et al., 2012, 2016; Van der Wal et al., 2000; Jensen et al., 2014; Madsen et al., 2007).

In this study we assess if there is a potential for interspecific competition between the Svalbard herbivores in spring by first observing them in a field study and second using camera traps to assess co-occurrence. In the field study we aimed to describe how co-occurrence influences herbivore behaviour. We assumed that behaviours where one species was disturbing or preventing access to foraging grounds for another could indicate the potential for interference competition. In the camera-trap study we aimed to quantify the effects of the number of potential herbivore competitors, snow-cover extent, and vegetation type on the spatiotemporal distributions of herbivores in two years characterised by early and late snow melt. Low potential for competition would be indicated by no effect of one herbivore on the other. Moreover, extensive snow-cover was expected to increase the co-occurrence of herbivores (e.g., reindeer numbers higher with presence of geese and vice versa in interaction with snow) as the availability of open vegetation under such conditions is limited, which would also indicate low potential for interference competition. Alternatively, negative effect of occurrence of one herbivore on the numbers of the other, either alone or with extensive or full snow-cover, would indicate potential for interference competition.

2. Methods

2.1. Study area

The study area was in the central part of Spitsbergen, the largest island in the Svalbard archipelago (Fig. 1). The landscape is mountainous with glaciers and broad glacial valleys with extensive river systems. The four study locations, Hanaskogdalen, Endalen, Janssonhaugen and Gjelhallet, are within, or in close connection to Adventdalen and Sassendalen, two of the major valleys in Nordenskiöld Land (Fig. 1). In these valleys, where continuous vegetation cover is found, four habitat types can be distinguished: 1) exposed, well-drained ridges with a sparse vegetation cover dominated by *Dryas octopetala*, 2) heath typically dominated by either *Luzula confusa*, *Cassiope tetragona* or *Salix polaris*, 3) mesic moss tundra characterised by a thick moss-layer and high diversity of grass and forb species, and 4) wetland dominated by moss and graminoids (Elvebakk, 1994).

Svalbard has a high-Arctic climate, characterised by low temperatures and precipitation, and high seasonal variability (Hanssen-Bauer et al., 2019). Average winter and summer temperatures are estimated to -13.9 and 4.5 , respectively (Hanssen-Bauer et al., 2019; measured at Svalbard Airport, based on a 1971–2000 average). Precipitation usually falls as snow, and snow-cover may persist from October until June, however, large interannual variation occurs (Killie et al., 2021). Periods of above-zero temperatures with rain in winter are common (Peeters et al., 2019; Vickers et al., 2022), which often results in basal ice-layers covering the vegetation. Topography and wind-patterns contribute to large variability in snow distribution in the landscape. Local snow-cover properties like depth and duration, in combination with hydrology and permafrost-related processes, supports habitats with different vegetation compositions (Elvebakk, 1994).

2.2. Study species

The resident herbivores, Svalbard reindeer and Svalbard rock ptarmigan, are both widespread (Le Moullec et al., 2019; Pedersen et al., 2017). Svalbard reindeer use small seasonal home ranges ($< 5 \text{ km}^2$; Tyler and Øritsland, 1989), and movement within and between seasons is limited compared to most other reindeer sub-species. The reindeer live in a nearly predator-free environment, with only rare observations of polar bear (*Ursus maritimus*) and Arctic fox (*Vulpes lagopus*) predation (Derocher et al., 2000; Prestrud, 1992; Stempniewicz et al., 2021). The main drivers of reindeer population dynamics are density-dependence caused by food limitation and winter weather variability, such as rain-on-snow events, causing basal ice and inaccessible foraging grounds (e.g., Albon et al., 2017; Hansen, Gamelon et al., 2019; Hansen et al., 2019). Foraging ecology in spring is influenced by timing of snow melt, and habitat selection is based on quantity of the important food plants at this time of year, *L. confusa* and *S. polaris*, rather than plant quality (Van der Wal et al., 2000). Svalbard rock ptarmigan occurs in low densities (Marolla et al., 2021) and availability of breeding habitats of high quality is limited (Pedersen et al., 2017). Foraging ecology in spring is influenced by snow-cover and the territories are found in early thaw areas where *S. polaris* is the dominating forage item (Unander et al., 1985; Unander and Steen, 1985).

Two species of migratory geese, pink-footed and barnacle goose, use the study area as both pre-breeding foraging grounds and breeding areas. They arrive in early to mid-May and both populations have increased substantially over the last decades (Heldbjerg et al., 2021; Tombre et al., 2019). Even though the two species of geese show increasing sympatry on breeding grounds, there is little overlap in diet and feeding ecology (Fox et al., 2007; Fox et al., 2005). Barnacle geese mostly eat moss and grass (Fox et al., 2009; Soininen et al., 2010), while pink-footed geese in the spring almost exclusively feed on below ground plant parts as soon as the ground unfreezes sufficiently (Anderson et al., 2012; Fox et al., 2006).

2.3. Study design and data collection

In this study we conducted two different field data campaigns: 1) A field study where we observed herbivore behaviour (spring 2020), and 2) a camera-trap study to create a time-series of herbivore counts and snow-cover extent (spring 2020 and 2021) to assess co-occurrence. Below we detail the study designs and field data collections.

