RESEARCH/REVIEW ARTICLE

Spatial patterns of goose grubbing suggest elevated grubbing in dry habitats linked to early snowmelt

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Abstract

The western Palaearctic tundra is a breeding habitat for large populations of European geese. After their arrival in spring, pink-footed geese (Anser brachyrhynchus) forage extensively on below-ground plant parts, using a feeding technique called grubbing that has substantial impact on the tundra vegetation. Previous studies have shown a high frequency of grubbing in lowland fen vegetation. In the present study, we examined the occurrence of grubbing in other habitat types on Spitsbergen, in the Arctic archipelago of Svalbard. Goose grubbing was surveyed along 19 altitudinal transects, going from the valley bottom to altitudes dominated by scree. Grubbing was more frequent in the wet habitat type at low altitudes compared to the drier habitat type at higher altitudes. For the dry habitat type, a higher frequency of grubbing was found in study plots with a south-east facing exposure where snowmelt is expected to be early. This suggests that pink-footed geese primarily use dry vegetation types for grubbing when they are snow-free in early spring and the availability of snow-free patches of the preferred wet vegetation types in the lowlands is limited. Dry vegetation types have poorer recovery rates from disturbance than wet ones. Sites with early snowmelt and dry vegetation types may therefore be at greater risk of long-term habitat degradation. We conclude that the high growth rate of the Svalbard-breeding pink-footed goose population suggests that increasing impacts of grubbing can be expected and argue that a responsible monitoring of the effects on the tundra ecosystem is crucial.

Arctic tundra ecosystems harbour unique biodiversity which provides a range of ecological functions and services. They are inherently fragile and, due to low primary production, tundra ecosystems recover slowly from disturbances (Walker 1996; Jefferies et al. 2006). Herbivory by high-density populations of geese can be a major source of disturbance in tundra vegetation. Some goose species forage for below-ground plant parts—roots and rhizomes (Jefferies et al. 2003; Fox et al. 2006)—in the spring. This so-called grubbing activity is particularly destructive for vegetation. It creates holes in the vegeta-tion and may create vegetation-free craters at high grubbing intensities (Jefferies et al. 2003; van der Wal et al. 2007; Sjogersten et al. 2008; Speed et al. 2009; Speed, Cooper et al. 2010; Speed, Woodin et al. 2010). Furthermore, grubbing exposes the organic layer to wind and flooding, and thereby increases the impact of erosion processes (van der Wal et al. 2007). The recovery of grubbed areas is slow, depends on the grubbing intensity and is faster in wet than in dry habitats (Handa et al. 2002; Jefferies & Rockwell 2002; Speed et al. 2009; Speed, Cooper et al. 2010), and can produce persistent

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stable states characterized by near irreversible changes in soil properties (Jefferies et al. 2003). However, while grubbing in general has negative effects on vegetation cover and productivity, studies have shown that moss removal has positive effects on the soil temperature in the rooting zone of vascular plants and leads to enhanced grass growth (van der Wal 2006; Gornall et al. 2009). In this way, goose grazing and grubbing can have profound consequences for the structure and function of tundra habitats, and strong top–down effects on both plant productivity and community structure have been documented (e.g., Bazely & Jefferies 1997; van der Wal et al. 2007; Speed, Cooper et al. 2010; Sjögersten et al. 2012). A classical example is the salt marshes along the Hudson Bay coast in the Canadian Arctic. These have been subject to large-scale vegetation loss and habitat degradation caused by grubbing by lesser snow geese (*Anser caerulescens caerulescens*; Kerbes et al. 1990; Jefferies & Rockwell 2002; Jefferies et al. 2003; Walker et al. 2003; Jefferies et al. 2006). In this case, the transition to an alternative habitat state had negative consequences for both the lesser snow geese as well as other species in the ecosystem (Milakovic et al. 2001; Milakovic & Jefferies 2003; Rockwell et al. 2003).

