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Spatiotemporal distribution and co-occurrence of Arctic herbivores in spring

Anna Caroline Grimsby
Master's thesis in Biology BIO-3950 April 2022



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Cover photograph: © Lina Lettau - Svalbard reindeer and barnacle geese grazing in Endalen

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Abstract

Biotic interactions play an important role in the structure and dynamics of food-webs and may drive the spatial distribution of species. In the Arctic, spring snow-cover limits the availability of resources at a critical time for resident and migratory herbivores, which could lead to resource competition. This study takes a first step towards understanding the potential for competition between the major Svalbard herbivores; Svalbard reindeer (*Rangifer tarandus platyrhynchus*), Svalbard rock ptarmigan (*Lagopus muta hyperborea*), pink-footed goose (*Anser brachyrhynchus*) and barnacle goose (*Branta leucopsis*) during spring when resources are limited. The behaviour of co-occurring herbivores was observed with the aim of describing behaviours that could indicate interference competition. Further, camera-trap data was used to quantify the effects of snow-cover extent, vegetation type and presence of potential competitors on the spatiotemporal distributions of reindeer and geese. Reindeer and geese in Svalbard were found to generally forage in the same areas, especially in moss tundra. Observations suggested that reindeer was the behaviourally dominant competitor, but even though geese were regularly disturbed by close encounters with reindeer, no direct interference interactions were observed. Quantitative analyses confirmed that their spatiotemporal distributions were mainly driven by snow-cover extent and vegetation type. While it was clear that reindeer did not avoid geese, the avoidance of reindeer by geese could not be rejected. Chasing of ptarmigans was observed from both reindeer and geese, however the potential for competition between these species is not further assessed in this study due to a low number of ptarmigan observations. Extensive snow-cover seemed to slightly increase the co-occurrence of reindeer and geese, and the effect is expected to be stronger in years of late snowmelt. The shared space use by these species could potentially lead to exploitative competition, however this should be further studied by assessing dietary overlap, especially in relation to timing of snowmelt which is predicted to change with climate warming. This study adds to the current knowledge of spatial ecology of reindeer and geese in Svalbard and gives insight to the potential for competition between these Arctic herbivores during spring.

Key words: Arctic herbivores, spatiotemporal distribution, co-occurrence, competition, behaviour, snow-cover, camera-traps, Svalbard

1 Introduction

Identifying the drivers of species' spatial ecology is crucial for our understanding of community structure and biodiversity, especially in relation to ongoing climate warming and increasing anthropogenic disturbance of wildlife habitats (Constable et al., 2022; McCarty, 2001; Walther et al., 2002). Tolerance to abiotic conditions, like climate and environment, controls the distribution of species on a regional scale, however the role of biotic interactions should not be underestimated (Barbaro et al., 2019; Leach et al., 2016; Pearson & Dawson, 2003; Wisz et al., 2013). At the local scale, strong links between spatial distribution and interspecific interactions can be observed. For example, facilitative interactions benefit at least one of the participating species and cause harm to neither, which may have positive effects on species co-occurrence, while competition often leads to spatial segregation (Amarasekare, 2003; MacArthur & Levins, 1967; Schoener, 1983). Competitive interactions can arise between species with similar niches, in particular in resource-limited ecosystems (Connor & Simberloff, 1979). This interaction can have significant negative effects on fitness components and population dynamics, either directly through interference competition, or indirectly through resource depletion (Chen et al., 2020; Smith & Fox, 2017; Tannerfeldt et al., 2002). To avoid the consequences of competition, and allow coexistence, ecologically similar species may select different habitats, or utilize different resources. For example, studies have found that the distribution of mountain hare (*Lepus timidus*) is constricted to high altitudes and deep forests when it occurs in the same locations as the brown hare (*Lepus europaeus*; Thulin, 2003). Another example, involving the three Arctic herbivores musk oxen (*Ovibos moschatus*), Arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus muta*), illustrates that the quantitative dietary overlap between herbivores can be low even though they forage in the same resource-limited area (Schmidt et al., 2018). Habitat or resource partitioning is not necessarily always a result of density-dependent competition where a species selects a less preferred habitat when it occurs in sympatry with a dominant competitor (Connell, 1980; Morris et al., 2000). However, habitat use and patterns in spatiotemporal distribution and co-occurrence can provide useful insights to understanding the potential for interactions between species.

Ecosystems are intrinsically dynamic, and the strength of inter-specific interactions will often change with temporal fluctuations in resource availability (Kelt et al., 2019; Ostfeld & Keesing, 2000). Resource fluctuations might be caused by irregular events like high

temperatures causing increased plant productivity or rain-on-snow events locking vegetation in ice, or they can be a result of seasonality (Hansen et al., 2013; Van der Wal & Stien, 2014; Yang et al., 2008). In highly seasonal landscapes, periods of limited access to resources could intensify resource competition (Seyer et al., 2020). In the Arctic, long winters and a short growing season additionally limit the availability of resources. Finding access to forage through snow and ice constitutes a major challenge for resident herbivores to fulfil energy requirements necessary to survive and reproduce (Forchhammer et al., 2008; Hansen et al., 2013). Arctic herbivores therefore often rely on body reserves during the winter and in early spring when reserves are depleted and snow starts to melt, there is a pressure to get the most out of the short growing season (Mortensen et al., 1983; Reimers et al., 1982; Tomassini et al., 2019; Tyler, 1986). The same applies to migratory Arctic-breeding geese, who are often dependent on tundra vegetation to fulfil resource demands for successful reproduction after a long migration (Gauthier et al., 2003; Klaassen et al., 2006). Presence of snow on goose nesting sites at the time when they arrive on the tundra have cascading effects on reproductive success (G. H. Jensen et al., 2014; Madsen et al., 2007; Prop & de Vries, 1993). Spring snowmelt and the following green-up is patchy due to topography-related variations in snow distribution in the landscape (Liston & Elder, 2006). This causes available resources to be limited to small patches of snow-free vegetation at a critical time (i.e., prior to reproduction) when forage demands are high for the herbivores. Therefore, there is an increased potential for interspecific competition in early spring when most forage is still covered by snow.

Spring is a season undergoing rapid climatic changes, especially in the Arctic (Constable et al., 2022; Hanssen-Bauer et al., 2019). Warmer temperatures advance the onset of snowmelt, which have significant consequences in regards to phenological events across taxa (Høye et al., 2007; Thackeray et al., 2016). Changes in the timing of life-history events can have complex ecosystem consequences, like decoupling or mismatch of trophic interactions and altered relations between key species (Post & Forchhammer, 2008; Renner & Zohner, 2018; Thackeray et al., 2010; Wheeler et al., 2015). Therefore, understanding species interactions and how they are linked to the distribution and melting of snow in spring is of critical importance.

Svalbard is a low-productive tundra ecosystem in the high-Arctic where climate is changing rapidly (Førland et al., 2011; Hanssen-Bauer et al., 2019; Peeters et al., 2019). The terrestrial food web is relatively simple (Descamps et al., 2017; Ims et al., 2013), and the vertebrate

herbivore guild consists of only two widespread resident species: Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Svalbard rock ptarmigan (*Lagopus muta hyperborea*). In addition, the two herbivorous migratory goose species pink-footed goose (*Anser brachyrhynchus*) and barnacle goose (*Branta leucopsis*) are present on the tundra in the breeding season. In such simple high-latitude food-webs interactions can be strong (Post et al., 2009; Seyer et al., 2020). Even though the herbivore species on the Svalbard tundra have different life-histories, they share several food plants (Anderson et al., 2012; Bjørkvoll et al., 2009; Eidesen et al., 2015; Soininen et al., 2010; Unander et al., 1985). Additionally, a preliminary assessment of predictive habitat suitability models for reindeer, ptarmigans and pink-footed geese indicated shared habitats between the herbivores (Pedersen et al., 2017; Ravolainen et al., 2018; Speed et al., 2009). Generally, reindeer and ptarmigan habitats are thought to overlap in mid-elevation ridges, while pink-footed geese and reindeer would share suitable habitats in more moist valley bottom areas (Ravolainen et al., 2018). All three herbivores seem to have overlapping habitats in productive hot-spots on the tundra, such as in moss tundra (Ravolainen et al., 2018). In these habitats, the potential for interactions could be high, and the Svalbard herbivores might compete for the most productive foraging grounds, either through resource depletion or interference competition.

In Greenland, physical interference by Canada geese (*Branta canadensis*) is thought to suppress access to high quality forage for Greenland white-fronted geese (*Anser albifrons flavirostris*) at a sympatric site (Kristiansen & Jarrett, 2002). The two species of geese in Svalbard do not display the same behaviour (Fox & Bergersen, 2005), but interference competition is possible between geese and the two resident herbivores, reindeer and ptarmigans. Additionally, pink-footed geese in Svalbard use a destructive foraging technique where plant roots are pulled out of the ground (hereafter grubbing). Grubbing has a large impact on tundra vegetation and could potentially cause vegetation state shifts (Ravolainen et al., 2020; Speed et al., 2009), leading to negative effects on the other herbivore species. For instance, in the Canadian Arctic, degraded vegetation caused by grubbing has been identified as a cause of the decline in the local ptarmigan population (Sandercock et al., 2005). Although the pink-footed geese in Svalbard mostly feed in wet habitats (Speed et al., 2009) while ptarmigans occupy territories in drier heath-vegetation (Pedersen et al., 2017), their foraging grounds could overlap in spring when snow-cover is still high and the geese forage at drier, higher elevation sites which melts out earlier (Anderson et al., 2012; Pedersen, Tombre, et al., 2013). These early melting habitats are important also for reindeer, which are known to select

habitats of advanced snowmelt in spring where plant biomass is higher (Van der Wal et al., 2000). Snow-cover and the timing of melting thus has the potential to alter distributions of herbivores (Anderson et al., 2016) and might lead to more frequent co-occurrences. There is a need to understand the potential for competitive interactions between all the four herbivore species and how this potential is linked to snow-cover and vegetation types, yet no studies have investigated this.

