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Low spatial habitat overlap of herbivores in the High Arctic tundra

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ABSTRACT

Herbivores play a crucial role in shaping tundra ecosystems through their effects on vegetation, nutrient cycling, and soil abiotic factors. Understanding their habitat use, co-occurrence, and overlap is therefore essential for informing ecosystem-based management and conservation. In the High Arctic, only a marginal proportion of the land area is vegetated, and climate change is impacting herbivore population sizes and their habitats. In this study, we assessed the spatial habitat overlap of a vertebrate herbivore community based on: 1) regional predictive summer habitat suitability models for the resident Svalbard reindeer (*Rangifer tarandus platyrhynchus*), resident Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and the migratory pink-footed goose (*Anser brachyrhynchus*), and 2) presence of fecal pellets, reflecting the annual habitat use of reindeer, ptarmigan, and geese, including the pink-footed goose and barnacle goose (*Branta leucopsis*). Our findings revealed that only small proportions of the available land cover (~ 12,516 km²; all land area excluding glaciers and freshwater) are suitable for each of the species (habitat suitability [HS] > 0.5): reindeer (22 %), ptarmigan (11 %), and pink-footed goose (4 %). Overlapping suitable habitat [HS > 0.5] for reindeer and goose accounted for only 3 % of the total vegetated area (~ 8848 km²) and was primarily found in heath and moist habitats dominated by mosses, graminoids, and herbaceous plants. The overlapping suitable habitat for reindeer and ptarmigan covered 8 % of the vegetated area, in higher elevation ridges with

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vegetation on drier substrates. The shared habitat for ptarmigan and goose, and all three species of herbivores, was less than 1 % of the vegetated area. Additionally, an assessment of fecal pellets suggested that the highest overlap in habitat use among reindeer and goose occurred in bird cliff moss tundra, followed by moss tundra and heath habitats. The small proportion of the vegetated area suitable for all three herbivores indicates a high degree of habitat differentiation. Therefore, different habitats need to be considered for the management and conservation of resident and migratory herbivore species in this High Arctic Archipelago. Moreover, our results underscore the importance of the small but productive parts of the landscape that were used by all herbivores.

1. Introduction

The Arctic is under pressure from climate change and increased human activities (Constable et al., 2022), and shifts to new climate regimes may even give rise to new ecosystems with unknown properties and food web dynamics (Ims and Ehrlich, 2013). A current challenge is predicting how climate change will affect flora and fauna that are intimately linked through the food web and shared habitats (Barrio et al., 2016; Malhi et al., 2022; Mellard et al., 2022). For example, both geese (Abraham et al., 2005; Speed et al., 2009) and reindeer (Van, Wal, 2006; Sundqvist et al., 2019) can have a strong impact on vegetation. Yet, it is not known to what extent these herbivores overlap in habitat use in the Arctic (but see Boulanger-Lapointe et al., 2022 for a sub-Arctic example), which could lead to direct or indirect interspecific competition over forage resources (Ims et al., 2013; Ravolainen et al., 2020). In addition, the herbivore's combined effects on vegetation may be additive or compensatory (Barrio et al., 2022a). Identifying the distribution and extent of the shared habitat of co-occurring herbivores offers a starting point for understanding resource partitioning and species interactions (e.g., competition, facilitation and mutualism; Koffel et al., 2021).

The distribution of herbivores in landscapes is regulated by multiple factors, and they may overlap at multiple spatial and temporal scales (Senft et al., 1987). At the circumpolar scale, herbivore diversity is strongly related to primary productivity and predator presence (Barrio et al., 2016; Speed et al., 2019). In the High Arctic, vegetation cover is patchy (Raynolds et al., 2019), often resulting in uneven herbivore distribution in the landscapes (Barrio et al., 2016). The heterogeneity of the landscapes may result in contrasting predictions for spatial overlap among herbivore species. On one hand, different herbivores diverge in mobility (mammals vs. birds), breeding strategies (migrant vs. resident) and feeding ecology, which suggests that herbivores show different distributions in the landscapes. Within a season, spatial heterogeneity in drainage, water supply and the type of substrate, nutrient content, and disturbance of soils can cause sharp contrasts in High Arctic vegetation (Raynolds et al., 2019; Ravolainen et al., 2020), which also influence the distribution of co-occurring herbivores (Speed et al., 2009; Pedersen et al., 2017; Pedersen et al., 2023). On the other hand, low and patchy primary production, and relatively high biomass of herbivores in High Arctic ecosystems (Speed et al., 2019) may suggest that herbivores should show a high degree of spatial co-occurrence in vegetated areas.

Climate change in the High Arctic affects vegetation (Berner et al., 2020; Myers-Smith et al., 2020), migration strategies (Clairbaux et al., 2019), species distribution (Jenkins et al., 2016; Jensen et al., 2008; Marolla et al., 2021), and species interactions (Berg et al., 2008; Gilg et al., 2009; Barrio et al., 2016). The High Arctic Archipelago of Svalbard is experiencing many of these changes because it is the tundra region with the greatest temperature increases over the last decades (Nordli et al., 2020; Isaksen et al., 2022). The food web is depauperate and consists of few vertebrate herbivores (Descamps et al., 2017); the resident, endemic sub-species, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Svalbard rock ptarmigan (*Lagopus muta hyperborea*) and the migratory geese, pink-footed goose (*Anser brachyrhynchus*) and barnacle goose (*Branta leucopsis*). Reindeer and geese are the most prevalent and widespread vertebrate herbivores in the Svalbard tundra (Le Moullec et al., 2019; Johnson et al., 2020), while ptarmigan are distributed across the archipelago, in low but increasing densities (Marolla et al., 2021). The reindeer and geese populations have substantially increased since the 1980s, while the reindeer population has doubled (Le Moullec et al., 2019; estimate from 2016), the pink-footed goose and the barnacle goose have increased five-fold and eight-fold, respectively (Tombre et al., 2019; Heldbjerg et al., 2021).