A significant number of geese that winter in temperate Europe use the western Palaearctic tundra in the summer season (Madsen et al. 1999; Fox et al. 2010). Most of these populations have increased significantly over the last few decades due to conservation efforts, intensified agricultural practices and a warmer climate (Abraham et al. 2005; Fox et al. 2005; Kery et al. 2006; Bauer et al. 2008; Fox et al. 2010). The Arctic tundra is therefore linked to European land use and conservation policies and management strategies for migrating goose populations. Extreme consequences of grubbing, such as observed in the Canadian Arctic, have not yet been reported for the tundra in the western Palaearctic. However, several western Palaearctic goose populations have high population growth rates. For example, in the High-Arctic archipelago of Svalbard, the population of pink-footed geese (*Anser brachyrhynchus*) has doubled over the last two decades, from 32 000 to 40 000 individuals in the 1990s to almost 80 000 at present (Madsen, unpubl. data; Madsen & Williams 2012). With a warmer climate, continued growth in the population is expected (Jensen et al. 2008). This causes concern regarding their impact on the High-Arctic tundra habitats in their breeding ranges (e.g., Madsen & Williams 2012).

Vegetation changes caused by goose grubbing have already been documented in Svalbard (van der Wal 2006; van der Wal et al. 2007; Speed et al. 2009). Grubbing has been found to be most prevalent in fen habitats which are low elevation areas with early thawing of the moss layer and with preferred food plants for geese (Wisz et al. 2008; Speed et al. 2009). In the present study, we examine the occurrence and magnitude of grubbing along altitudinal transects from the valley floor to mountain slopes. The study design incorporates a gradient from rich to sparse vegetation and wet to dry/mesic habitats at different altitudes. Environmental variables important for the timing of snowmelt were included, as snowmelt has been suggested to influence the likelihood for grubbing (Speed et al. 2009). The results are discussed in relation to the resilience of the tundra when exposed to an increasing population of pink-footed geese.

Material and methods

Study area

In the High-Arctic archipelago of Svalbard, Norway (62 700 km^2), 85% of the land is covered by glaciers, barren rocky or sparsely vegetated ground, while the remaining 15% is vegetated (Johansen et al. 2012). Our study area was located in the north-eastern part of the peninsula of Nordenskiöld Land on the archipelago's largest island, Spitsbergen. The study area encompassed two valleys, Adventdalen and Hanaskogdalen, surrounded by peaks reaching 1200 m a.s.l. (78°15′ N, 17°20′ E; Fig. 1). The study area is located in the middle Arctic tundra zone, dominated by rivers and open valleys with wetland, ridge and heath vegetation that never grows more than 5–10 cm above ground (Elvebakk 2005). The terrestrial ecosystem of Svalbard is characterized by a low diversity of vertebrates and an absence of fluctuating small mammals and specialist predators, commonly found in other Arctic ecosystems (Ims & Fuglei 2005). The terrestrial ecosystem is, however, supplemented by large populations of migratory birds in spring, which utilize the plant production during a short and intense Arctic summer with 24-hour daylight (e.g., Pierce 1997; Fox et al. 2010).