In recent years, populations of reindeer and both species of geese have been increasing in Svalbard (Helldbjerg et al., 2020; Le Moullec et al., 2019; Tombre et al., 2019). Increases of herbivore populations can lead to range expansions or changes in spatial niche breadth, which could intensify potential inter-specific competition. For example, it has been documented that the prevalence of grubbing by pink-footed geese increases in less preferred dry sites concomitant with population growth (Pedersen, Speed, et al., 2013). Predictions of the distribution of pink-footed geese with a warmer climate suggest that population size will further increase, and their spatial distribution in Svalbard will be expanded (R. A. Jensen et al., 2008). This could lead to an increased overlap in habitat use with the other herbivore species, with unknown effects on population dynamics. When it comes to the two species of geese, previous studies have revealed niche segregation both in diet and habitat use during most parts of the breeding season (Fox et al., 2009; Fox & Bergersen, 2005). However, to this date no study has assessed the spatiotemporal distributions and co-occurrence of all four major herbivores in Svalbard during the critical spring season when resources are limited.

This study takes a first step towards understanding the potential for inter-specific competition between resident Svalbard reindeer and Svalbard rock ptarmigan, and migratory pink-footed and barnacle geese in Svalbard, during spring when access to forage is limited. In the first part of this study, observations of herbivore behaviour were carried out at a common foraging ground to collect evidence for interactions between the species. Based on these observations I aimed to describe the behavioural dominance between the different species and the types of interactions that could potentially indicate competition. Potential interference interactions between the herbivores were expected to be detected as a behaviour from one species that disturbed or prevented access to foraging grounds for the other. As the herbivores have significant body size differences, it was expected that the larger-sized species would be the dominant competitor in such a scenario. Second, I used time-series data collected from automatic wildlife cameras to quantify the effects of vegetation type, snow-cover extent, and the presence of potential competitors on the spatiotemporal distribution of the herbivores. The

cameras were placed in different vegetation types where habitat suitability is overlapping for several of the species, more specifically in *Dryas* ridges, moss tundra, and vegetation that has been previously heavily grubbed by pink-footed geese. I expected to see a negative effect of extensive snow-cover on the general presence of herbivores, and a more frequent use of dry ridge habitats by reindeer and geese when snow-cover was high, based on the results of Pedersen, Tombre, et al. (2013) and Van der Wal et al. (2000). Co-occurrence of reindeer and geese was expected to be higher in more productive moss tundra habitats, as these provide suitable forage for both species. However, if the species were to avoid each other to decrease competition, I predicted that the presence of the dominant competitor would have a negative effect on the presence of the other species. This response could be independent of vegetation type, or the herbivores might change their habitat use as a result of avoidance. Any avoidance was expected to be weaker when snow-cover was extensive, as the herbivores would be forced to aggregate in the same small patches of open vegetation and might therefore co-occur more often.

2 Methods

2.1 Study area

The study area included three locations within the Adventdalen valley system (78°10'N, 16°05'E). Adventdalen is located in Nordenskiöld Land in the central part of Spitsbergen, Svalbard. Svalbard has a high-arctic climate, which is characterized by low temperatures and precipitation, and high seasonal variability (Hanssen-Bauer et al., 2019). On the west coast of Spitsbergen, however, warm Atlantic water is transported into the Arctic Ocean by the West Spitsbergen current, causing relatively mild temperatures compared to the average for the latitude (Piechura et al., 2001). Average winter and summer temperatures in Adventdalen are estimated to -13.9 and 4.5, respectively (measured at Svalbard Airport, based on a 1971-2000 average; Hanssen-Bauer et al., 2019). The valley is often snow-covered from October until June, however large interannual variation occurs. Periods of above-zero temperatures and rain in winter are common, which often results in basal ice-layers covering the vegetation (Peeters et al., 2019).

Adventdalen is a broad glacial valley with an extensive braided river system (Fig. 1). Topography and wind-patterns contribute to a large variability of snow distribution in the landscape. Local snow-cover properties like depth and duration, in combination with hydrology and permafrost-related processes gives rise to habitats that support different vegetation compositions. Typically, plant communities are structured in a ridge-snowbed gradient or in wet sites by the hydrological conditions and accumulation of peat (Elvebakk, 1994). In Adventdalen, four major vegetation types can be distinguished as: 1) barren ridges with a sparse vegetation cover of *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 that often supports a variety of forbs and grasses, and 4) moss- and graminoid- dominated wetland (Eischeid et al., 2021; Ravolainen et al., 2020).

2.2 Study species

The resident Svalbard reindeer and Svalbard rock ptarmigan are both widespread on the Svalbard archipelago (Le Moullec et al., 2019; Pedersen et al., 2017). Svalbard rock ptarmigans occur in low densities (Fuglei et al., 2020; Soininen et al., 2016), and availability of breeding habitats of high quality is limited (Pedersen et al., 2017). Svalbard reindeer use small seasonal home ranges, and their movement within and between seasons is very low

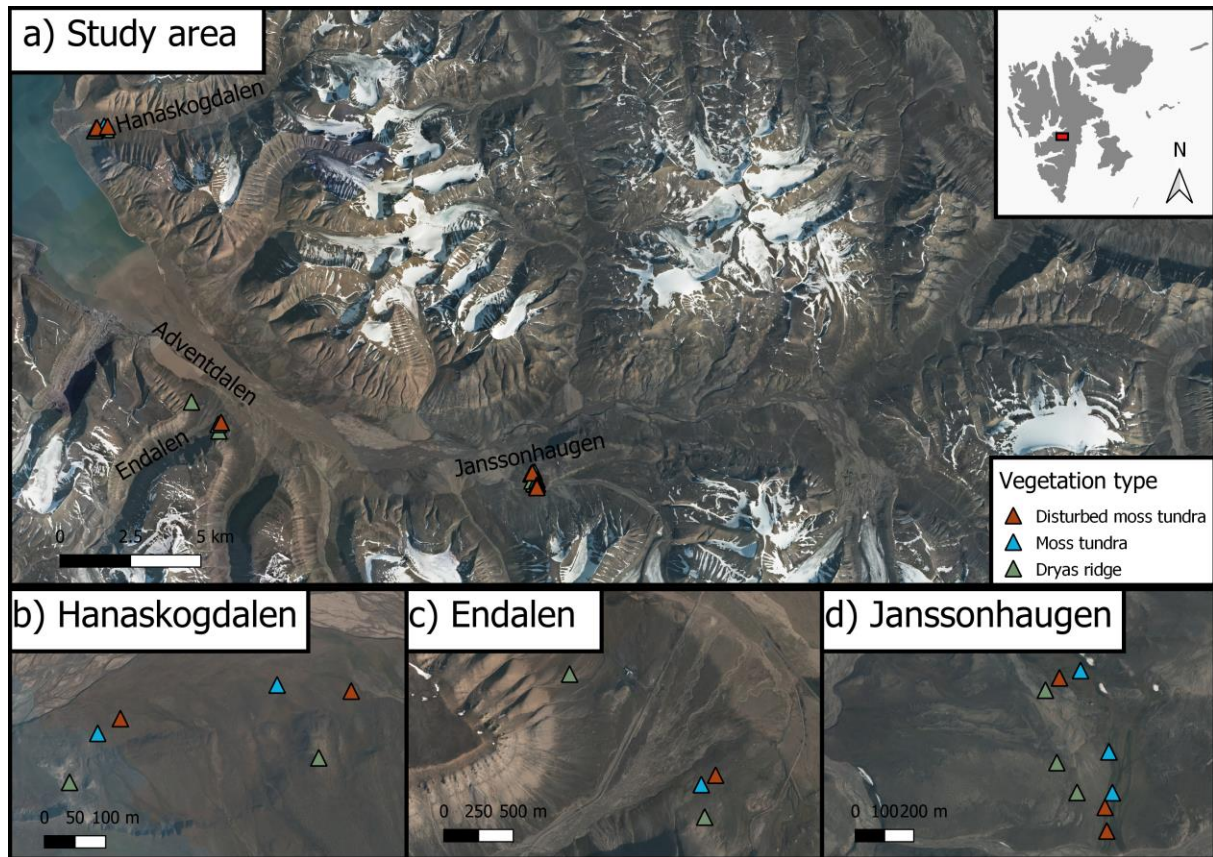


Figure 1. General study area and location of camera-trap sites (coloured triangles). Sites are distributed in three focal vegetation types defined by the study design: *Dryas* ridges (green triangles), moss tundra (blue triangles) and disturbed moss tundra (brown triangles; characterised by disturbance caused by high intensity of goose grubbing or permafrost-related processes). The map in the upper right corner places the study area within Svalbard. The upper panel (a) shows an overview of the study area, while the placement of sites within the three locations: b) Hanaskogdalen, c) Endalen and d) Janssonhaugen is illustrated in the smaller panels. Each site covers an area of 30 x 30 meters. Note that the scale is different in the smaller map panels. Orthophoto retrieved from the Norwegian Polar Institute (2022).

compared to most other reindeer populations (Tyler & Oritsland, 1989). The species live in a nearly predator-free environment. Polar bear (*Ursus maritimus*) attacks and killing of calves by Arctic fox (*Vulpes lagopus*) have been observed but are rare (Derocher et al., 2000; Prestrud, 1993; Stempniewicz et al., 2021). Main drivers of population dynamics are density-dependence caused by food limitation and winter weather variability such as rain-on-snow events, causing icing of foraging grounds (Albon et al., 2017; Hansen et al., 2019). Foraging ecology in spring is influenced by timing of snowmelt, and habitat selection is based on plant quantity rather than quality, in particular of the important food plants at this time of year, *L. confusa* and *S. polaris* (Van der Wal et al., 2000). The Adventdalen study population range from about 1300 to 1700 individuals (year 2014-2020; Environmental monitoring of Svalbard and Jan Mayen, 2021).