The Svalbard herbivores represent a range of functionally different animals. The reindeer are ruminant, while the ptarmigan and geese are hindgut fermenters. The predominant feeding mode for ptarmigan is browsing (Unander et al., 1985), while the reindeer and barnacle goose graze, and the pink-footed goose feeds by grubbing in the spring and early summer (pulling up roots of vascular plants) (Fox et al., 2007; Fox et al., 2009). Although a limited proportion of the non-glaciated land area in Svalbard is suitable habitat for reindeer (Pedersen et al., 2023), ptarmigan (Pedersen et al., 2017), and geese (Speed et al., 2009), the degree of overlap in habitat suitability has not been assessed. Such information informs ecosystem-based management and ecological monitoring, particularly in the context of the conservation of habitats and monitoring herbivores' impact on vegetation.

In this paper, we identify and characterise areas of habitat overlap among Svalbard reindeer, Svalbard rock ptarmigan, and migratory geese. First, we use archipelago-wide predictive habitat suitability models of the reindeer, ptarmigan, and pink-footed goose (Speed et al., 2009; Pedersen et al., 2017; Pedersen et al., 2023) to assess spatial overlap during the short Arctic summer. Second, we used the presence of fecal pellets of herbivores in focal habitat types to assess year-round spatial overlap in habitat use by herbivores.

2. Methods

2.1. Study area

Svalbard is a High Arctic Norwegian archipelago (74–81°N, 10–35°E; 62,700 km²), encompassing more than 500 islands, with the largest being Spitsbergen (Fig. 1). Svalbard currently comprises 60 % glaciers, 25 % barren and sparsely vegetated areas, and only 15 % of fully vegetated areas. Of the vegetated areas, about 22 % is classified as moss and herbaceous-dominated vegetation in wet, moist, and mesic habitats (Johansen et al., 2012). Deeply indented fjords characterise the areas along the west and north coasts. Mountains, with summits reaching up to around 1700 m above sea level, cover much of Spitsbergen. Svalbard has a relatively mild climate compared to other Arctic regions, shifting from a typically humid, oceanic climate in the west to a colder and drier climate in the northern and eastern parts (Førland et al., 2012). The archipelago spans three bioclimatic zones ranging from Arctic polar desert (zone A, e.g., in northern and eastern parts of the archipelago), Northern Arctic tundra (zone B, e.g., large areas along the west coast of Spitsbergen) to Middle Arctic tundra (zone C, e.g., central Spitsbergen) (CAVM Team, 2003).

The field data collection was conducted in the central, western, and northwestern regions of Spitsbergen (Fig. 1). Glacial valleys with wetland, ridge, and heath vegetation, are rarely above 20 cm in height, and coastal plains dominate this area (Elvebakk 1999). The most productive areas with continuous vegetation can be found along the coast and in valley bottoms (Johansen et al., 2012). Dwarf shrubs (*Salix polaris* and *Dryas octopetala*), grasses, sedges, forbs, and mosses dominate, and form different vegetation types (Van der Wal, 2006). Hillsides above approximately 200 m elevation are only sparsely vegetated and mainly barren and rocky.

2.2. Study species

The Svalbard archipelago has a relatively simple terrestrial food web due to the lack of rodents and specialist predators (Descamps et al., 2017). There are only a few herbivore species residing on the archipelago, including the resident, endemic sub-species, Svalbard reindeer and Svalbard rock ptarmigan, and the migratory pink-footed, barnacle, and brent goose (*Branta bernicla*). In our study, we have not included the brent goose, which appear mostly in the Eastern part of the archipelago in much smaller numbers compared to the other two goose species (Clausen et al., 2013).

The Svalbard reindeer is non-migratory, appears in small groups or as single animals, and tends to stay within small home ranges

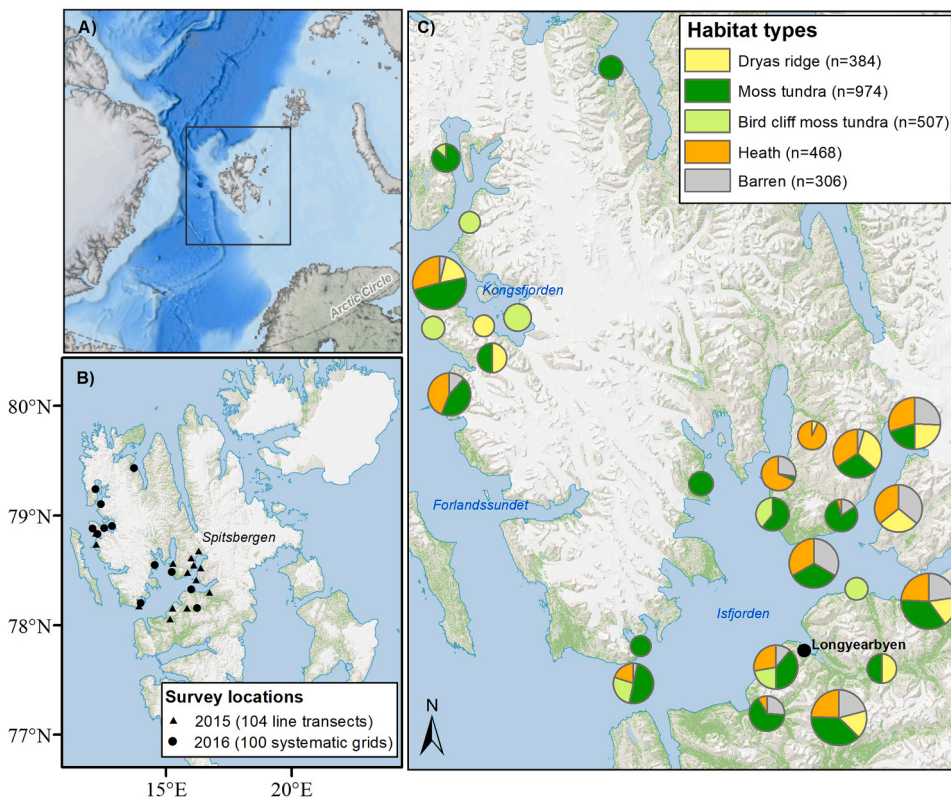


Fig. 1. Overview of A) geographic location of Svalbard (black rectangle); B) survey locations for presence of fecal pellets of herbivores in plots conducted in 2015 and 2016; and C) number of sampling units in habitat types surveyed. See Johansen et al. (2012) and Appendix 1 for detailed descriptions of habitat types.