2.3.1. Field study of herbivore behaviour

The field study aimed to give qualitative background for the analysis of camera-trap data by describing herbivore behaviours that could reflect interspecific interference competition. Observations took place during spring 2020 (May 15th to June 5th) in the southwest part of Adventdalen (i.e., in the vicinity of Endalen, Fig. 1c), where all four species (reindeer, ptarmigan, and the two goose species) were present. At this time of the year snow-cover often limit the access to forage, which creates a potential for competitive interactions (but see Fox et al., 2005). Observations were conducted every other day, or with intervals of up to four days when weather conditions were poor, as this affected detection negatively. Co-occurring herbivores (i.e., a group of individuals of two or more herbivores [ptarmigan, reindeer, and/or geese] with maximum 50 m between each other) were located at random points, usually a different one each time, within an area of approximately 9 km². The average time used to locate a group was 35 min, and the total sampling effort comprised about 31 h. In total, 24 observations of co-occurring herbivores were conducted, always by the same observer, and each observation lasting maximum one hour. Individuals were monitored with the use of range finder binoculars throughout the whole one hour, or until the group dissolved, if this happened prior to the maximum observation time. The behaviours of the two goose species were not separated, as any potential interaction with either reindeer or ptarmigans was expected to be similar for both species as they are ecologically similar (Fox et al., 2005). Behaviours that could indicate potential for interspecific interference competition were defined a priori based on the review by Hermann (2017), and classified as either: 1) *alertness*, where the activity of one individual caused alertness (i.e., raised head, calling or standing up from resting position) of another, 2) *movement away*, where one individual moved away (i.e., walked or flew) within three minutes after being alerted by the activity of another individual or 3) *chasing*, where one individual intentionally chased another.

2.3.2. Camera-trap study of herbivore co-occurrence and spatiotemporal distribution

To investigate herbivore co-occurrence and spatiotemporal distribution, we created a spatially replicated time-series of herbivore counts from camera-traps of the type Reconyx Hyperfire 2 Professional Series cameras (Reconyx Inc, Wisconsin, US) that were established at existing vegetation monitoring sites in Adventdalen during early spring 2020 (n = 19), and in Sassendalen in spring 2021 (n = 11). The sites follow a stratified randomised design, based on Ravolainen et al. (2020), and were distributed within two focal vegetation types, *Dryas* ridges (n = 10) and moss tundra (n = 20) (Fig. 1). One camera was placed at each site and positioned in accordance with a standardised protocol to ensure that images included the outline of the respective sites (30 × 30 m). The outer delineation of the counting area within the images, was marked in the terrain with an aluminium stick initially, but frost heaves made them unstable and therefore most images were visually delineated. Images were recorded from the camera-trap sites during the snow melt period in spring, from approximately when migrating geese arrived on the tundra (May 10th to June 10th in Adventdalen in 2020 and 2021, and May 22nd to June 10th in Sassendalen in 2021). Time lapse images were taken with intervals of 20 min, as recommended by Hamel et al. (2013). This generated a time-series of 72 images per day from each camera. See Appendix A (Fig. A1, Table A1) for an overview of number and examples of images and sample sizes available for analysis.

2.4. Data analysis

2.4.1. Pre-processing of camera-trap data

Camera-trap images were processed in the Reconyx MapView Professional software (Reconyx Inc, 2016). This software allows images to be scored individually and thereafter exported to a dataset. Image data was further processed in RStudio, version 2021.9.1.372. At each image, we manually counted the number of herbivores of each species and assessed the snow-cover extent. Snow-cover extent was visually estimated and recorded in one of the following categories: 'limited' (0–50% snow-cover), 'extensive' (50–95% snow-cover) and 'full' (95–100% snow-cover). To account for potential differences in co-occurrence related to snow-cover extent early and late in the season, we further divided the 'extensive' category into two new categories: 'extensive (early)' for observations of extensive snow-cover extent before day of year (DOY) 147, and 'extensive (late)' for observations of extensive snow-cover extent including or after DOY 147. Before arriving at a final dataset for analysis, we removed images of poor quality due to weather conditions or technical problems with the cameras, images with presence of humans or fresh snowmobile tracks and all images from one camera because of no herbivore observations. The final dataset included a total of 88787 images (2020, N = 39695; 2021, N = 49092; including both presence and absence of animals; Appendix A, Table A1) with a total count of 1081 reindeer, 5676 pink-footed geese, 2584 barnacle geese and 65 ptarmigans present on the images (Appendix B, Fig. B1 and B2 for annual sample sizes). As the number of ptarmigans at the camera-trap sites was low, this species was excluded from the subsequent quantitative analyses (Appendix B, Fig. B1 and B2). Counts of the two species of geese were combined, as in the field study, because any potential interaction with reindeer was expected to be similar for both species (Fox et al., 2005).

To reduce autocorrelation in our data, which is a common challenge in camera-trap studies (Sollmann, 2018), we aggregated the camera-trap data to three-hour intervals because this was the maximum time-interval with the least autocorrelation where herbivores were expected to have an impact on each other's presence. Each three-hour interval consists of nine images, and the number of herbivores were summarised to a total count over the interval (see Appendix A, Table A1 for sample sizes after aggregation). Images from 2021 were scored by two different persons, and observer bias was estimated by double-scoring a subset of the images, however, the percent of images scored differently was low enough to be ignored (percent images scored differently, reindeer = 1.5%, geese = 1.3%, snow cover = 5.1%; Appendix C, Table C1).

2.4.2. Modelling co-occurrence and spatiotemporal distribution

To quantify the effects of environmental conditions and the number of herbivores on the spatiotemporal distribution of either one

of them, we applied generalised linear mixed models (GLMMs) using the function ‘glmmTMB’ in the glmmTMB package in R (Brooks et al., 2017). As response variables we used: 1) Total count of reindeer in time-interval j at camera-trap site i , R_{ij} , and 2) total count of geese in time-interval j at camera-trap site i , G_{ij} . A global model was assembled for each response variable (termed ‘reindeer model’ and ‘goose model’). We explored the data using the protocol by Zuur et al. (2010) to detect possible outliers, zero-inflation, or collinearity (Appendix D1, Table D1 and D2) and determine the correct distribution of the response variable and relationships between response and predictor variables (e.g., quadratic effects or interaction terms).