Two species of migratory geese, pink-footed goose and barnacle goose, use the study area as pre-breeding foraging grounds. They arrive in early/mid-May and both populations have increased substantially over the last decades (Heldbjerg et al., 2020; Tombre et al., 2019). In the case of the pink-footed goose, a five-fold increase in population size between 1965 to 2012 can be attributed to land use changes on wintering grounds, conservation efforts and a warmer climate (Madsen & Williams, 2012). Since then, the population size has decreased, probably mostly due to an increased hunting pressure on wintering grounds (Johnson et al., 2020). The size of the Svalbard pink-footed goose population is currently estimated to about 68 000 individuals (Heldbjerg et al., 2020). The Svalbard barnacle goose population experienced an eight-fold increase from the 1960s until 2008, after the species was protected and breeding sanctuaries were established in Svalbard (Mitchell et al., 2010), and is currently estimated to about 40 000 individuals (Wildfowl & Wetlands Trust, 2021). Even though the two species of geese show increasing sympatry on breeding grounds due to the population increases, there is relatively little overlap in diet and feeding ecology (Fox et al., 2009; Fox & Bergersen, 2005). Barnacle geese mostly eat moss and grass (Fox et al., 2009; Soininen et al., 2010), while pink-footed geese almost exclusively feed on below ground plant parts as soon as the ground unfreezes sufficiently (Anderson et al., 2012; Fox & Bergersen, 2005; Van der Wal et al., 2007).

2.3 Study design and data collection

The study involved two separate types of data collection: 1) an observational study of herbivore behaviour, and 2) a time-series of herbivore counts related to snow-cover extent and vegetation types based on camera-trap images. The observational study was undertaken as a preliminary study aimed to describe the types of interactions that could potentially indicate competition. The data from this part of the study gave a qualitative description as a background for the interpretation of the quantitative analyses of the camera-trap data. Both parts of the study were based around 19 camera-trap sites that were established in the Adventdalen valley system during early spring 2020. The sites are also part of an ongoing vegetation monitoring study (Ravolainen, 2019), and follow a stratified randomised design. Sites are grouped in three locations within, or in close connection to Adventdalen (Endalen (n=4), Janssonhaugen (n=9) and Hanaskogdalen (n=6)) and distributed within three focal vegetation types: i) *Dryas* ridges (n=7), ii) moss tundra (n=6), and iii) disturbed moss tundra (n=6; Fig. 1). The *Dryas* ridge sites are located in well-drained and exposed ridges, have a sparse vegetation cover, and are dominated by the plant species *D. octopetala*, while moss



Figure 2. Image from one of the camera-traps illustrating a fully snow-covered site (95-100% snow-cover). The camera is located at a moss tundra site. Notice the reindeer foraging on a small patch of open vegetation.

tundra sites are located in moist terrain, characterized by a thick moss-layer and have a high diversity of grass and forb species (Eischeid et al., 2021). The disturbed moss tundra sites are characterised by disturbance caused by high intensity of goose grubbing or permafrost-related processes. Each site covers an area of 30x30 meters.

2.3.1 Observational study of herbivore behaviour

Observations of herbivore behaviour took place in the south-west part of Adventdalen, from 15th of May until the 5th of June. This period was considered to hold the highest potential for observing competitive interactions between species as snow-cover was limiting access to forage and all herbivore species were present on the tundra. Locations of the observations were based around two of the camera-trap sites: one *Dryas* ridge site, and one moss tundra site, both located in Endalen (Fig. 1). These sites were chosen due to their logistical availability for repeated field visits, and their proximity to known ptarmigan territories. Fieldwork was performed every other day or adjusted to weather conditions to avoid observations in poor sight that could cause detection biases. Each field day involved

observations of herbivore behaviour when two or more species were occurring together in groups. Observations lasted for one hour, or until the group dissolved. Groups were observed on locations close to the camera-trap sites and connecting roads. The observations were made from a distance of minimum 200 meters, to reduce disturbance from the observer and avoid breaking the integrity of the data collected from the nearby camera-traps. Species groups that were observed were composed of reindeer and either species of goose, reindeer and ptarmigan, as well as ptarmigan and either species of goose. Groups consisting only of the two species of geese were not observed, as their behaviour is already described (Fox et al., 2009; Fox & Bergersen, 2005). The individuals had to be close enough to each other to make an interaction between them likely, approximated to 50 meters. Competitive behaviours were classified as either chasing, where one individual intentionally chases another, or disturbing. The latter was defined as any reaction from one individual caused by the activity of another, and could involve alertness, moving away or standing up from rest.

2.3.2 Camera-trap images

To create a replicated time-series of herbivore counts, cameras were recording images from each of the 19 camera-sites during the snowmelt period in Adventdalen (10th of May – 10th of June). This period included the arrival of geese on the tundra (first observation on camera-trap sites at 16th of May), and hence represented a development in the number of geese present on the tundra. The cameras used were Reconyx Hyperfire 2 Professional Series cameras (Reconyx Inc, Wisconsin, US). One camera was placed at each site and positioned in accordance with a standardised protocol to ensure that image outline approximately corresponded to the outline of the respective site (30 x 30 meters). Further, the outlines of the sites were marked with aluminium sticks to be visualised in images (Fig. 3). Time lapse images were taken with intervals of 10 minutes, generating a time-series of 144 images per day from each camera-trap. The chosen time interval was thought to balance the trade-off of optimising detection rates while minimising counting effort. Motion sensors for image capture were deactivated as detection rates of herbivores by automatic motion-triggers decreased significantly with increasing distance from the camera, which would cause a detection bias within the site. Additionally, motion-triggers can create biases in studies of several species due to behavioural differences that affect detection rates (Hamel et al., 2013). Images were thus collected from the camera-traps from 00:00 on the 10th of May until 23:50 on the 10th of June, generating an amount of 4607 images per camera and in total 87 533 images for analysis.



Figure 3. Image from one of the camera-traps illustrating the co-occurrence of a reindeer (upper left corner) and two pink-footed geese at a disturbed moss tundra site. In the background of the image, an aluminium stick can be seen that marks the outline of the site. The site covers an area of 30x30 meters. In the foreground of the image are some smaller patches of snow, total coverage of snow in this image is classified as mosaic – small patches (5-50% snow-cover).

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 tagged individually with information like number of herbivores present or extent of snow-cover. Further, data is exported directly in a dataset containing information about each image per row. Herbivores were counted from each image, within the outline of the site (30 x 30 meters, marked with a stick; Fig. 3). Snow-cover extent was visually estimated as a percentage of cover within the site and recorded in each image as one of the following categories: 1: 0-5% snow-cover (open vegetation), 2: 5-50% snow-cover (mosaic, small patches of snow), 3: 50-95% snow-cover (mosaic, large patches of snow), and 4: 95-100% snow-cover (fully covered). See examples of snow-cover estimates in Fig. 2 and 3. Some of the images from the camera-traps were obscured due to poor weather conditions or technical problems with the cameras. These images were removed

from the dataset, leaving a total of 84010 images. A total count of 895 reindeer, 4050 pink-footed geese, 2889 barnacle geese and 75 ptarmigans were recorded from the images (Supplementary material; Fig. S1). As the occurrence of ptarmigans at the camera-trap sites was too low, this species was excluded from the quantitative analyses. Counts of the two species of geese were combined, as any potential interaction with reindeer was expected to be the same for both species (based on observations from the preliminary observational study).

2.4.2 Statistical analysis

All data analyses were performed in RStudio, version 2021.9.1.372 (RStudio Team, 2021). Data exploration was conducted according to the protocol by Zuur et al. (2010) to detect possible outliers, zero-inflation or collinearity and determine the correct relationship between dependent and independent variables. Two response variables were chosen for the analyses: i) total count of reindeer per camera-trap site per time-unit, and ii) total count of geese per camera-trap site per time-unit. As counts were repeated every 10 minutes, the observations were not independent. This was visible in the raw data as counts of geese and reindeer were temporally autocorrelated (based on AutoCorrelation Function (ACF) plots). Temporal non-independence is a common problem with camera-trap data, and a solution is to change the length of time-intervals (Sollmann, 2018). The data were therefore aggregated at three time-intervals: 1 hour (hourly data), 3 hours (3-hourly data) and 24 hours (daily data). The potential behavioural effects that the herbivores would have on each other's presence at a site was expected to be detected within one or maximum three hours, however the three different aggregations were made to consider the consistency of results across temporal scales. For each aggregated dataset, herbivore counts within the chosen time-interval were summarised to a total count over the interval. For snow-cover measures, a mean value was assigned at each time-interval, giving values ranging from 1:4. Therefore, snow-cover was used as a continuous rather than categorical variable later in the analyses.

Generalized linear mixed models (GLMMs) with a negative binomial distribution and a log link function were applied to the herbivore counts, to assess which factors drive the spatial distribution of reindeer and geese. Analyses were carried out using the `glmmTMB` package in R (Brooks et al., 2017). For each temporal scale (hourly, 3-hourly and daily) and each herbivore, a global model was assembled that included a count of the other herbivore within the chosen time-interval at each site as an explanatory variable to assess whether they were affecting each other's presence. The count variables were log-transformed ($\ln(x+1)$) when

used as explanatory variables to improve model convergence. Two environmental explanatory variables were included: vegetation type (categorical with three levels: *Dryas* ridge, moss tundra and disturbed moss tundra) and snow-cover ([1:4], used as continuous variable), in addition to three interactions: geese/reindeer \times vegetation type, geese/reindeer \times snow-cover and vegetation type \times snow-cover. Initially, a day-of-year (DOY) variable was included in the global model to account for arrival time of geese, however this variable was removed after data exploration as it was collinear with snow-cover (Supplementary material; Table S1). Camera-trap site was included as a random intercept in the models to account for the dependency structure of counts within each site. A first-order autoregressive covariance term (AR1) was added to account for temporal autocorrelation of counts within camera-trap sites. The two global models from each temporal scale thus took the form:

i) Reindeer as response

$$\text{Reindeer} \sim \text{Geese} + \text{VegType} + \text{Snow} + \text{Geese} \times \text{VegType} + \text{Geese} \times \text{Snow} + \text{VegType} \times \text{Snow} + \text{Camsite} + \text{AR1}$$

ii) Geese as response

$$\text{Geese} \sim \text{Reindeer} + \text{VegType} + \text{Snow} + \text{Reindeer} \times \text{VegType} + \text{Reindeer} \times \text{Snow} + \text{VegType} \times \text{Snow} + \text{Camsite} + \text{AR1}$$

where Reindeer and Geese are counts of reindeer and geese at each camera-trap site within the respective time-interval. VegType = vegetation type, Snow = snow-cover. Camsite is the random intercept of camera-trap site, assumed normally distributed, and residuals are following an autoregressive structure (AR1).