(Tyler and Øritsland, 1989). The population size is estimated to be around 22,000 individuals and is driven by the availability of foraging resources, density dependence, and climatic variability (Albon et al., 2017; Hansen et al., 2019; Le Moullec et al., 2019). In summer, reindeer select quantity over quality of forage plants (Van der Wal et al., 2000), and graze commonly in lowland moss tundra, wetlands, meadows, and lower foothills where the vegetation consists of grasses, sedges, forbs, dwarf willow, and mosses (Staaland, 1986; Bjørkvoll et al., 2009).

The Svalbard rock ptarmigan is the only overwintering herbivore bird species in the archipelago, with densities ranging from 3 to 5 males per km² in the spring (Fuglei et al., 2020; Marolla et al., 2021) and restricted availability of breeding areas (Pedersen et al., 2017). A recent increase in population size is related to major changes in winter temperature (Marolla et al., 2021). The Svalbard rock ptarmigan feeds on a variety of woody and herbaceous plants and grasses, while the chicks specialise in the bulbils of alpine bistort (*Bistorta vivipara*) (Unander et al., 1985).

The pink-footed goose and barnacle goose populations arrive from the wintering areas in May and breed in Svalbard. The abundance of both goose species has increased substantially over the last decades (Tombre et al., 2019; Heldbjerg et al., 2021) due to conservation actions and milder temperatures at their overwintering sites that have improved their physical condition and survival rates (Kery et al., 2006). The pink-footed goose breeds and forages in lowland tundra, while the barnacle goose is mainly confined to coastal wet tundra near lakes or rivers and commonly breeds in bird cliff areas (Fox et al., 2007; Jensen et al., 2008). Upon arrival in spring, both goose species use the same habitats, but they apply different foraging techniques (Fox et al., 2007; Fox et al., 2009). Barnacle geese feed mainly by grazing above-ground plant material, while pink-footed geese feed mostly by excavating below-ground parts of plants such as roots and rhizomes (i.e., the technique is termed grubbing). The grubbing activity creates holes in the vegetation, removal of the moss layer, and may create vegetation-free craters at high grubbing intensities (Fox and Bergersen, 2005; Fox et al., 2006).

2.3. Digital spatial data layers

To assess spatial overlap among the herbivores in the summer season, we took advantage of three archipelago-wide habitat suitability models available as raster layers. The first is the Svalbard reindeer model describing summer habitat suitability based on GPS-marked females and positional data from July and August (2009–2018; Pedersen et al., 2023). The second is the Svalbard rock ptarmigan model describing breeding habitat suitability based on count data of territorial males in April (2000–2011; Pedersen et al., 2017), which reflects breeding territories that the males defend until mid-July (Unander and Steen, 1985; Pedersen et al., 2012). The third is the pink-footed goose model describing the grubbing habitat suitability based on extensive field surveys of goose grubbing activity in May to early June (2006–2007; Speed et al., 2009), which reflects pre-breeding areas for pink-footed geese. These three models predict the likelihood of occurrence on a scale from 0 to 1 by extrapolating findings from smaller study areas to a larger spatial scale. Appendix 2 summarises the characteristics of each habitat suitability model. There is no existing habitat suitability map available for the barnacle goose.

To assess the vegetation characteristics of the habitats shared by the herbivores, we used a digital vegetation map of the Svalbard archipelago (Johansen et al., 2012; Johansen and Tømmervik, 2014). Field investigations revealed that the original classes were less precise on the archipelago-wide scale, thus the original vegetation classes (37 spectral classes, spatial resolution 30 m × 30 m) were aggregated into coarser classes. First, the available land cover was defined as the sum of the vegetated and unvegetated classes available to the herbivores (class 6–31, 33–37), excluding freshwater bodies and glaciers (class 1–6, 32). The vegetated class contained all classes mentioning vegetation (class 8, 10–22, 25, 33–37) and the unvegetated class consisted of mainly polar desert and gravel areas (class 7, 9, 23, 24, 26–31). Following Pedersen et al. (2023) appendix B, we further divided the vegetated class into: 1) moss tundra (class 8, 10–15, 19, 20, 25, 33–37), heath (class 16–18, 21–22), and 3) barren (class 7, 9, 23, 24, 26–27, 28, 30–31), as moss tundra and heath are important seasonal habitats for herbivores and large proportions of Svalbard is sparsely vegetated (barren). To assess the elevational characteristics of the habitats shared by herbivores, we used a digital elevation model (DEM; Norwegian Polar Institute, 2023) with an original spatial resolution of 20 m × 20 m.

All raster layers were resampled to the layer with the lowest pixel cell resolution (100 m × 100 m) using the nearest neighbour method in R with the *resample* function in the package 'raster'. Since the raster layers had slightly different spatial extents, they were cut and masked to the smallest spatial extent (Appendix 2, Figs. S2-1 and S2-2 excluding sea, fjords, glacier and water bodies, area = 12,515.9 km²). For each habitat suitability raster, we excluded all pixels with a habitat suitability value <0.2, which was considered unsuitable habitat, with the *reclassify* function in the 'raster' package (Appendix 2, Figs. S2-2).

2.4. Field data collection

To assess the habitat use of the herbivore community, we identified the presence of feces in multiple survey locations during the summers of 2015 and 2016 in habitats relevant to year-round space use of the herbivore community (Fig. 1). We selected valleys or peninsulas to cover the Isfjorden area and the west coast of Spitsbergen from Isfjorden in central Spitsbergen and north to Liefdefjorden. The 2015 survey aimed to describe general habitat characteristics of lowland areas used by herbivores and focused on three common habitat types: 1) moss tundra represented by moist moss and herbaceous vegetation in the foot-hills, which included areas used by seabirds (bird cliff moss tundra); 2) heath represented by drier vegetation, which included areas with *Dryas octopetala* vegetation on ridges (*Dryas* ridge); and 3) barren represented by gravel, rock, or sand and limited vegetation (Appendix 1). The 2016 survey locations were pre-selected based on the existing vegetation map by Johansen et al. (2012). These field sites included both moss tundra and *Dryas* ridge habitat types. Within the moss tundra class, we included two categories: 1) moss tundra impacted by sea birds (bird cliff moss tundra) and 2) moss tundra without impacts of seabirds (Appendix 1). In 2015, a photo was taken of each plot, which

was later used to assign the habitat types as used in the 2016 survey to ensure the habitat types were consistent over years (Appendix 1).