For the reindeer model, fixed predictor variables included G_{ij} (discrete, range [0:55]), vegetation type (categorical with two levels; *Dryas* ridge and moss tundra), snow-cover (categorical with four levels; limited, extensive (early), extensive (late) and full), DOY (discrete, range [130:162]) and DOY^2 , in addition to the interactions $G_{ij} \times$ snow-cover and snow-cover \times vegetation type. To improve model convergence, the predictor G_{ij} was log-transformed ($\ln(x + 1)$) and DOY was scaled. For vegetation type and snow-cover, reference levels were set to moss tundra and limited, respectively. We applied a GLMM with a log-link function, assuming a negative binomial error distribution. Year nested within camera-trap site was included as a random intercept to account for the dependency structure of herbivore counts. Moreover, we corrected for autocorrelation in the residuals by adding a first-order autoregressive covariance term (AR1) to the model. We assembled a set of 13 candidate models, including the global model, a null model and 11 models of decreasing complexity (Table 1a). The variables G_{ij} , snow-cover and vegetation type were retained in all the models in the candidate model set, as they were essential to our aims. The best model was selected using the second-order Akaike’s Information Criterion (AICc; Burnham, Anderson, 2002), calculated using the function ‘aictab’ in the AICcmodavg package in R (Mazerolle, 2020). Models with $\Delta AICc < 2$ were regarded to perform equally well (Burnham et al., 2011), and if several models had $\Delta AICc < 2$ the most parsimonious model was selected.

For the goose model, prior to analysis we removed all observations from *Dryas* ridge sites ($N = 3262$) from the dataset, as the number of geese in these habitats was very low (470 geese in 3262 observations, compared to 7790 geese in 6790 observations from moss tundra sites, see Fig. 3). The fixed predictor variables in the global model included R_{ij} (discrete, range [0:37]; log-transformed ($\ln(x + 1)$)) and the same additive predictors as in the reindeer model, except vegetation type. Additionally, we included the interaction $R_{ij} \times$ snow-cover. The variables R_{ij} and snow-cover were retained in all the models in the candidate model set, as they were essential to our aims. We applied a GLMM with a log-link function assuming generalised Poisson distributed errors. As above, year nested within camera-trap site was included as a random intercept, and a first-order autoregressive covariance term (AR1) was added to the model. A set of seven candidate models, including the global model, a null model and five models of decreasing complexity, was assembled (Table 1b), and the best model was selected using AICc, as described above.

Table 1

Model selection table for candidate models explaining the spatiotemporal distribution of reindeer (a) and geese (b). The fixed predictors include number of geese or reindeer present at camera-trap sites within three hours (continuous, log-transformed; rein [0:3.64], geese [0:4.03]), snow-cover extent (categorical; limited, extensive (early), extensive (late) and full), vegetation type (categorical; *Dryas* ridge and moss tundra), day of year (DOY; continuous, scaled; [-1.91:1.66]), and quadratic effect of day of year (DOY^2 ; continuous, scaled; [0:3.64]), in addition to interaction terms. The fixed predictors, number of respective herbivores, vegetation type (only in reindeer model) and snow-cover in addition to the random effect (camera_ID/year) and the AR1 term to correct for temporal autocorrelation, were retained in all models of the candidate set. VegType = vegetation type, Snow = snow-cover extent, k = number of parameters included in each model. The selected models are indicated with bold letters.

(a) Reindeer model											
Model	Geese	Snow	VegType	DOY	DOY^2	Geese \times Snow	Snow \times VegType	k	AICc	$\Delta AICc$	AICc weight
Global	x	x	x	x	x	x	x	19.00	4219.08	4.37	0.04
1	x	x	x	x	x	x		16.00	4223.57	8.86	0.00
2	x	x	x	x	x		x	16.00	4215.30	0.59	0.24
3	x	x	x	x	x			13.00	4219.87	5.16	0.02
4	x	x	x	x		x	x	18.00	4218.97	4.26	0.04
5	x	x	x	x		x		15.00	4223.71	9.00	0.00
6	x	x	x	x			x	15.00	4215.31	0.60	0.24
7	x	x	x	x				12.00	4220.13	5.41	0.02
8	x	x	x			x	x	17.00	4218.20	3.49	0.06
9	x	x	x			x		14.00	4223.65	8.94	0.00
10	x	x	x				x	14.00	4214.71	0.00	0.32
11	x	x	x					11.00	4220.14	5.43	0.02
Null								6.00	4244.91	30.20	0.00

(b) Goose model											
Model	Reindeer	Snow	DOY	DOY^2	Reindeer \times Snow	k	AICc	$\Delta AICc$	AICc weight		
Global	x	x	x	x	x	15.00	10490.37	4.23	0.11		
1	x	x	x	x		12.00	10486.14	0.00	0.89		
2	x	x	x		x	14.00	10541.75	55.61	0.00		
3	x	x	x			11.00	10537.25	51.11	0.00		
4	x	x			x	13.00	10547.95	61.81	0.00		
5	x	x				10.00	10543.50	57.36	0.00		
Null						6.00	10618.74	132.59	0.00		

Model fit was evaluated for the global models by residual diagnostics, using the DHARMA package in R (Hartig, 2021) including inspection of qq-plots, residuals plotted against predicted values for assessing heteroscedasticity, ACF plots of model residuals and test statistics for correct distribution, dispersion, and outliers (See Appendix E, Fig. E1 for ACF plots of model residuals). Model predictions, based on the best fitted model for reindeer and geese, were made for each fixed predictor using the function 'ggpredict' in the ggeffects package in R (Lüdtke, 2018). This function predicts values for the response for each continuous predictor variable by keeping all other variables constant at their mean values, while the categorical variables were set to their reference level.