Evaluation of global model fits was done by visually inspecting qq-plots and plots of standardized residuals against fitted values and covariates. Residual diagnostics were performed using the DHARMA package in R (Hartig, 2021). ACF plots were inspected to assess independence of residuals. A set of 10 candidate models of decreasing complexity, derived from each of the six global models (one for each response variable at each temporal scale), were chosen for model selection (Tables 2, 4). All candidate models were based on biologically relevant hypotheses, as described in the introduction, and the vegetation type and snow-cover variables were retained in all the models in the candidate set. Candidate models were compared with Akaike's Information Criterion (AIC; Burnham & Anderson, 2002),

using the function 'aictab' in the AICcmodavg package in R (Mazerolle, 2020). This function produces AICc values, which is a modified version of AIC for small sample sizes. The sample sizes in this study were not small, however AICc values approximates AIC values when sample sizes are large and are therefore often recommended as a default (Symonds & Moussalli, 2011). Generally in AIC model selection, the candidate model with the lowest AIC value is regarded the best approximating model, and remaining models are ranked by ΔAIC values, however there is some debate as to when a candidate model can be considered uninformative (Burnham et al., 2011; Symonds & Moussalli, 2011). In this study, I regarded all models with $\Delta AICc < 2$ as essentially as good as the best model (Burnham & Anderson, 2002). Further, I rejected models that were not contained in a 95% confidence set of models computed for each of the six sets of candidate models. The confidence set of models represent a 95% confidence that one of the models within this set is the best model, and is computed by ranking all models from the best until cumulative AICc weights exceeds 0.95 (Burnham & Anderson, 2002). The selected models chosen to explain the spatial distribution of reindeer and geese in relation to vegetation type, snow-cover and presence of other herbivores, were the models assigned the lowest AICc value, at the 3-hourly temporal scale. This time-interval was chosen as there was minimal temporal dependence of residuals in these models, and the potential behavioural effects of the presence of other herbivores was thought to disappear after the duration of this time-interval. Model predictions were made from the selected model for each of the herbivores, using the function 'ggpredict' in the ggeffects package in R (Lüdtke, 2018).

3 Results

3.1 Co-occurrence and behaviour based on observational study

In the study area in Endalen, where co-occurring reindeer, geese and ptarmigans were observed, at least one group was located every field day, and in total 24 observations were made. This included 19 observations of reindeer and geese, two of reindeer and ptarmigans, and five of geese and ptarmigans. In 10 of the 19 observations of co-occurring geese and reindeer, geese were disturbed by reindeer, but never intentionally chased. The behaviours indicating that the geese were disturbed included flying away (4 of 10 observations), calling, interrupted resting or eating, or walking away. In the other 9 of the 19 observations of co-occurring geese and reindeer, the two species stayed close, but were not disturbed by each other. In one of the two observations of co-occurring reindeer and ptarmigans, a reindeer intentionally chased the ptarmigan, and ptarmigans were chased or disturbed by geese in two of five observations. In all cases, the ptarmigans moved just a few meters away, and continued feeding shortly after. Reindeer never displayed any behaviours indicating that they were disturbed by either geese or ptarmigans.

3.2 Spatial distribution of reindeer and geese based on camera-trap data

Generally, reindeer were present in both *Dryas* ridge vegetation, moss tundra and disturbed moss tundra, at all levels of snow-cover (Fig. 5a). Moss tundra habitats, both disturbed and undisturbed, were more frequently used compared to *Dryas* ridges, when snow-cover was low (below 5%; Fig. 5a). The same pattern was seen in the temporal distribution of reindeer, where *Dryas* ridge habitats were used early in spring, until they switched around June 5th (DOY 155), whereafter reindeer were mainly observed in moss tundra habitats (Fig. 5c). The total number of reindeer present at camera-trap sites was higher after this date (Fig. 5c). Geese were present in both moss tundra and disturbed moss tundra, and in very low numbers in the *Dryas* ridge habitats (Fig. 5b). They were not present at any of the camera-trap sites when snow-cover was most extensive (above 95%; Fig. 5b). The general presence of geese at the camera-trap sites peaked on May 25th (DOY 145), and at the beginning of the study period they were not present at any of the camera-trap sites (Fig. 5d). Reindeer and geese both occurred at 15 of 19 camera-trap sites over the length of the whole study period, but co-occurrence within one hour was only 45 of 14148 times (0.03 %), based on the total number

of hourly summarized counts obtained from camera-trap images (Table 1). Reindeer and geese co-occurred at camera-trap sites within one hour 18 times more often in moss tundra habitats compared to *Dryas* ridges (Fig. 4).

Table 1. Number of co-occurrence of reindeer and geese within different temporal scales, based on camera-trap data. In this respect, co-occurrence is defined as occurrence of both geese and reindeer at one camera-trap site within the respective time-unit. Observations indicate the total number of observations per time-unit.

Temporal scale	1 hour	3 hours	1 day	1 month
Observations	14148	4757	606	19
Co-occurrence	45	58	76	15
Proportion	0.003	0.01	0.12	0.79

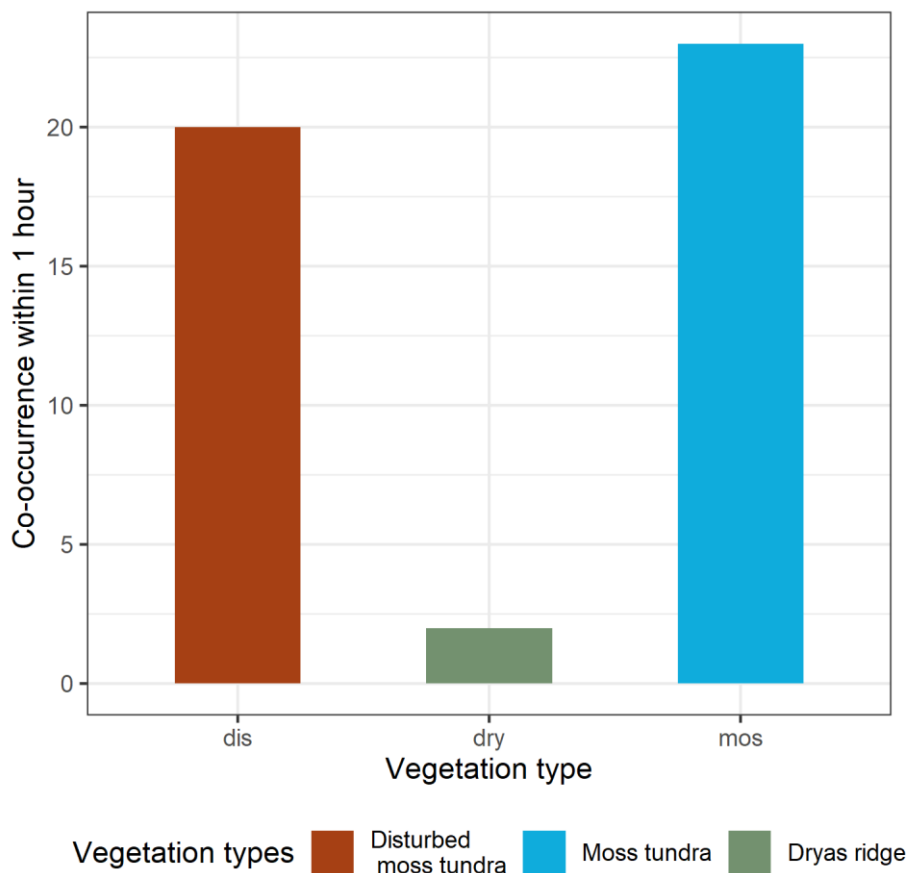


Figure 4. Number of observations of co-occurring reindeer and geese at camera-trap sites within one hour, in each of the three vegetation types (dry = *Dryas* ridge, mos = moss tundra, dis = disturbed moss tundra). Co-occurrence is defined as occurrence of both geese and reindeer at one camera-trap site within one hour. The total number of hourly observations was 14148.