The presence or absence of feces of each herbivore type was assessed in $0.5 \text{ m} \times 0.5 \text{ m}$ plots along 30-meter transects (2015, $n = 104$) or in a systematic grid orientated in the cardinal directions with eight plots of $0.5 \text{ m} \times 0.5 \text{ m}$ size (2016, $n = 100$) following the published protocols of Barrio et al., (2022b). Feces are correlated with herbivore density and activity (e.g., Krebs et al., 2001;

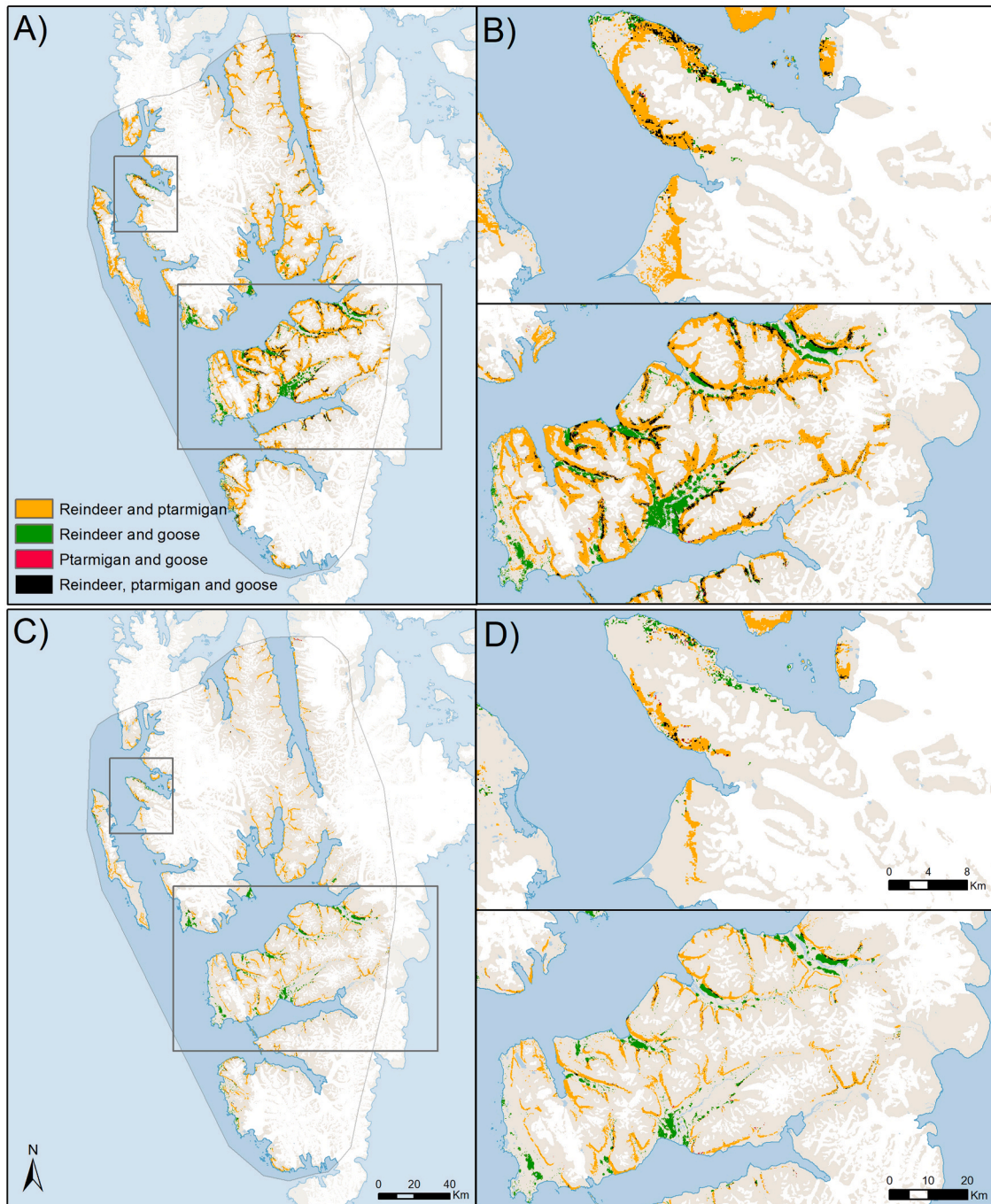


Fig. 2. Spatial habitat overlap based on the predictive habitat suitability models for the three herbivores, the Svalbard reindeer *Rangifer tarandus platyrhynchus*, the Svalbard rock ptarmigan *Lagopus muta hyperborea* and the pink-footed goose *Anser brachyrhynchus*, in the study extent of the Svalbard archipelago (left panels) and in the core monitoring areas (right panels; after Ims et al., 2013b). A and B) Shared habitat where habitat suitability in individual models are set to > 0.2 . C and D) Shared habitat where habitat suitability in individual models are set to > 0.5 . See method section for details on calculations and categorization of shared habitats.

Bråthen et al., 2007) and the detection of accumulated feces provides a static index of herbivore presence. Within each plot, we surveyed for reindeer summer (pellets aggregated with softer consistency) and winter feces (single, hard pellets). The summer and winter feces of ptarmigan could not be distinguished from each other in the field resulting in seasons being combined. In addition, the summer feces of pink-footed and barnacle geese could not be distinguished from each other resulting in both goose species being combined. The proportion of plots that contained fecal pellets served as an index of herbivore abundance. In total, 1352 plots were surveyed for feces and each plot was assigned to a class from the main habitat types, moss tundra, bird cliff moss tundra, heath, *Dryas* ridge, and barren (Fig. 1, Appendix 1).