3. Results

3.1. Observations of behaviour and co-occurrence

From the total of 24 observations, 20 observations included reindeer, 23 included geese, and 6 included ptarmigans (Appendix F, Table F1). In one of 20 observations, a reindeer was alerted by geese, and moved away immediately. Reindeer were never alerted by ptarmigans, and chased by neither geese nor ptarmigans. Geese were alerted by the activity of reindeer in 10 out of 23 observations. In 3 of these 10 observations, the geese flew or walked away within three minutes after being alerted by reindeer. Geese were never alerted by ptarmigans, and never chased by either reindeer or ptarmigans. Ptarmigans were never alerted by reindeer or geese, but was in one of the six observations chased by reindeer, and another of the six observations chased by geese.

3.2. Characteristics of spring snow melt and herbivore data from camera-traps

The ground was still fully snow-covered (i.e., full snow-cover; 95–100%) in most of the camera-trap sites until May 14th in 2020 [DOY 135] and to May 25th in 2021 [DOY 145]. The snow melting period (i.e., extensive snow-cover; 50–95%) began on average eight to eleven days earlier in 2020 compared to 2021. In 2020, the mean date for when snow melt started at the camera-trap sites was two days earlier in *Dryas* ridges than in moss tundra, while in 2021 it was five days earlier. The mean date for the start of the snow melting period in *Dryas* ridge sites was May 16th in 2020 [DOY 137] compared to May 25th in 2021 [DOY 145]. The mean date for the start of

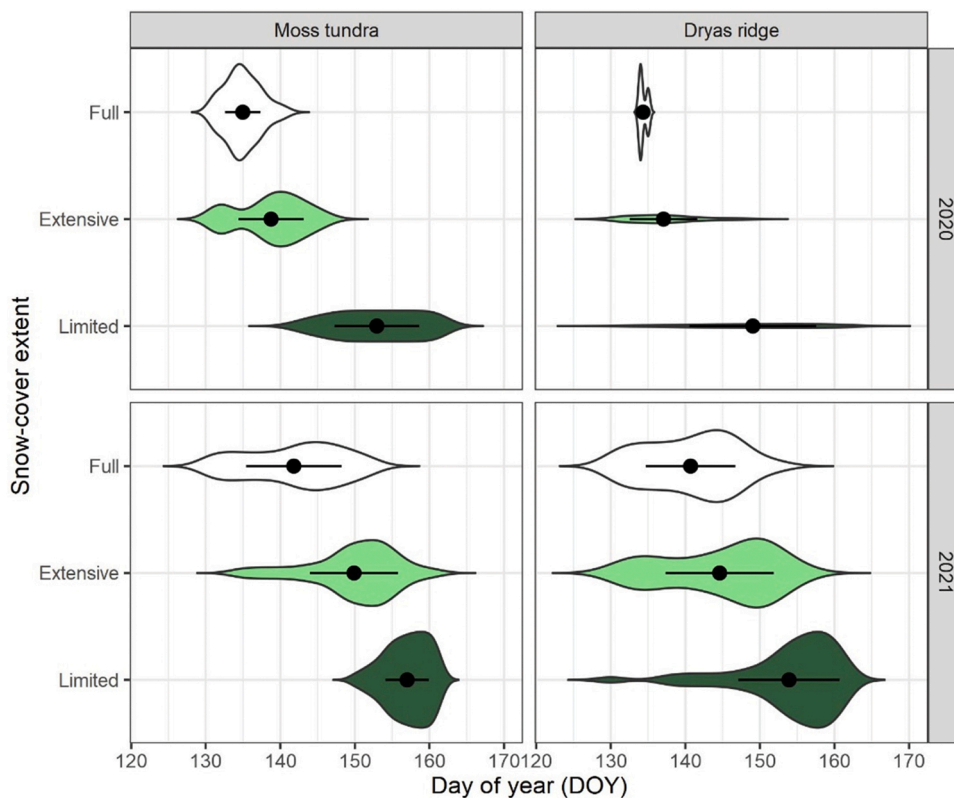


Fig. 2. Violin plots of the distribution of snow-cover extent at camera-trap sites in each vegetation type (moss tundra and *Dryas* ridge) by Julian date and year. Points and lines represent the mean date and standard deviation, respectively, of each snow-cover category for the camera-trap sites (2020: N = 19, 2021: N = 26), while the outline of the violins show the kernel probability density of the snow-cover categories at different dates. DOY 130 corresponds to May 9th in 2020, and to May 10th in 2021. Limited = 0–50% snow-cover; extensive = 50–95% snow-cover; full = 95–100% snow-cover.

the snow melting period in moss tundra sites was on May 18th in 2020 [DOY 139] compared to May 30th in 2021 [DOY 150]. The mean date for when the study sites were exposed (i.e., limited snow-cover; 0–50%) was about five days earlier in 2020 compared to 2021. In moss tundra, the mean date for when most of the snow had melted was June 1st [DOY 153] in 2020 compared to June 6th [DOY 157] in 2021. In *Dryas* ridges, the mean date for when most of the snow was melted was May 28th [DOY 149] in 2020 compared to June 3rd [DOY 154] in 2021. See Fig. 2 for graphical description of characteristics.