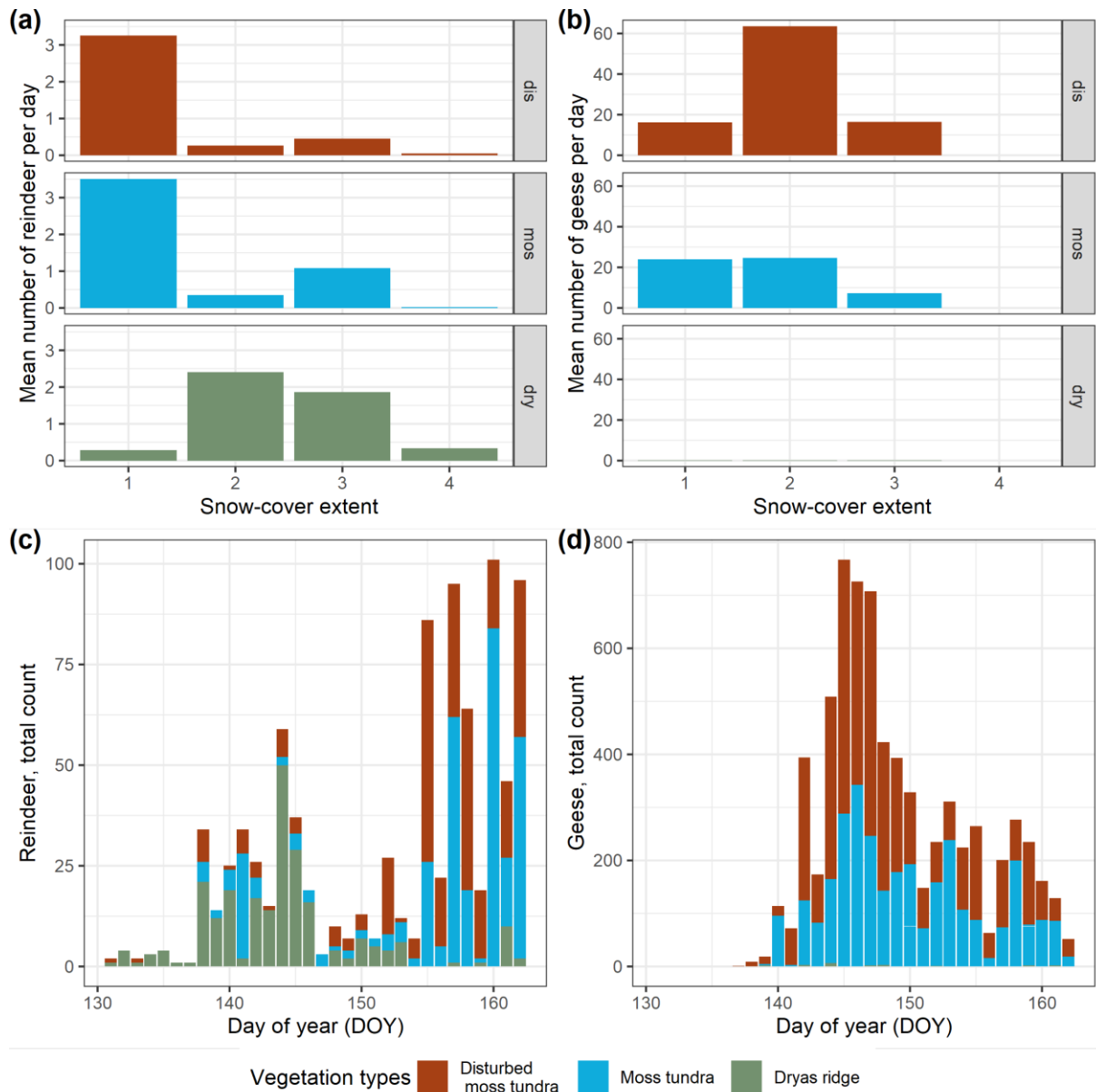


Figure 5. Upper subplots: Mean number of reindeer (a) and geese (b) counted per day at camera-trap sites in each vegetation type (horizontal panels), in relation to snow-cover extent. The colours represent the presence of reindeer or geese in each vegetation type (dry = *Dryas* ridge (green), mos = moss tundra (blue), dis = disturbed moss tundra (brown)). Snow-cover extent is categorised as: 1: 0-5% snow-cover (open vegetation), 2: 5-50% snow-cover (mosaic, small patches of snow), 3: 50-95% snow-cover (mosaic, large patches of snow), and 4: 95-100% snow-cover (fully covered). Lower subplots: Total count of reindeer (c) and geese (d) from camera-trap sites at each day of the study period. Note that the scale on the y-axis is not the same in the left and right subplots.

3.2.1 Reindeer models

Model selection of reindeer models showed clear support for the best model from each temporal scale, with only four models in total having $\Delta\text{AICc} < 2$ (Table 2). Models were consistent across temporal scales, and the effects of snow-cover and *Dryas* ridge vegetation were negative in all models contained in the 95% confidence sets, while the interaction between these two effects was always positive. This interaction term (*Dryas* ridge vegetation

× snow-cover) had clear support in model selection across temporal scales as it was contained in all the models making up the 95% confidence sets (Table 2). There was no significant effect of the presence of geese in any of the models contained in the 95% confidence set of models from either the hourly, 3-hourly or daily data. This shows that the presence of geese at a certain site had no effect on the probability to observe reindeer at the same site within any of the time-intervals explored in this study.

Table 2. Model selection table showing 95% confidence set of best-ranked GLMMs (models whose cumulative AICc weight ≤ 0.95) examining the spatiotemporal distribution of reindeer in relation to vegetation type, snow-cover and presence of other herbivores, at each temporal scale. The fixed effects include snow-cover ([1:4], used as continuous variable), vegetation type (categorical; *Dryas* ridge, moss tundra and disturbed moss tundra) and total counts of geese per camera-trap site within the selected time interval (continuous), in addition to interactions. The vegetation type and snow-cover variables were retained in all models of the candidate set, as was the random effect (camera ID) and the AR1 term to correct for temporal autocorrelation. The candidate set for each temporal scale consisted of 10 models of decreasing complexity, derived from the global model. The selected model is indicated with bold letters. VegType = vegetation type, Snow = snow-cover, k = number of parameters included in each model.

Temporal scale	Model	Geese	Snow	VegType	Geese x Snow	Geese x Vegtype	Snow x VegType	k	AICc	Δ AICc	AICc weight
Hourly	1		x	x			x	10	2888.78	0.00	0.80
	2	x	x	x	x		x	12	2892.44	3.66	0.13
	3	x	x	x	x	x	x	14	2895.23	6.45	0.03
3-hourly	1		x	x			x	10	2316.15	0.00	0.56
	2	x	x	x			x	11	2318.14	1.99	0.21
	3	x	x	x	x		x	12	2319.54	3.39	0.10
	4	x	x	x		x	x	13	2319.89	3.74	0.09
Daily	1	x	x	x		x	x	13	1274.56	0.00	0.48
	2	x	x	x	x	x	x	14	1276.57	2.01	0.18
	3		x	x			x	10	1276.88	2.32	0.15
	4	x	x	x			x	11	1277.30	2.74	0.12
	5	x	x	x	x		x	12	1279.38	4.82	0.04

From the hourly data, there was clear support for the best model, which included the explanatory variables vegetation type and snow-cover, and the interaction term vegetation type × snow-cover (Table 2). The best model from the daily data additionally contained the geese variable, and the interaction geese × vegetation type (Table 2). From the 3-hourly data, the model with the lowest AICc value included the vegetation type and snow-cover variables, and the interaction term vegetation type × snow-cover. However, the second-best model at this temporal scale had Δ AICc = 1.99, and was therefore considered as good as the best

model. This model additionally included the geese variable, however the effect was not significant in the model. The selected model explaining the spatiotemporal distribution of reindeer is presented in Table 3. There was a clear negative effect of snow-cover (-0.724, SE: 0.298; estimates on the log scale) on the number of reindeer present at camera-trap sites. The effect of *Dryas* ridge vegetation compared to the two other vegetation types was also negative (-2.848, SE: 0.845). The interaction term snow-cover \times *Dryas* ridge vegetation was positive (Table 3). These results indicate that reindeer were generally less present in areas of extensive snow-cover and in *Dryas* ridge vegetation compared to moss tundra vegetation, however when snow-cover was extensive they were more frequently present in *Dryas* ridges, as visualised in prediction plots (Fig. 6c, d).

Table 3. Parameter estimates for the explanatory variables in the model selected to explain the spatiotemporal distribution of reindeer. Estimates are given on the log-scale and shown with standard errors, z values and P-values. Explanatory variables include snow-cover ([1:4], used as continuous variable) and vegetation type (categorical; *Dryas* ridge, moss tundra and disturbed moss tundra), in addition to the interaction between these variables. The estimates for vegetation type effects are comparisons to the reference level, which is set to disturbed moss tundra. ‘VegTypeDry = vegetation type *Dryas* ridge, ‘VegTypeMos’ = vegetation type moss tundra.

	Estimate	Std.error	z value	P-value
Intercept	-6.350	0.565	-11.241	<0.001
Snow-cover	-0.724	0.298	-2.427	0.015
VegTypeDry	-2.848	0.845	-3.370	<0.001
VegTypeMos	-0.422	0.761	-0.555	0.579
Snow-cover x VegtypeDry	1.348	0.424	3.181	0.001
Snow-cover x VegTypeMos	0.058	0.449	0.128	0.898

Random effects: camera-trap var = 2.443 e-07; AR1 corr = 0.10 var = 45.41

3.2.2 Goose models

There was some uncertainty in model selection of the goose models. In total, 14 models had $\Delta\text{AICc} < 2$ (Table 4), but parameter estimates were consistent between models. Effects of *Dryas* ridge vegetation and extensive snow-cover were significant and negative in all models contained in the 95% confidence sets across temporal scales. There was a significant negative effect of the presence of reindeer in two of the models in the 95% confidence set of models, however these models had $\Delta\text{AICc} = 3.18$ and 4.95 (Table 4). Thus, a negative effect of the presence of reindeer on the probability to observe geese within the same site is unlikely but can not be rejected.

Table 4. Model selection table showing 95% confidence set of best-ranked GLMMs (models whose cumulative AICc weight ≤ 0.95) examining the spatiotemporal distribution of geese in relation to vegetation type, snow-cover and presence of other herbivores, at each temporal scale. The fixed effects include snow-cover ([1:4], used as continuous variable), vegetation type (categorical; *Dryas* ridge, moss tundra and disturbed moss tundra) and total counts of reindeer per camera-trap site within the selected time interval (continuous), in addition to interactions. The vegetation type and snow-cover variables were retained in all models of the candidate set, as was the random effect (camera ID) and the AR1 term to correct for temporal autocorrelation. The candidate set for each temporal scale consisted of 10 models of decreasing complexity, derived from the global model. The selected model is indicated with bold letters. VegType = vegetation type, Snow = snow-cover, k = number of parameters included in each model.

Temporal scale	Model	Reindeer	Snow	VegType	Reindeer x Snow	Reindeer x Vegtype	Snow x VegType	k	AICc	Δ AICc	AICc weight
Hourly	1		x	x			x	10	10900.20	0.00	0.19
	2	x	x	x	x			10	10900.49	0.29	0.17
	3	x	x	x		x	x	13	10900.55	0.35	0.16
	4	x	x	x	x	x		12	10900.75	0.55	0.15
	5	x	x	x		x		11	10901.32	1.12	0.11
	6	x	x	x			x	11	10901.49	1.28	0.10
	7		x	x				8	10901.89	1.69	0.08
3-hourly	1	x	x	x	x	x	x	14	6563.87	0.00	0.41
	2	x	x	x	x	x		12	6564.82	0.96	0.25
	3	x	x	x		x	x	13	6565.64	1.78	0.17
	4	x	x	x	x		x	12	6567.05	3.18	0.08
	5	x	x	x		x		11	6567.37	3.50	0.07
Daily	1	x	x	x		x	x	13	2137.00	0.00	0.35
	2	x	x	x		x		11	2137.68	0.67	0.25
	3	x	x	x	x	x	x	14	2138.52	1.51	0.17
	4	x	x	x	x	x		12	2138.87	1.87	0.14
	5	x	x	x	x		x	12	2141.95	4.95	0.03
	6	x	x	x			x	11	2142.17	5.16	0.03

From the hourly data, all models in the 95% confidence set of models had Δ AICc < 2 (Table 4). These models also had some leftover temporal autocorrelation in the residuals, and were therefore ascribed little explanatory power. From the daily data, there were four models with Δ AICc < 2 (Table 4). The best model at this temporal scale included all additive effects, and the interaction terms reindeer \times vegetation type and snow-cover \times vegetation type, while the three next-best models included different combinations of the interaction terms (Table 4). From the 3-hourly data, the selected model was the global model, including all additive and interaction effects (Tables 4, 5). Two other models at this temporal scale had Δ AICc < 2 and were regarded as good as the best model, however they were both simplifications of the selected model (Table 4).