Field permits were obtained in the national parks and nature reserves, and all sampling was done non-destructively by foot and in accordance with the Svalbard Environmental Protection Act.

2.5. Data analysis

To identify shared habitats of the herbivores, we analysed: 1) summer spatial overlap using the habitat suitability models for reindeer (Pedersen et al., 2023), ptarmigan (Pedersen et al., 2017), and pink-footed goose (Speed et al., 2009) and 2) annual spatial habitat overlap using the observed presence of fecal pellets in plots for all herbivores (including barnacle goose, but most likely not brent goose since they breed in other locations than our survey sites (Madsen et al., 1989)). All data preparation and analysis were conducted in R 3.3.2. and presented with ArcMap 10.7.1 (ESRI, 2011).

2.5.1. Habitat overlap based on habitat suitability models

We calculated habitat overlap between all species combinations at two suitability thresholds within both the total available land cover and the total vegetated area. First, we calculated the area (sum of number of pixels) from the habitat suitability (HS) maps where the herbivore species had more than 20 % probability of occurrence ($HS > 0.2$). Second, we calculated the area where the herbivore species had more than 50 % probability of occurrence ($HS > 0.5$). The latter threshold has been used previously to define suitable herbivore habitat in the Arctic (Beumer et al., 2019; Pedersen et al., 2023). Moreover, habitat overlap was defined as the sum of number of pixels where two or more species had more than 20 % or 50 % probability of occurrence. We calculated shared habitat for the following species combinations: 1) reindeer and ptarmigan, 2) reindeer and goose, 3) ptarmigan and goose, and 4) reindeer, ptarmigan, and goose. The shared habitat was calculated both from the total available land cover, defined as the sum of number of pixels within the spatial extent (Appendix 2, Figs. S2–1), excluding glaciers and water bodies (53 % of total land cover in study extent), and the total vegetated area was defined as the sum of all pixels in vegetated classes in the original vegetation map (Johansen et al., 2012; 34 % of total land cover in study extent). Furthermore, we calculated suitable areas across elevation gradients and habitat types (moss tundra, heath, and barren) for each of the herbivore combinations within the total available land cover and vegetated area. In addition, we calculated habitat overlap on a continuous scale (HS 0–1) for the pairwise species suitability combinations: 1) reindeer and ptarmigan, 2) reindeer and goose, 3) ptarmigan and goose, using Schoener's D (Schoener, 1968). Schoener's D is one of the most common indices used for spatial niche overlap of habitat suitability models. The index ranges from 0 to 1 with values close to one indicating a high degree of spatial niche overlap.

2.5.2. Habitat overlap based on fecal pellets

To investigate spatial habitat overlaps in fecal pellets, we calculated the percentage of plots with presence of feces following these combinations of herbivore species: 1) reindeer and ptarmigan, 2) reindeer and goose, 3) ptarmigan and goose, and 4) reindeer, ptarmigan, and goose. During data collection, ptarmigan summer and winter feces were grouped because they could not be distinguished from one another. In the data analyses, we also grouped reindeer's summer and winter feces together for consistency. This allowed us to describe year-round habitat use by reindeer and ptarmigan. Both goose species (barnacle and pink-footed goose) were grouped, which allowed us to describe habitat use by geese after their arrival in spring through the breeding period. The proportional

Table 1

Overview of suitable habitat (km^2) for Svalbard reindeer (*Rangifer tarandus platyrhynchus*), Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and pink-footed goose (*Anser brachyrhynchus*) within vegetated and available land cover (vegetated areas, excluding glacier and water bodies; see 2.3 for details) in the study extent (see polygon in Fig. 2). Areas are calculated based on the sum of number of pixels of habitat suitability > 0.2 and > 0.5 . Numbers in parentheses are percent of the vegetated area (8848.3 km^2) and the total available land cover (12,515.9 km^2) from the smallest shared spatial extent.

Species and combinations	Area in km^2 (%)		Area in km^2 (%)	
	Habitat suitability (>0.2)		Habitat suitability (>0.5)	
	Vegetated	Available land cover	Vegetated	Available land cover
Reindeer	4024.0 (45)	4822.4 (39)	2496.6 (28)	2732.4 (22)
Ptarmigan	2331.5 (26)	2952.4 (24)	1072 (12)	1366.9 (11)
Goose	807 (9)	876.5 (7)	454.9 (5)	485.8 (4)
Reindeer and goose	552.6 (6)	571.4 (5)	226 (3)	229.8 (2)
Reindeer and ptarmigan	2107.7 (24)	2522.3 (20)	696.4 (8)	781.3 (6)
Ptarmigan and goose	209.2 (2)	220.9 (2)	32.7 (<1)	35 (<1)
Reindeer, ptarmigan, and goose	198.1 (2)	206.9 (2)	23.2 (<1)	24.1 (<1)

use of each habitat class by these species combinations was then determined, and Schoener’s D was calculated as a measure of pairwise spatial niche overlap.

3. Results

3.1. Habitat overlap based on habitat suitability models

The spatial overlap of suitable habitats for Svalbard reindeer, Svalbard rock ptarmigan, and pink-footed geese was mostly found in the lowlands and along the coast of Central Spitsbergen, particularly in Nordenskiöld Land (Fig. 2). Within the total available land cover area to herbivores, limited proportions were suitable ($HS > 0.2$) habitat for reindeer (39 %), ptarmigan (24 %), and pink-footed goose (7 %) separately, with even less areas at the higher threshold ($HS > 0.5$; reindeer (22 %), ptarmigan (11 %), and pink-footed goose (4 %)) (Table 1). Using the highest threshold ($HS > 0.5$), overlapping suitable habitat for reindeer and ptarmigan covered 8 % of the vegetated area, in higher elevation ridges with vegetation on drier substrates below 200 m. Overlapping suitable habitat ($HS > 0.5$) for reindeer and geese covered only 3 % of the total vegetated area, in heath and moist habitats dominated by mosses, graminoids, and herbaceous plants at 0–50 m, while habitat overlap for ptarmigan and geese was negligible (<1 %) (Table 1; Fig. 3). Reindeer and geese shared habitat in the valley bottoms, whereas reindeer and ptarmigan shared habitat along ridges (Fig. 3). However, suitable habitats for both ptarmigan and geese were typically also suitable for reindeer (Table 1, Fig. 2). Reindeer and ptarmigan shared moss tundra habitats and to a lesser degree heath habitat (Fig. 3). Reindeer and ptarmigan had the largest shared habitat (Schoener’s $D = 0.51$), followed by reindeer and geese (Schoener’s $D = 0.31$), and lastly ptarmigan and geese (Schoener’s $D = 0.21$).