Reindeer occurred daily in 19% and 20% of the observations in 2020 (N = 606) and 2021 (N = 700), respectively. Geese occurred daily in 29% and 34% of the observations in 2020 and 2021, respectively. Reindeer and geese co-occurred in 9% and 12% of the total observations in 2020 and 2021, respectively. Of the observations where reindeer were present at camera-traps, geese occurred at the same camera-trap site within the same day 49% and 63% of the times in 2020 and 2021, respectively. Of the observations where geese were present at the camera-traps, reindeer occurred at the same site within the same day 32% and 36% of the times in 2020 and 2021, respectively. On the three-hourly interval, used in the subsequent modelling, reindeer were found in 4% of the observations in both years. Geese were present in 11% and 14% of the total observations in 2020 and 2021, respectively. Co-occurrence on the three-hourly interval was 1% of the total observations in both years. Of the observations with reindeer occurrence, co-occurrence with geese was 19% in 2020 and 34% in 2021. Of the observations with goose occurrence, co-occurrence with reindeer was 6% in 2020 and 10% in 2021 (Appendix G, Table G1).

The mean number of reindeer in the vegetation types was unevenly distributed between the years and snow-cover categories (Fig. 3). The highest reindeer numbers were found in moss tundra when snow-cover was limited and in *Dryas* ridges when snow-cover was extensive early in the season (Fig. 3). Reindeer numbers had similar temporal distributions across the study period in 2020 and 2021 (Fig. 4). The mean number of geese was evenly distributed between the years and was found almost exclusively in moss tundra (Fig. 3). Geese numbers increased early in the study period and thereafter decreased (Fig. 4). In 2020, the first observation of geese at camera-trap sites was on May 17th (DOY 138), and the number peaked at 398 geese on May 25th (DOY 145; Fig. 4). In 2021, the first observation of geese was on May 16th (DOY 136), and peak number of geese reached 500 on May 31st (DOY 151; Fig. 4).

3.3. Herbivore co-occurrence and spatiotemporal distribution

In the reindeer model selection, number of geese, snow-cover extent and vegetation type were kept as additive model terms, as well as the interaction vegetation type \times snow-cover (Fig. 5, Table 1). Full snow-cover and extensive snow-cover early in the season, negatively influenced the number of reindeer. The effect of extensive snow-cover late in the season was not significant (Figs. 5 and 6). When snow-cover was extensive early in the season, the number of reindeer in *Dryas* ridges was significantly higher than in moss

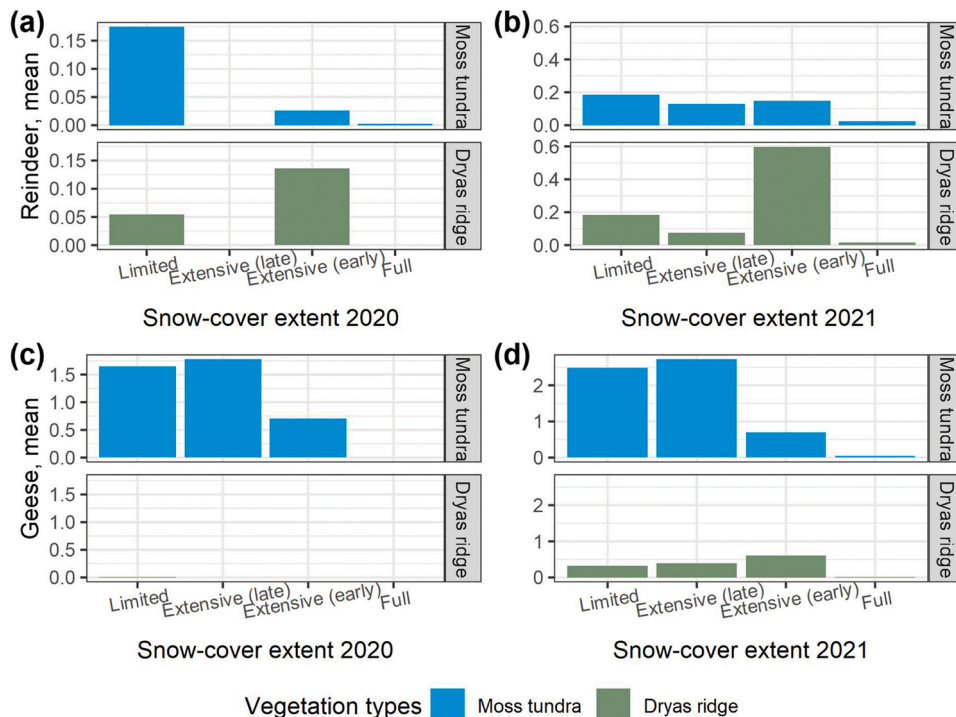


Fig. 3. Mean number of reindeer (a, b) and geese (c, d) counted every three hours at camera-trap sites in each vegetation type (horizontal panels) in relation to snow-cover extent in year 2020 (a, c) and 2021 (b, d). Blue colour represents moss tundra vegetation and green colour *Dryas* ridge vegetation. Snow-cover extent is categorised as: Limited (0–50% snow-cover), extensive (late) (50–95% snow-cover including or after DOY 147), extensive (early) (50–95% snow-cover before DOY 147), and full (95–100% snow-cover). Note that the scale on the y-axis varies between subplots.