Study design and field protocol

In this study, we selected 19 transects spanning an altitudinal gradient from valley bottoms to altitudes dominated by scree (Fig. 1). Our design covered gradients from rich to sparse vegetation, and wet to dry/mesic habitats. Transects were distributed in three study areas: Fivelflyene and Isdammen (in Adventdalen) and Hanaskogdalen. Within each study area, the starting positions of the first plot within the first transect was picked from a
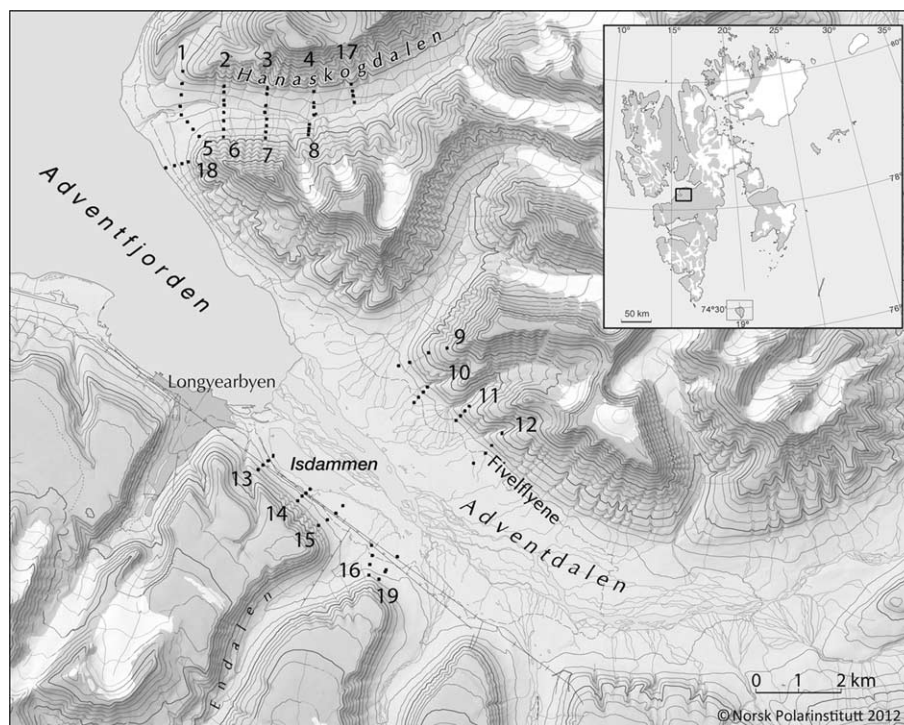
Fig. 1 The study areas in Adventdalen (Isdammen and Fivelflyene) and Hanaskogdalen, Svalbard, where evidence of grubbing was registered. The sampling plots (four in each transect; total $n = 76$) in the 19 altitudinal transects are marked with black dots on the map. Illustration: Oddveig Øien Ørvoll, Norwegian Polar Institute, 2012.

sample of random points within the lowest altitude zone (i.e., valley bottoms). The starting positions of additional transects were placed at 1-km intervals from the first position along a straight line following the valley contours. Each transect varied in length depending on the length of the vegetated part of the slopes (mean = 597 m; range = 240–1210 m). Each transect contained four evenly spaced sampling plots ($N = 76$ sampling plots), three with greater than 50% vegetation cover and one with less than 25% vegetation cover (Fig. 3). In cases where a sampling plot did not meet the vegetation cover criteria of greater than 50%, the plot was moved along the transect line to where greater than 50% vegetation cover was reached. Each sampling plot consisted of a 15×15 m marked square placed perpendicular to the mountain slope. We surveyed goose grubbing in each sampling plot by using eight 50×50 cm frames (total $N = 608$) systematically placed in the corners and in the middle of each side of the squared plot. Cumulative goose grubbing was surveyed on 1–16 July 2011, after the short and relatively intense period of pink-foot goose grubbing in May/June (Fox et al. 2009). We defined evidence of grubbing activity as the presence of moss fragmentation or beak holes, that is, holes in the moss and vegetation

cover whereby the goose removes below-ground plant parts such as rhizomes, roots and tubers roots (Fox et al. 2005; van der Wal et al. 2007; Speed et al. 2009). Using a 0.25-m^2 sampling frame, we recorded whether grubbing was "present" or "absent." The habitat type of each sampling plot was classified into one of the 18 habitat types described for Svalbard by Johansen et al. (2012). See Table 1 for details regarding the habitat classification and re-grouping of habitats for statistical analysis.