The largest habitat overlap ($HS > 0.5$) for all three species was in the elevation class 50–100 m (Fig. 3), but common suitable habitat was found up to an elevation of 350 m. Overall, the largest habitat overlap was found for reindeer and ptarmigan, especially between 50–200 m elevations. Reindeer and goose habitat overlap was largest at low elevations and decreased gradually with elevation. Similarly, ptarmigan and goose habitat overlap were mostly found at low elevations, typically between 50–150 m.

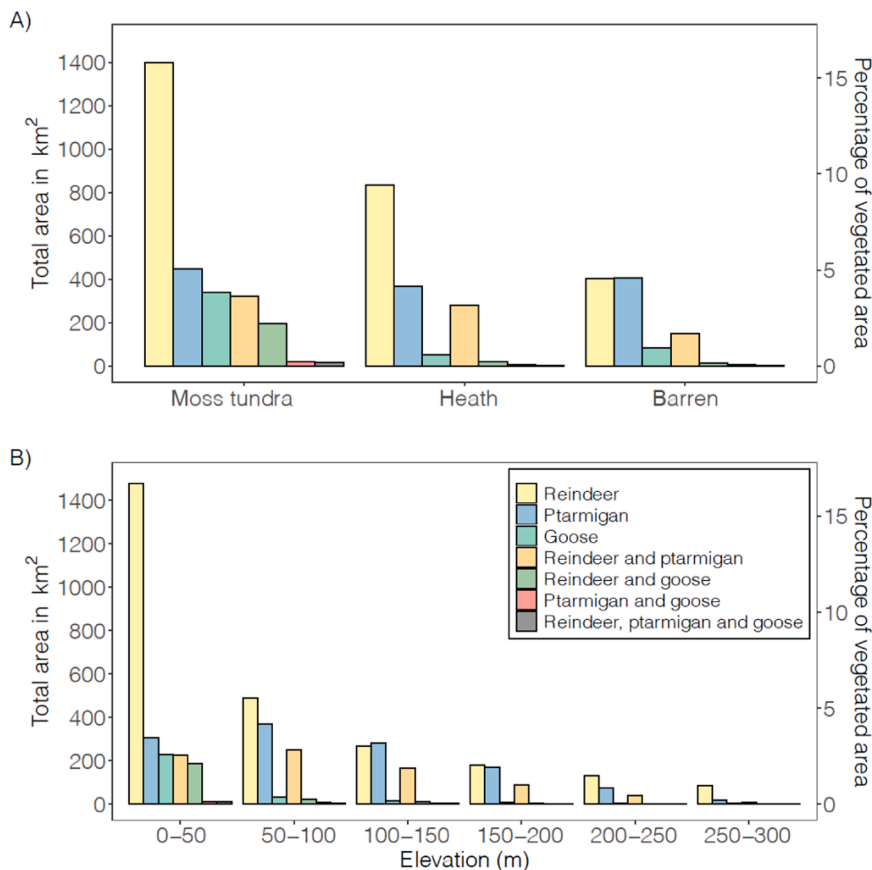


Fig. 3. Estimates of spatial habitat overlap (km²) by different herbivore communities in A) common habitat types (see Appendix 1) and B) different elevation intervals, based on the overlay analysis of predictive habitat suitability models (thresholds > 0.5) for the Svalbard reindeer (*Rangifer tarandus platyrhynchus*), the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and the pink-footed goose (*Anser brachyrhynchus*). Spatial habitat overlap is reported in absolute area of overlap for the species combinations (km², left axis) and as a percentage of vegetated area (right axis).