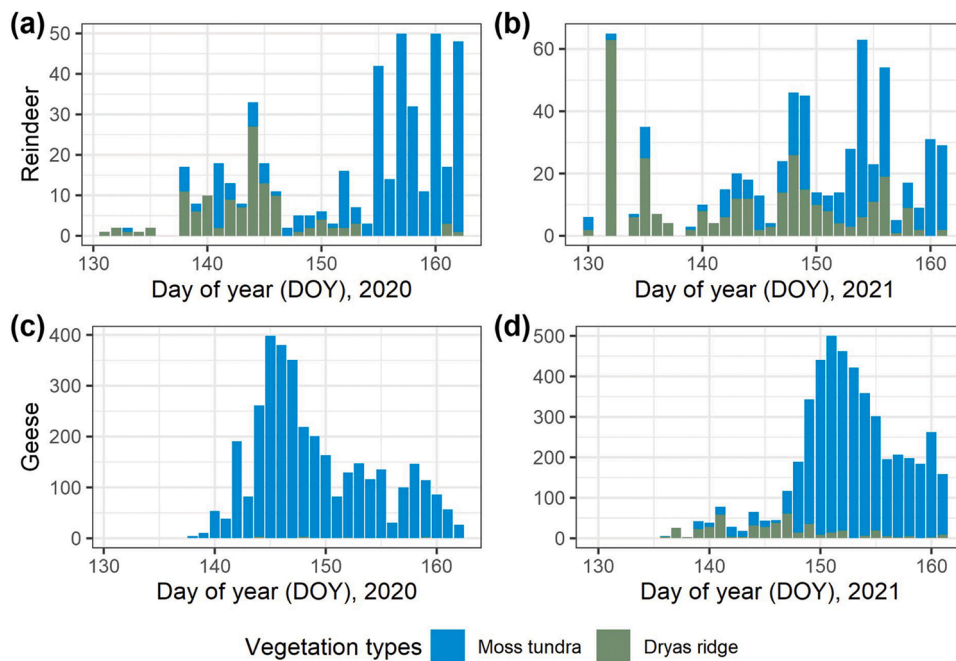


Fig. 4. Total count of reindeer (a, b) and geese (c, d) at each day of the study period in year 2020 (a, c) and 2021 (b, d). Blue colour represents moss tundra vegetation and green colour *Dryas* ridge vegetation. Note that the scale on the y-axis varies between subplots.

tundra (Figs. 5 and 6). There was no effect of the number of geese (Figs. 5 and 6). See Appendix H, Table H1 for estimated variance of random effects.

In the goose model selection, number of reindeer, snow-cover, DOY and DOY^2 were kept as additive model terms (Table 1). Full snow-cover, and extensive snow-cover late in the season had a negative effect on the number of geese (Figs. 5 and 6). DOY had a positive effect, while DOY^2 had a negative effect (Fig. 5), resulting in a bell-shaped distribution of the predicted number of geese over the season (Fig. 6). Reindeer number or extensive snow-cover early in the season did not have effect on geese numbers (Fig. 5).

4. Discussion

Our investigation of the spring spatiotemporal distribution of a high-Arctic herbivore community showed that reindeer and geese used the same foraging areas in spring, and occurrence of none of the herbivores impacted the numbers of the other, which indicate a low potential for competition. Rather, the spatiotemporal distribution of geese and reindeer was driven by snow-cover extent and vegetation type, independent of the number of the other herbivore present. The observations in the field study showed that no direct aggressive interactions were observed between the reindeer and geese, also suggesting limited potential for competition. Svalbard rock ptarmigan occurred in too low numbers to be analysed.

The result of no impact of one of the herbivores on the other suggests low potential for competition. Instead, the physical environment, such as snow-cover and vegetation type, played a larger role in determining the herbivores' spatiotemporal distribution. Reindeer utilised moss tundra habitats in accordance with former habitat descriptions and female reindeer habitat selection during calving (Beumer et al., 2017; Garfelt-Paulsen et al., 2021). However, early in the spring season, when snow-cover was extensive, reindeer utilised the *Dryas* ridge habitats more often than moss tundra. This corresponds to Bjørkvoll et al. (2009), who found a high proportion of the evergreen *D. octopetala* in the diet of Svalbard reindeer at this time of the year. In 2021, when snow melt was late, reindeer utilised the *Dryas* ridge habitats late in the season more often than in 2020, which was an early snow melt year. This habitat is wind-exposed, and consequently has a thinner snow-cover and melts out earlier in spring than the moss tundra habitat. The timing of snow melt will not only influence the start of the growing season, but also the nutrient quality and quantity of forage plants (Livensperger et al., 2016; Mårell et al., 2006; Semenchuk et al., 2016). The interacting effect of snow-cover and vegetation type early in spring on reindeer spatiotemporal distribution, demonstrate the ability of reindeer to seek out the best foraging habitats prior to parturition when energy demands are high (Garfelt-Paulsen et al., 2021; but see Veiberg et al., 2017). Geese almost exclusively utilised moss tundra habitat (i.e., we found very low numbers of geese in *Dryas* ridge habitat), in accordance with former descriptions of both geese species' pre-breeding areas (Fox et al., 2007; Fox et al., 2005; Fox et al., 2006). Spatiotemporal distribution of geese was solely driven by snow-cover (Anderson et al., 2012; Anderson et al., 2016) and spring migration phenology (Fox et al., 2006), which impacted number of geese in the study areas. It is likely that the decreasing presence of geese towards the end of the study period in both years (Fig. 4, Fig. 6) is due to geese either leaving the area to breed in other locations or geese being on the nest and not captured by the cameras.