In the selected model, the effect of *Dryas* ridge vegetation was negative (-8.003, SE: 1.699), as was the effect of snow-cover (-1.338, SE: 0.365; Table 5), indicating that geese generally avoided sites with *Dryas* ridge vegetation and extensive snow-cover. This is visualised in the prediction plots (Fig. 6a, b). The interaction vegetation type \times snow-cover was not significant in the selected model or the other models with $\Delta\text{AICc} < 2$ from the 3-hourly data (Tables 4, 5). There was a significant positive effect of the interaction reindeer \times *Dryas* ridge vegetation in the selected model, and in the two next-best models (Tables 4, 5), meaning that geese were more frequently present in *Dryas* ridge sites where there were more reindeer. The interaction reindeer \times snow-cover was not significant in the selected model (Table 5), however there was a significant positive effect of this interaction in the second-best model, indicating that geese co-occurred more often with reindeer when snow-cover was extensive (Supplementary material; Table S2). This model had $\Delta\text{AICc} = 0.96$, and was therefore considered essentially as good as the selected model (Table 4).

Table 5. Parameter estimates for the explanatory variables in the model selected to explain the spatiotemporal distribution of geese. Estimates are given on the log-scale and shown with standard errors, z values and P-values. Explanatory variables include snow-cover ([1:4], used as continuous variable), vegetation type (categorical; *Dryas* ridge, moss tundra and disturbed moss tundra) and the presence of reindeer at a certain camera-trap site within the selected time-interval (continuous), in addition to interaction effects. The estimates for vegetation type effects are comparisons to the reference level, which is set to disturbed moss tundra. ‘VegTypeDry = vegetation type *Dryas* ridge, ‘VegTypeMos’ = vegetation type moss tundra.

	Estimate	Std.error	z value	P-value
Intercept	-0.049	0.924	-0.053	0.958
Reindeer	-0.515	0.442	-1.165	0.244
Snow-cover	-1.338	0.365	-3.669	<0.001
VegTypeDry	-8.003	1.699	-4.710	<0.001
VegTypeMos	1.050	1.259	0.834	0.404
Reindeer x Snow-cover	0.573	0.297	1.927	0.054
Reindeer x VegTypeDry	1.617	0.703	2.300	0.021
Reindeer x VegTypeMos	-0.220	0.341	-0.644	0.520
Snow-cover x VegtypeDry	1.088	0.866	1.256	0.209
Snow-cover x VegTypeMos	-0.771	0.515	-1.497	0.134

Random effects: camera-trap var = 0.761; AR1 corr = 0.94 var = 8.488.

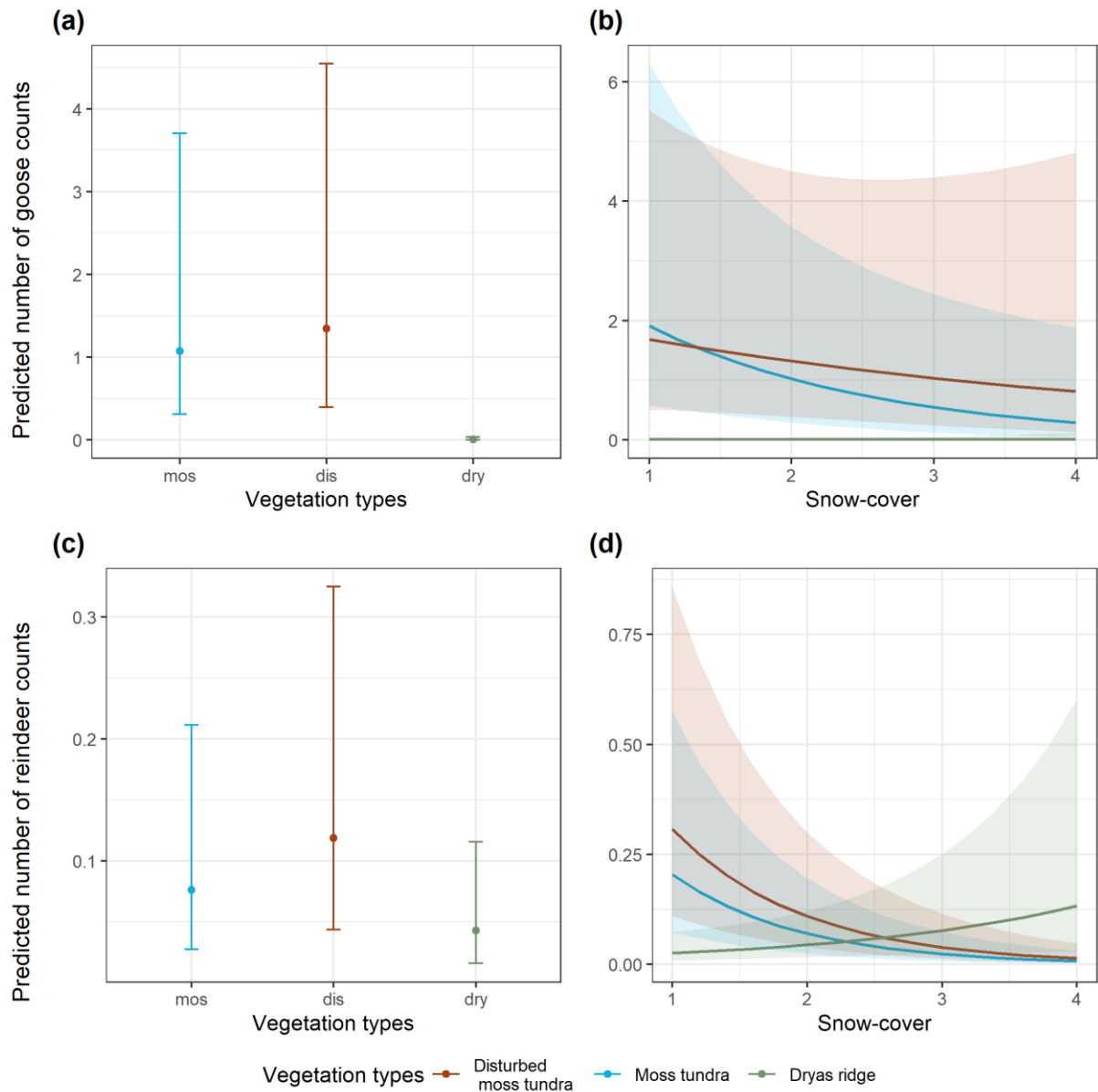


Figure 6. Left subplots: Predicted number of geese (a) and reindeer (c) present at camera-trap sites in each of the three vegetation types (dry = *Dryas* ridge, mos = moss tundra, dis = disturbed moss tundra), as predicted by the selected GLMMs. Right subplots: Predicted number of geese (b) and reindeer (d) present at camera-trap sites in relation to snow-cover extent in *Dryas* ridges (green), moss tundra (blue) and disturbed moss tundra (brown). Snow-cover extent is categorised as: 1: 0-5% snow-cover (open vegetation), 2: 5-50% snow-cover (mosaic, small patches of snow), 3: 50-95% snow-cover (mosaic, large patches of snow), and 4: 95-100% snow-cover (fully covered), however the variable is used as a continuous variable in the models. Predicted values are conditioned on the fixed effects only. Error bars and bands indicate 95% confidence intervals (CI).

4 Discussion

This study investigated the behaviour and habitat use of four high-Arctic herbivores: the residents Svalbard reindeer and Svalbard rock ptarmigan, and the migratory pink-footed goose and barnacle goose, as a first step towards understanding the potential for inter-specific competition in spring, when access to forage is limited. Observations from the preliminary study of herbivore behaviour indicated that there is a hierarchy of behavioural dominance based on size among the herbivores, where reindeer is the dominant competitor. No direct aggressive interactions were observed between reindeer and geese. Expectedly, the results from the GLMM showed that the spatiotemporal distribution and habitat use of reindeer in Svalbard was not affected by the presence of geese (Table 3). However, even though geese were regularly disturbed by reindeer, no consistent effect of reindeer presence could be detected in the goose models (Table 5). Rather, the spatiotemporal distributions of reindeer and geese on the Svalbard tundra in early spring were mainly driven by vegetation type and the extent of snow-cover (Tables 3, 5). Ptarmigans were the least dominant competitor in the presence of reindeer and geese and were chased by both. This behaviour could potentially exclude ptarmigans from important feeding or breeding grounds. Unfortunately, the number of ptarmigan observations was too low in this study (Supplementary material; Fig. S1), and the potential for interference competition between this species and reindeer or geese is yet to be quantified.

Based on the results of this study it is clear that reindeer and geese in Svalbard use the same foraging areas in spring, even at a fine spatial scale (30x30 meters; Table 1). Model selection of reindeer models further indicated that reindeer do not avoid geese and distribute themselves in different vegetation types independently of the presence of geese (Tables 2, 3). These findings are supported by my observations of reindeer behaviour in groups with geese, and in accordance with preliminary assessments of shared habitats between reindeer and pink-footed geese (Ravolainen et al., 2018). Intra-guild competition is rarely studied in reindeer populations and such interactions are often complicated by relations to predation (Kojola et al., 2021). Svalbard reindeer experience low predation pressure, and a previous study suggest that their spatial distribution is most likely independent of predation risk (Garfelt-Paulsen et al., 2021). This study found that interference interactions with, or avoidance of species at the same trophic level is unlikely, and thus the spatiotemporal distribution of Svalbard reindeer is

mainly driven by interactions with lower trophic levels (i.e., forage plants) and mediating effects of snow-cover rather than predation or competition.