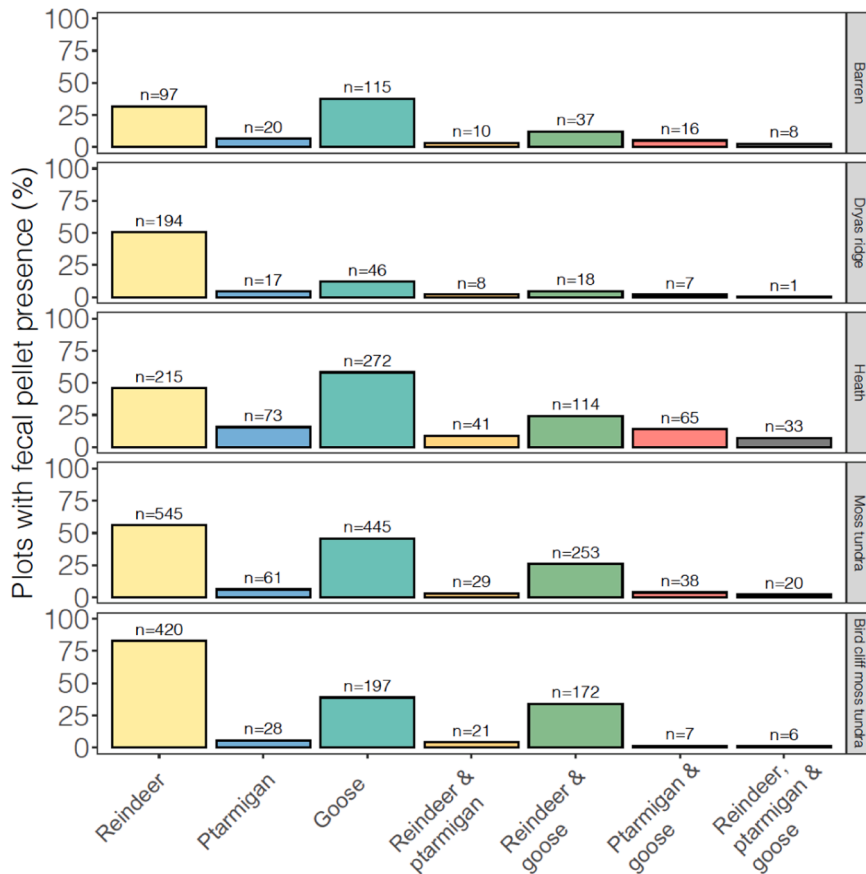


Fig. 4. Spatial overlap (%) in the habitat use of Svalbard reindeer (*Rangifer tarandus platyrhynchus*), Svalbard rock ptarmigan (*Lagopus muta hyperborea*) and geese (pink-footed goose *Anser brachyrhynchus* and barnacle goose *Branta leucopsis* combined) based on presence of plots with fecal pellets of each herbivore type in 2015 and 2016 (data combined) in each of the five habitat classes (see Appendix 1 for information on habitat classes). n = total number of fecal pellets observed. Total number of plots per vegetation class = Dryas ridge (384), moss tundra (974), bird cliff moss tundra (507), heath (468), barren (306).

3.2. Habitat overlap based on fecal pellets

We found low spatial overlap of the presence of feces for the herbivore community of resident and migratory species (Fig. 4). Moss tundra, both with and without fertilising effects from seabird colonies, had the overall largest proportions of reindeer and goose feces. We found the greatest overlap in habitat use between reindeer and geese in bird cliff moss tundra habitats. Heath was the only habitat where reindeer, ptarmigan and goose had substantial overlap. Schoener’s D was highest between reindeer and geese (Schoener’s $D_{2015} = 0.47$, Schoener’s $D_{2016} = 0.34$), followed by ptarmigan and geese (Schoener’s $D_{2015} = 0.18$, Schoener’s $D_{2016} = 0.03$), and then reindeer and ptarmigan (Schoener’s $D_{2015} = 0.11$, Schoener’s $D_{2016} = 0.04$).

4. Discussion

Our study of spatial habitat overlaps of the herbivore community in Svalbard showed that only small proportions of the vegetated area are suitable for, or used by, the herbivores jointly. This indicates that, despite the limited forage availability of the High Arctic landscapes, selective use of habitat leads to segregation between the herbivore species. The greatest spatial overlap occurred in the most productive habitats, such as moss tundra, and particularly those located below seabird cliffs. Thus, these habitats are important shared habitats in pairwise comparisons between the herbivores, although reindeer and ptarmigan also shared habitats in drier vegetation at mid-elevation.

Our finding that moss tundra, both with and without fertilisation from seabirds, emerged as the habitat type with the largest spatial overlap in modelled habitat suitability and observed use by reindeer and geese, aligns with previous studies that have focused on single herbivore species separately (Pedersen et al., 2023; Speed et al., 2009). Habitats that correspond to our relatively broad category moss tundra, which encompasses a range of moist and wet vegetation dominated by mosses and herbaceous vascular plants, are important for different geese species (Slattery & Alisauskas 2007; Gauthier et al., 2013) and for reindeer/caribou (Skarin 2008; White & Trudell 1980) during the summer season. Our results also coincide with results from a recent landscape-scale analysis of time-laps camera

images showing that reindeer and geese had high co-occurrence in moss tundra (Grimsby et al., 2023). The spatial overlap analysis indicates that moss tundra and lowlands of the valleys offer important, preferred shared resources for reindeer and geese, despite the small proportion of the total vegetated landscape that this kind of vegetation covers.

The habitat overlap we found based on fecal counts, particularly in seabird-influenced moss tundra, is likely conservative because accumulated feces decompose significantly slower in the heath habitats (up to 4–5 years) than moss dominated habitats (Helle et al., 1990; Skarin, 2008). Additionally, reindeer are occasionally observed to feed on goose feces, subsequently removing them from the landscape (Van der Wal and Loonen, 1998). Reindeer summer habitat suitability at the Svalbard archipelago-scale increases with shorter distance to bird cliffs (Pedersen et al., 2023), and there is local-scale evidence from Hornsund in the southwestern coast of Spitsbergen on herbivores use of this habitat (Jakubas et al., 2008), suggesting that seabird-fertilized moss tundra is an important habitat for the herbivores. Seabird-fertilized moss tundra that is spatially restricted to but widely distributed along the coastal High Arctic tundra is known to have a disproportionate effect on nutrient flux from the terrestrial to the marine system (Otero et al., 2018), and, as shown here, is an important habitat for the herbivore community with potential ramifications to the terrestrial food web interactions that remain to be further investigated.

The high spatial overlap of reindeer and geese occurred in areas that support grass and forb-rich communities, embedded in often thick moss cover, potentially impacting the tundra vegetation state (Ravolainen et al., 2020). The congregation of large herbivore numbers in specific vegetation types (Jilkova et al., 2021), occurring in small parts of the landscape, can be either formed or maintained by the herbivores themselves (Jakubas et al., 2008; Ravolainen et al., 2020; Van der Wal et al., 2004; Van der Wal, 2006; Vanderpuye et al., 2002). Depending on the abundance levels of herbivores and subsequent grazing and other activities (e.g., grubbing, trampling), as well as fertilisation from sea birds or the herbivores, moss tundra habitats can develop in different directions, such as towards more herbaceous dominance or more moss dominance (Ravolainen et al., 2020). The extent to which the use of moss tundra habitats by herbivores is related to or leads to stable or unstable vegetation patch dynamics (Jefferies et al., 1994; Ravolainen et al., 2020), potentially leading to changed landscape diversity in the High Arctic, remains to be investigated. Additional studies that investigate the potential causes and consequences of changed habitat configuration in the High Arctic are needed if we want to identify effective management approaches for the growing densities of resident (Le Moullec et al., 2019) and migrant grazers like geese (Madsen et al., 2017; Johnson et al., 2020) that impose widespread small scale disturbances on the landscape (Bjerke et al., 2017; Eischeid et al., 2021). This need is particularly important given the relatively slow re-growth capacity of dominant plants inhabiting Arctic landscapes coupled with the rapid climate change (Isaksen et al., 2022).