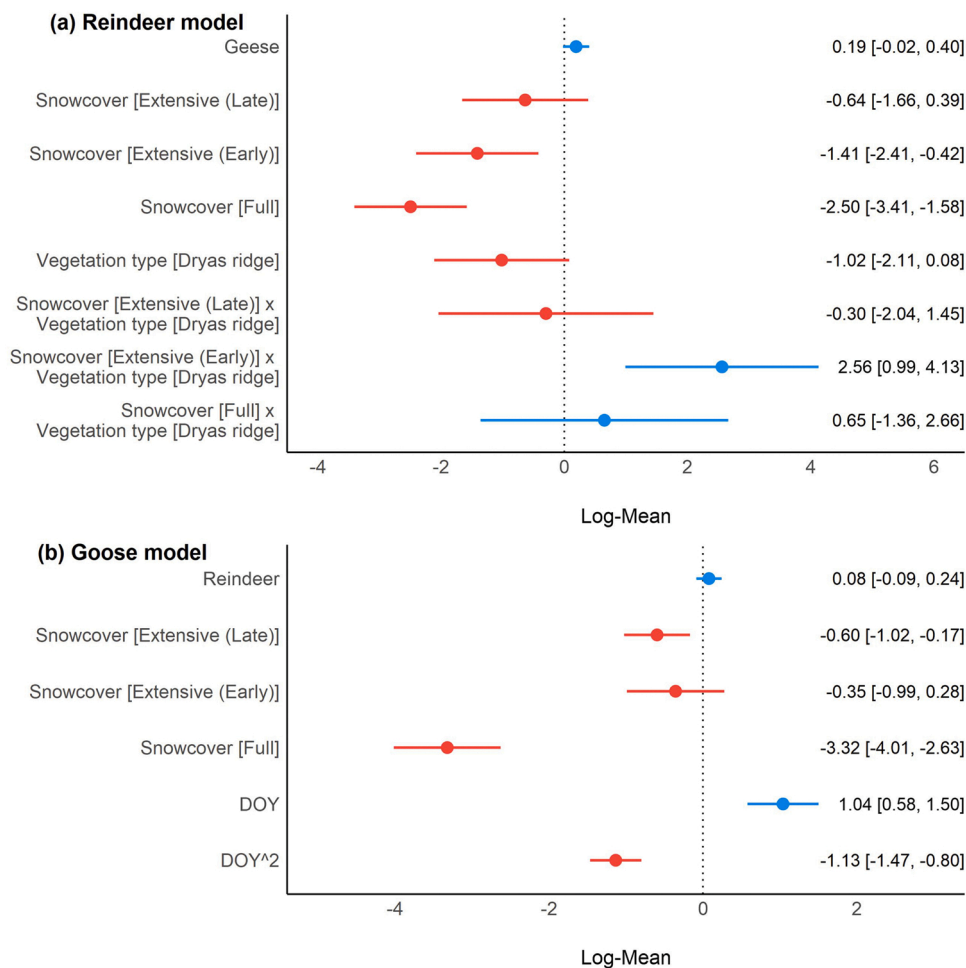


Fig. 5. Parameter estimates (red = negative effects; blue = positive effects) for the fixed predictor variables in the selected models explaining the spatiotemporal distribution of (a) reindeer and (b) geese in spring. Estimates are given on the log-scale and shown with 95% confidence intervals (in brackets). Effects are statistically significant if the confidence interval is not crossing zero. Fixed predictors include number of geese or reindeer present at camera-trap sites within three hours (continuous, log-transformed; reindeer [0:3.64], geese [0:4.03]), snow-cover extent (categorical; limited, extensive (early), extensive (late) and full), vegetation type (categorical; *Dryas* ridge and moss tundra), day of year (DOY; continuous, scaled; [-1.91:1.66]), and quadratic effect of day of year (DOY²; continuous, scaled; [0:3.64]), in addition to interaction terms. Number in brackets are ranges. The estimates for snow-cover effects and vegetation type are comparisons to the reference level, which is set to limited and moss tundra, respectively.

Contrary to our expectations, there was no effect of the interaction between snow-cover extent and the number of potential competitors on the distributions of either reindeer or geese. This result stands strong because we found similar it in both the early (2020) and the late (2021) snow melt year. Reindeer and geese feeding together in small patches of vegetation have been observed in years when snow melt is late in Svalbard (Å.Ø. Pedersen, *pers.comm.*), but our study shows that they utilise the same areas also when larger part of the landscape is available in an early snow melt year. There are, however, few studies conducted in spring in the Arctic to compare this result to (but see Anderson et al., 2012, 2016 and Fox et al., 2009 on snow influence on geese distribution and Pedersen et al., 2006 on co-feeding of ptarmigan and reindeer under severe snow conditions in early spring). Snow melt variability in the high-Arctic is considerable, the most recent analysis of the MODIS satellite-records showing that 2020 had the earliest snow melt since year 2000 (Karlsen et al., 2022). During these two decades the Karlsen et al. (2022) analysis shows that our study areas had approximately 6 delayed snow melt years, 6–7 early snow melt years, and 7 average years, highlighting the variability that the herbivores experience in the spring season. Our results suggest that they are currently able to co-occur during the range of snow melt timing that has been documented (Karlsen et al., 2022; but note 2021 was not included in their study).

In this study we found that both geese and reindeer shared habitats in spring, particularly moss tundra, however, this co-occurrence does not necessarily mean shared forage plants. For example, a study investigating the dietary overlap between muskoxen, hares and ptarmigans in Greenland found that diets were specialised, and even more so when the extent of snow-cover increased, despite the herbivores were feeding in the same areas (Schmidt et al., 2018). Resource partitioning is recognised as a common mechanism promoting coexistence among Arctic herbivores (Fox et al., 2009; Ihl, Klein, 2001; Klein, Bay, 1994), and the extent of quantitative