My observations suggested that reindeer is the behaviourally dominant herbivore in Svalbard, and geese were in fact observed leaving an area after being disturbed by close encounters with reindeer. Therefore, it could be expected that a negative effect of the presence of reindeer would be detected in the models explaining the distribution of geese, which would indicate an avoidance of reindeer. However, the selected model showed no significant effect of reindeer presence (Table 5). Even though a negative effect of the presence of reindeer was significant in two of the models in the 95% confidence sets, meaning that the effect can not be rejected, there is not enough statistical power to confirm that geese do avoid reindeer. There is also no significant negative effect of the interaction between the presence of reindeer and vegetation type in the models (Table 5). This means that geese forage in moss tundra and *Dryas* ridge vegetation independently of the presence of reindeer in these habitats. Direct interference competition has the potential to exclude the less dominant competitor from selecting the preferred foraging grounds (Kristiansen & Jarrett, 2002). The results from this study suggest that this is not the case for reindeer and geese in Svalbard, and aggressive behaviour or avoidance do not seem to be important drivers of habitat use. Potential future interactions between reindeer and geese would be expected to be asymmetrical, as geese are disturbed by reindeer but not opposite, and might be defined as ammensalism rather than competition. Asymmetry in species interactions are common, and this study highlights the importance of understanding the context of interactions (Cazelles et al., 2016; Chen et al., 2020; Morris et al., 2000).

Even though a negative effect of reindeer presence was not confirmed in goose models, there was a significant interaction between snow-cover extent and presence of reindeer in the second-best model (Supplementary material; Table S2). This indicates that geese more frequently co-occur with reindeer when snow-cover is extensive compared to when it is mostly melted, which confirms my expectation. The statistical significance of the effect is not strong, however this could be due to the early snowmelt in the current study year. At the time the geese arrived on the tundra this year, large patches of open vegetation were already available. In years of late snowmelt, the availability of open vegetation might be limited to very small patches at the time of arrival, which could force the herbivores to aggregate. Reindeer and geese feeding together in small patches of open vegetation have been observed

in Svalbard in years when snowmelt is late (Å.Ø. Pedersen, *pers. comm.*). The mediating effect of snow-cover extent on co-occurrence of reindeer and geese might therefore be more pronounced in late-melting years. Snow-cover extent and timing of snowmelt is expected to change with climate warming (Constable et al., 2022; Hanssen-Bauer et al., 2019), and it is therefore important to further study how co-occurrence of reindeer and geese relates to variations in snowmelt timing.

The shared space use of reindeer and geese in Svalbard during spring represent a contrast to landscape partitioning in other Arctic herbivore communities during winter (Schaefer et al., 1996). Extensive snow-cover in spring causing increased co-occurrence and use of shared foraging areas could lead to strong overlap in resource use. This may increase the potential for competition through resource depletion. However, shared space use does not mean shared resource use. In Greenland, muskoxen open up vegetation in winter by making feeding craters in the snow, where also hares and ptarmigans feed, and the same is seen for reindeer and ptarmigans in Svalbard (Pedersen et al., 2006). 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, even though the herbivores were feeding in the same craters (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 overlap in reindeer and goose diets in Svalbard during spring when snowmelt is late is not yet known. Even though resources are shared, the total availability might not be limited, and seasonal variations of the availability of resources could exceed the negative consequences of competition in periods of limited availability (Kelt et al., 2019). These aspects need to be further investigated to understand the potential for exploitative competition between the Svalbard herbivores.

Based on the results from the GLMMs, it seems that Svalbard reindeer generally feed more often in moss tundra habitats rather than the drier, less densely vegetated *Dryas* ridges (Fig. 6c, Table 3). This is in accordance with results from summer habitat suitability models and female reindeer habitat selection during calving (Garfelt-Paulsen et al., 2021; Ravolainen et al., 2018), and likely reflect a selection for vegetation containing high biomass of forage plants (Van der Wal et al., 2000). However, models show a clear interaction between the presence of reindeer in different vegetation types and the extent of snow-cover (Tables 2, 3). This result indicates that reindeer more frequently use *Dryas* ridge habitats when snow-cover

is extensive (Fig. 5a, 6d). These habitats usually have a thinner snow-cover and melts out earlier in spring. In a snow manipulation study where snowmelt was experimentally advanced and delayed in separate plots, Van der Wal et al. (2000) found that earlier snowmelt advances plant phenology. The advanced plots were selected by reindeer, likely due to the higher biomass of *S. polaris* and *L. confusa*, which are important food plants at this time of year. Bjørkvoll et al. (2009) also found a relatively high proportion of the evergreen *D. octopetala* in the diet of Svalbard reindeer in late winter, which provide green tissue even when extensive snow-cover is still limiting the availability of live plant biomass. Thus, the increased use of *Dryas* ridge habitats when snow-cover is extensive is in accordance with previous studies of habitat selection by Svalbard reindeer, and indicates that they follow the phenological development of plants in the landscape (Bjørkvoll et al., 2009; Van der Wal et al., 2000).

Similarly to reindeer, geese were most often present in the moss tundra vegetation compared to *Dryas* ridges (Fig. 5b, 6a). However, even though the interaction between their presence in different vegetation types and the extent of snow-cover was included in the selected model, the effect was not significant (Table 5). Pink-footed geese have previously been found to feed more frequently in dry, early-melting habitats in early spring when snow-cover reduced the availability of the preferred wet fen habitats (Anderson et al., 2012; Pedersen, Tombre, et al., 2013; Speed et al., 2009). As pink-footed geese mainly feed by grubbing below-ground plants parts, the use of early-melting ridge habitats is likely due to earlier thawing of soil and easier extractability of plant roots, such as *Bistorta vivipara* (Anderson et al., 2012). Therefore, the lack of a significant interaction between snow-cover extent and presence in *Dryas* ridges is contrary to what was expected. However, even though the two species of geese were combined in the models, geese were rarely present in the *Dryas* ridge habitats overall. Barnacle geese have been observed feeding mostly along the edges of snow-patches (Fox & Bergersen, 2005), and since their diet mainly consist of moss (Fox & Bergersen, 2005; Prop & de Vries, 1993; Soiminen et al., 2010), they might not be as dependent on early-melting dry habitats as reindeer and pink-footed geese, which could explain the low occurrence in *Dryas* ridge sites in the current study. With regards to the pink-footed geese, the few observations in *Dryas* ridge sites, even when snow-cover was extensive, is opposite to what was found by Anderson et al. (2012) and Pedersen, Tombre, et al. (2013), however the results might not be contradictory. The *Dryas* ridge sites in this study are characterised by a sparse vegetation cover, while the 'dry' habitats defined by the study design of Anderson et al. (2012) and Pedersen, Tombre, et al. (2013) were not elaborately described in terms of vegetation. The

vegetation in Svalbard is heterogeneous at a fine spatial scale, and these habitats could have been more densely vegetated, or have included more of the pink-footed geese's preferred food plants, like *B.vivipara*. This could explain the higher occurrence of pink-footed geese in drier habitats in these studies. Another explanation for the low presence of pink-footed geese in *Dryas* ridge sites in the current study could be that the availability of the preferred wet fen habitats was already high at the time that geese arrived at the tundra as snowmelt was early this year (Anderson et al., 2016; Pedersen, Tombre, et al., 2013).

There was a significant interaction between goose occurrence in different vegetation types and presence of reindeer, where geese more frequently used the *Dryas* ridge habitats when there was a higher presence of reindeer (Table 5). In a co-occurrence perspective, this could be interpreted as an indication of facilitation, however a more likely biological explanation is that this observed co-occurrence is due to favourable properties, not measured in this study, of some of the *Dryas* sites. For example, the vegetation classes used in this study are coarse, and more fine-scaled measures of vegetation composition or productivity could more accurately predict distributions and co-occurrence of reindeer and geese. I found that one of the *Dryas* sites had a particularly high number of both reindeer and geese, which likely explains the significant interaction between reindeer presence and vegetation type in the goose models. This site could be different to the other *Dryas* sites in regard to the availability of preferred food-plants that are shared between reindeer and geese. Additionally, the statistical significance of the effect might have been exaggerated as the number of geese present in *Dryas* ridge sites is overall low.

The more frequent presence of geese at one particular *Dryas* site could also be due to the close proximity of three pink-footed goose nests which were observed near this site from the 5th of June. Pink-footed geese breeding on sloping tundra sites generally feed in close proximity to nests to avoid nest predation (Anderson et al., 2015). Although this study primarily focused on the pre-breeding period for geese, factors influencing nest site selection might have affected the distribution of geese in the latter part of the study. Vegetation type and extent of snow-cover are likely the most important determinants of nest site, in addition to protection from predation from Arctic fox (Anderson et al., 2015, 2019), however terrain parameters like elevation, slope and aspect more accurately explain nest site selection by pink-footed geese on a fine spatial scale (Wisz et al., 2008). Barnacle geese are smaller than pink-footed geese and often nest on inaccessible cliffs or islands, likely due to their lower

ability to defend nests against predators (Løvenskiold, 1964). Timing of egg-laying in pink-footed geese is usually in late May or early June, but it is delayed by late snowmelt (Madsen et al., 2007). As the study year was an early-melting year, it is likely that the decreasing presence of geese towards the end of the study period is due to geese leaving the moss tundra habitats suitable for pre-nesting foraging to nest in more suitable habitats or in other locations. However, the modelled response to snow-cover extent and vegetation types in this study are thought to accurately explain the spatiotemporal distribution of geese in the pre-breeding period in the current study year.

I found that the presence of geese and reindeer in moss tundra was not different in those habitats that had been previously heavily grubbed (disturbed moss tundra). This could indicate that intensive grubbing by pink-footed geese does not affect the use of such habitats in following years by reindeer or geese. However, the design of the current study was not set up to assess the effects of grubbing. Moist moss tundra vegetation has a high resilience to grubbing (Speed et al., 2010), and the disturbed moss tundra sites in this study have likely recovered since the establishment in 2015-2017 when the major disturbance was detected in these sites. Additionally, grubbing is widespread on the tundra in Svalbard (Speed et al., 2009) and the non-disturbed moss tundra sites could just as well have been grubbed since the establishment of sites. Therefore, the disturbed and non-disturbed moss tundra sites in this study do not represent a true contrast in terms of grubbing impact, and a conclusion about the effects of grubbing on habitat use by reindeer or geese can not be reached in this study. It is widely recognised that herbivores can have large impacts on vegetation. Grubbing by pink-footed geese disrupts the insulative moss-layer, and exposes the soil to erosion and warming (Van der Wal et al., 2007), which can have large impacts on vegetation, and leave patches of bare ground on the tundra (Ravolainen et al., 2020). However, whether vegetation changes caused by herbivores lead to habitat degradation or increased productivity that sustains an increased grazing pressure through positive feedback loops is context-dependent (Bråthen et al., 2007; Jefferies & Rockwell, 2002; Van der Wal, 2006; Van der Wal et al., 2004, 2007). The combined effects of climate and herbivore impacts could cause vegetation state shifts in Svalbard (Petit Bon et al., 2021; Ravolainen et al., 2020), and further studies are needed to understand how Svalbard herbivores responds to such vegetation changes.