Vertebrate herbivore population abundances in Svalbard are changing and have changed since the goose grubbing habitat model was made (Speed et al., 2009). Reindeer total over 22,000 animals (Le Moullec et al., 2019) and the five-fold increase in the population sizes for pink-footed geese since the 1980s (Heldbjerg et al., 2021) causes archipelago-wide habitat disturbance noticed even when geese numbers were much smaller (Speed et al., 2009). On one hand, we documented a concentration of habitat overlap among herbivores in only parts of the landscape (low elevation, valley bottom and lowland foothills and slopes), while on the other hand, Eischeid et al. (2021) recently reported that a high percentage of moss tundra habitat is being disturbed at a local scale. These findings suggest the potential for large impacts of reindeer and geese, although with annual variations, in the limited habitat suitable for both species. Such combined impacts remain to be documented, as previous studies have focused mainly on one herbivore at a time (Speed et al., 2010a,b; Van der Wal et al., 2001).

Constraints of our analyses of spatial habitat overlaps include data availability, particularly related to the lack of available spatial habitat suitability raster layers throughout the breeding season of pink-footed geese and no existing habitat suitability maps for barnacle geese. Seasonal predictive habitat models are scarce and static and resolution hampers use of these to more detailed investigations than presented here. Although the detection of feces relates directly to reindeer and goose densities and fecal pellets are correlated with the abundance of herbivores (e.g., Barrio et al., 2022b; Krebs et al., 2001; Bråthen et al., 2007), decomposition rates are not addressed here, and animals may also defecate at other locations than where they feed.

Further, the detection of accumulated feces does not provide information on the temporal overlap of herbivores. Future studies may therefore combine large-scale spatial data (as done here) with high-resolution imagery that can differentiate the availability and quality of vegetation types at relevant temporal scales (Beamish et al., 2020) and emerging chemical (e.g., spectroscopy; Nopp-Mayr et al., 2020; Tuomi et al., 2023) and genetic approaches (e.g., DNA analysis; Joo et al., 2014; Kim et al., 2022) that can identify functional plant-herbivore interactions and potential competition among herbivores. For example, dietary DNA analysis demonstrated that bryophytes are an important food source of geese and ptarmigan in Svalbard in summer (Kim et al., 2022).

Understanding and predicting food web interactions are necessary for ecological monitoring and mitigating the effects of climate change (Mellard et al., 2022). The interactive effects of climate change on food web dynamics necessitate long-term ecological research, such as demonstrated in Greenland (Meltofte, 2008; Meltofte et al., 2008), Canada (Gauthier et al., 2013) and the more recent efforts to expand ecosystem-based monitoring in Svalbard through the Climate-ecological Observatory for Arctic Tundra (COAT) (Ims and Yoccoz, 2017). A common theme in such programs is the focus on understanding interactions among tundra species and how these species are influenced by climate change. Moreover, reindeer, ptarmigan, and geese contribute highly to ecosystem services (e.g., outdoor recreation and hunting; Madsen et al., 2017; Peeters et al., 2022) and are responsive in number and dynamics to a changing climate (Jensen et al., 2008; Hansen et al., 2013; Albon et al., 2017; Marolla et al., 2021). Besides, this study highlights an example of using remote sensing data coupled with field observations to estimate the spatial overlap of species. This may moreover provide a reference for future studies on climate change effects on both spatial and temporal interactions of herbivores in Svalbard's terrestrial ecosystem.

5. Conclusions

We found only a minor fraction of the vegetated land area to be suitable for the species of this High Arctic herbivore community. The habitat overlap between ptarmigan and geese is low, but reindeer and geese overlap in lowland habitats and ptarmigan and reindeer overlap in ridge habitats. This suggests that biotic interaction between ptarmigan and geese is limited at a large spatial scale, but that reindeer interacts with the other species over a diverse range of habitat types. The moss tundra, particularly when fertilized by seabirds, is suitable for all three herbivores, and constitutes the areas where spatial habitat overlap among the herbivores is highest, hence also likely to be impacted to a substantial extent by herbivores in the future (Ravolainen et al., 2020). The small proportion of the vegetated area suitable for all three herbivores indicates habitat differentiation among these herbivores. Therefore, different habitats need to be considered for the management and conservation of resident and migratory herbivore species in this High Arctic Archipelago.

CRedit authorship contribution statement

Ravolainen Virve: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Paulsen Ingrid M. G.:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis. **Eischeid Isabell:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Forbey Jennifer Sorensen:** Writing – review & editing, Methodology, Conceptualization. **Fuglei Eva:** Writing – review & editing, Resources, Investigation, Funding acquisition, Data curation, Conceptualization. **Hájek Tomáš:** Writing – review & editing, Methodology, Investigation. **Hansen Brage B.:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Loe Leif Egil:** Writing – review & editing, Methodology, Formal analysis. **Macek Petr:** Writing – review & editing, Methodology, Investigation. **Madsen Jesper:** Writing – review & editing, Resources, Methodology. **Soininen Eeva M.:** Writing – review & editing, Methodology, Investigation. **Speed James D.M.:** Writing – review & editing, Resources, Methodology. **Stien Audun:** Writing – review & editing, Methodology, Formal analysis. **Tømmervik Hans:** Writing – review & editing, Resources, Methodology. **Pedersen Åshild Ønvik:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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

Habitat suitability maps for Svalbard rock ptarmigan and Svalbard reindeer are available on the open-source, WebGIS for Svalbard at the Norwegian Polar Institute: <https://geokart.npolar.no/Html5Viewer/index.html?viewer=Svalbardkartet>. The data sets are also published as: Svalbard rock ptarmigan habitat suitability map [Data set]. Norwegian Polar Institute. <https://doi.org/10.21334/npolar.2023.6ae96b24>. Svalbard reindeer habitat suitability models [Data set]. Norwegian Polar Institute. <https://doi.org/10.21334/npolar.2023.fdd9eaf1>. The feces data set is published as: Herbivore fecal pellet dataset [Data set]. Norwegian Polar Institute. <https://doi.org/10.21334/npolar.2023.e1e3ea24>.

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Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02797](https://doi.org/10.1016/j.gecco.2024.e02797).

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