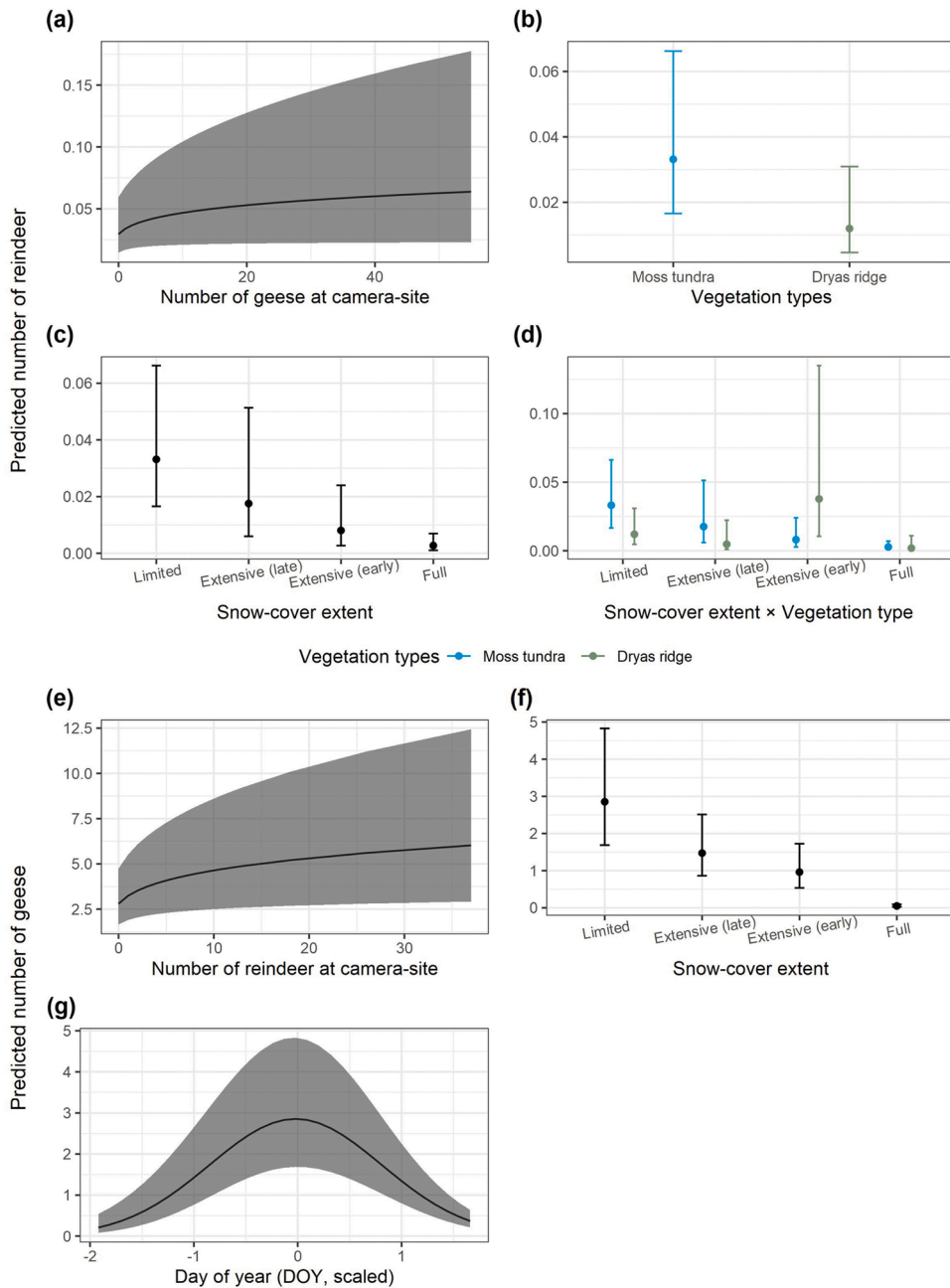


Fig. 6. Upper panel (a-d): Predicted number of reindeer present at camera-trap sites within three hours as a function of number of geese present at camera-trap site (a), vegetation types (b), snow-cover extent (c), and the interaction term vegetation type \times snow-cover extent (d), as predicted by the selected GLMM. Lower panel (e-g): Predicted number of geese present at camera-trap sites within three hours as a function of number of reindeer present at camera-trap sites (e), snow-cover extent (f) and day of year (DOY, scaled; g), as predicted by the selected GLMM. Predicted values are conditioned on the fixed predictors only. Error bars and bands indicate 95% confidence intervals (CI).

overlap in reindeer and goose diets in Svalbard during spring is not yet known. These aspects need to be further investigated to understand the potential for exploitative competition between the Svalbard herbivores. Given the low numbers of ptarmigans observed in the camera trap study and the exclusion of the species in analysis, we suggest that such a study should focus on reindeer and geese.

5. Conclusion

This study adds to the current knowledge about the spatiotemporal distribution and habitat use of resident and migratory herbivores during spring in high-Arctic Svalbard and is consistent with former meta-analysis (Barrio et al., 2013). Co-occurrence of geese

and reindeer occurred in moss tundra habitats. We found no negative effect of the number of reindeer or geese on each other's occurrence at camera-trap sites despite two years with contrasting timing of snow melt and no aggressive interactions between reindeer and geese — thereby the potential for competition is limited. We encourage further studies to assess, for example, the extent of spring dietary overlap among the herbivores to conclude on aspects of biotic interactions, such as various type of competition. The spatiotemporal distributions of reindeer and geese, now driven by the extent of snow-cover and vegetation type may, however, hold potential for exploitative competition over forage plants, particularly if herbivore populations continue to increase.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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CRedit authorship contribution statement

Anna Caroline Grimsby (ACG), Virve Ravolainen (VR), Dorothee Ehrich (DE) and Åshild Ønvik Pedersen (ÅØP) conceived the idea. ACG and ÅØP designed the observational study and ACG collected the data. ACG, ÅØP and VR designed the camera-trap study, and images were retrieved by several field technicians. ACC and Frida K. Brockmann scored the images and generated data. ACG wrote R-scripts with guidance from DE and ACG analysed the data with contributions from DE, VR, ÅØP and Ingrid M. G. Paulsen. ACG, VR and ÅØP wrote the first version of the manuscript. All authors commented on the manuscript before submission.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02521](https://doi.org/10.1016/j.gecco.2023.e02521).

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