There is no doubt that biotic interactions can affect spatial distributions and co-occurrence patterns of species (Barbaro et al., 2019; Leach et al., 2016; Pearson & Dawson, 2003).

Therefore, spatial data holds a great potential for understanding interactions, however the inference requires precaution (Blanchet et al., 2020). For example, co-occurrence of reindeer and geese in this study is contrasting between different temporal scales (Table 1). Within one month, reindeer and geese co-occur at 15 of 19 locations (79%), indicating a quite high co-occurrence, while co-occurrence within one hour is just 0.03%. Accounting for the temporal aspect of co-occurrence data is crucial in the understanding of interactions, especially in the case of mobile species such as mammals and birds (Wisz et al., 2013), and inferring interactions based on static presence-absence data should be questioned (Blanchet et al., 2020). Additionally, species interactions might be inconstant over time, and change with seasonal variations in resource availability (Kelt et al., 2019). In this study, I identified the period in which competitive interactions are most likely, based on knowledge of migration, reproductive phenology and the timing of resource limitation. Patterns of species distributions and co-occurrences should not be interpreted without such *a priori* knowledge (Blanchet et al., 2020).

Even though co-occurrence of reindeer and geese in this study was very low at a fine temporal scale, which could indicate avoidance, quantitative analyses showed that vegetation preferences and snow-cover extent were better predictors of spatiotemporal distribution of both species (Tables 3, 5). Negative effects of the presence of potential competitors were non-existing for reindeer, and only weak and with statistical uncertainty for geese. I also investigated to what degree habitat use is dependent on the presence of potential competitors and found that there was no biologically significant effect. The combined and often interacting effects of competition and environment can be difficult to distinguish, and therefore it is important to interpret co-occurrence and distributional patterns carefully (Godsoe et al., 2017). In this study, I used observations of behaviour as a background for the interpretation of the quantitative analyses, and acknowledge that the results of this study mainly give a first insight in the potential for interference competition and the extent of shared habitat among the herbivores. Resource depletion is possible as the herbivores forage in the same areas, however quantitative analyses of diet overlap (e.g. following the methods used by Schmidt et al., 2018) are required to understand the potential for this type of interaction, in addition to investigation of the availability of resources. Finally, the ultimate effects of competition can only be concluded with thorough experimental setup, and by studying fitness consequences and population dynamics over several years.

This study adds to the current knowledge about the spatial ecology of Svalbard herbivores during spring, by relating habitat use to snow-cover extent and co-occurrence with potential competitors. I found that strong interference competition or avoidance between reindeer and geese is unlikely, however geese are disturbed by reindeer and there is potential for an amensalistic interaction. Conclusions about the potential for competition between ptarmigan and reindeer or geese could not be reached in this study due to a low number of ptarmigan observations. Herbivores in Svalbard share habitats at a fine spatial scale, and exploitative competition is most likely to happen in moss tundra vegetation where occurrence of both reindeer, pink-footed geese and barnacle geese is high. Co-occurrence seems to increase with extensive snow-cover, and this effect is expected to be stronger in years of late snowmelt. However, shared space use does not necessarily imply shared resource use, and further studies should assess the extent of dietary overlap. Spatial distributions and co-occurrence of Svalbard herbivores should be related to variations in snowmelt timing, especially with regards to expected climate change effects (Hanssen-Bauer et al., 2019). Understanding inter-specific interactions is critical for the management of both herbivores and their habitat. In the current study year, spatiotemporal distributions of reindeer and geese were mainly driven by the extent of snow-cover and vegetation type, however competitive interactions might intensify as herbivore populations are increasing, and the development should be monitored.

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Supplementary material

Table S1. Spearman's rank correlation matrix for all continuous variables in the initial global models explaining the spatiotemporal distributions of reindeer and geese. DOY = day of year.

	Geese	Reindeer	Snow-cover	DOY
Geese	1			
Reindeer	0.033	1		
Snow-cover	-0.075	-0.042	1	
DOY	0.088	0.068	-0.777	1

Table S2. Parameter estimates for the explanatory variables in the second-best model explaining the spatiotemporal distribution of geese ($\Delta\text{AICc} = 0.96$). Estimates are given on the log-scale and shown with standard errors, z values and P-values. Explanatory variables include snow-cover ([1:4], used as continuous variable), vegetation type (categorical; *Dryas* ridge, moss tundra and disturbed moss tundra) and the presence of reindeer at a certain camera-trap site within the selected time-interval (continuous), in addition to interaction effects. The estimates for vegetation type effects are comparisons to the reference level, which is set to disturbed moss tundra. 'VegTypeDry = vegetation type *Dryas* ridge, 'VegTypeMos' = vegetation type moss tundra.

	Estimate	Std.error	z value	P-value
Intercept	0.407	0.790	0.516	0.606
Reindeer	-0.587	0.442	-1.327	0.185
Snow-cover	-1.597	0.266	-6.004	<0.001
VegTypeDry	-6.592	0.936	-7.043	<0.001
VegTypeMos	-0.410	0.805	-0.509	0.611
Reindeer x Snow-cover	0.629	0.298	2.114	0.035
Reindeer x VegTypeDry	1.891	0.713	2.651	0.008
Reindeer x VegTypeMos	-0.214	0.341	-0.628	0.530

Random effects: camera-trap var = 0.741; AR1 corr = 0.94 var = 8.817.

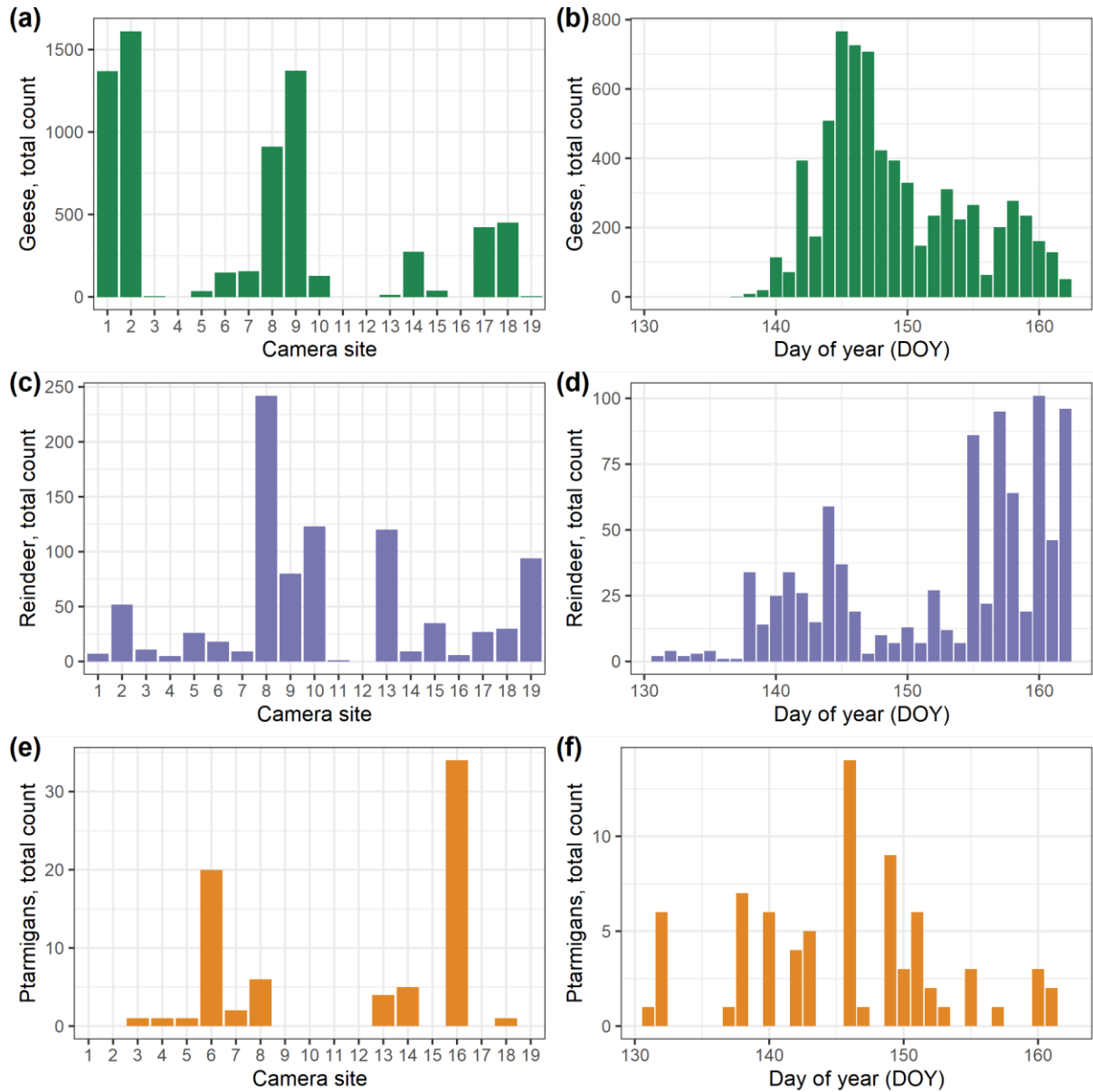


Figure S1. Total counts of geese (green; a and b), reindeer (purple; c and d) and ptarmigans (orange; e and f) in each camera-trap site (left subplots) and day of year (DOY; right subplots). The camera-trap sites 3, 4, 11, 12, 13, 16 and 19 are *Dryas* ridge sites, 1, 6, 7, 8, 15 and 18 are moss tundra sites, and 2, 5, 9, 10, 14 and 17 are disturbed moss tundra sites. Note that the scale on the y-axis is different in the sub-plots.