Statistical analysis

We analysed the proportion of frames in a sampling plot (number of frames grubbed/8) grubbed by pink-footed geese. The estimated probability of grubbing therefore refers to the presence/absence of grubbing at the 0.25-m^2 sampling frame. The data were analysed using generalized linear mixed effect models with a logit link function and binomial distribution for the response variable. The statistical models were fitted in R (R Development Core Team 2012) using the lme4 package (Bates et al. 2012). Because we had sample sizes from some habitat types, we re-grouped the Johansen et al. (2012) habitat types into two major habitat classes representing wet and dry

Table 1 Description of the eight habitat types sampled in the study plots (N =76). The habitat class number refers to one of the 18 habitat types described by Johansen et al. (2012). In the statistical analysis, habitat types from group 1, 3 and 4 were re-classified to a major habitat class termed "dry habitat" and group 2 was termed "wet habitat."

Habitat type	Map units	N[a]
Group 1	Areas without vegetation cover	
6	Dry, non-vegetated to sparsely vegetated barrens, slopes and ridges	2
Group 2	Wet habitat types with closed to dense vegetation cover	
10	Swamp and wet moss tundra	1
11	Mires and wet marsh tundra	2
12	Moist tussock tundra	23
Group 3	Heath and ridge communities with closed to dense vegetation cover	
13	Exposed dryas tundra	36
14	Established dryas tundra	10
Group 4	Slopes and dry meadows	
15	Arctic meadows	1
16	Exposed graminoid communities	1

[a]Number of study plots with each habitat type.

habitat types (Table 1). We explored predictor variables related to vegetation and topography. In particular, we explored topographical variables that could be expected to be related to the timing of snowmelt. The topographical variables considered were altitude (m a.s.l.), slope and aspect of the sampling plots, as extracted from a digital terrain model (DEM) with 20-m resolution provided by the Norwegian Polar Institute. The aspect is a circular variable (0–360°) and was converted to sine and cosine values, decomposing them into a north–south and east–west components. First, aspect values in degrees were converted to radians. Second, two variables were calculated representing "north exposure" = (cos[aspect in radians]) and "east exposure" = (sin[aspect in radians]), respectively. Sine values range from -1 (at due west) to 1 (at due east), while cosine values range from -1 (at due south) to 1 (at due north). Estimated effect sizes were back-transformed in R by calculating atan2 (sum[sine (aspect in radians)], sum [cosine (aspect in radians)]) (Batschelet 1981).

We calculated a heat load index (HLI) as a proxy for snowmelt following the protocol of Parker (1988). The index was based on the extracted slope and aspect values from the DEM by calculating cosine (aspect-225)*tan (slope) where aspect is expressed as degrees azimuth and slope angle is expressed in degrees.

In preliminary analyses, a one-way ANOVA was used to investigate the relationship between the two topographic variables, altitude and slope, and the habitat type. Both altitude and slope differed significantly between the two

habitat types (altitude [F (1, 74) = 16.01, P = 0.0001]; slope [F (1, 74) = 34.94, P = 0.0001]; Fig. 2). Therefore, only the habitat variable was retained as a predictor in the final statistical analysis. In the analysis of goose grubbing, three fixed effect predictors were therefore included; major habitat type (wet or dry), aspect and HLI and the two-way interactions "habitat type*aspect" and "habitat type*HLI." Aspect and HLI were correlated (Table 2) and entered separately in the tested models. Transect number was treated as random effect variable. We selected models based on Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham & Anderson 2004). To allow comparison of the two major habitat types, we estimate the odds ratios (OR) with 95% confidence intervals.

Results

Goose grubbing was documented in 18 of the 19 transects and in 194 of the 608 sampling frames (32%). Grubbing was documented along the entire altitudinal gradient in several transects, though not at the highest altitudes (Fig. 3). The selected model describing the probability of goose grubbing included additive effects of habitat type and the aspect of the sampling plot, and an interaction between habitat type and aspect (Table 2). The probability of grubbing was on average three times higher in the wetter habitat type than in the drier habitat types (OR Habitat (wet)/Habitat (dry) = 2.67 [1.92, 4.11]). Furthermore, in the dry habitats, grubbing was as frequent in plots with south-east facing exposure as in the wet habitat types, and low elsewhere (Fig. 4).
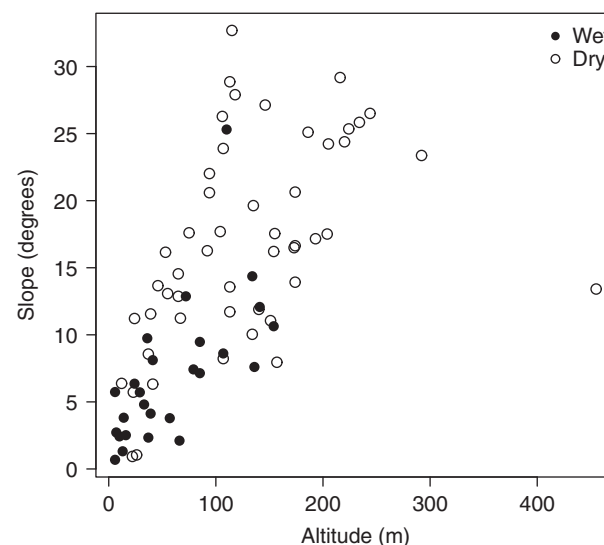

Fig. 2 Scatterplot showing the relations between altitude (m) and slope (degrees) for the dry and wet habitat types.

Table 2 Spearman's rank correlation matrix of continuous predictor variables which relate terrain characteristics to probability of goose grubbing in the study area. Significant correlations ($P < 0.05$) are indicated with asterisks.

	Altitude (m a.s.l.)	Aspect	Slope	Heat load index
Altitude	–	0.106	0.735*	0.133
Aspect	–	–	−0.006	0.318*
Slope	–	–	–	0.006

In contrast, the grubbing frequency was independent of aspect in the wet habitats (Fig. 4).

Discussion

This study confirms the finding that wet habitats are more frequently used as foraging sites for grubbing by pink-footed geese in Svalbard (Speed et al. 2009). However, we also find high and similar grubbing intensities in dry south-east facing habitats. The most likely explanation for the latter is that these dry habitat patches are available for grubbing before the wet habitats become snow-free, and therefore become exposed to intensive grubbing when the geese have no other option. Although south-west facing slopes receive the most solar radiation at these latitudes, local topography related to snow accumulation, snowdrift and shadow effects may cause the snowmelt patterns to differ from this expectation. Our results are in contrast to Hupp et al. (2001), who found snow-free areas to be less attractive to snow geese because: (1) available forage had been quickly exploited as ground became snow-free; and (2) as the soil became drier extraction of underground forage was difficult.
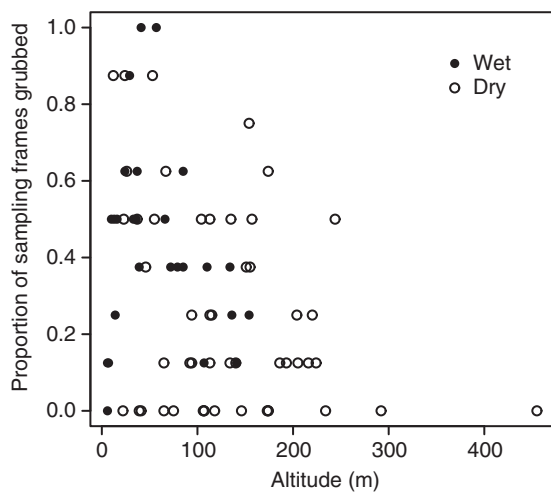

Fig. 3 Proportion of sampling frames grubbed in each sampling plot (no. frames grubbed/total no. sampling frames in study plot [8]) plotted against altitude (m) of the sampling plot.

Table 3 Parameter estimates and standard error (± SE) for the five evaluated models describing the probability of goose grubbing in the study areas in Adventdalen and Hanaskogdalen, Svalbard, according to Akaike's Information Criterion corrected for small sample size (AIC$_c$) and ΔAIC$_c$. Reference level (intercept) was set to habitat type "dry." Estimates are differences (contrasts) between the intercept and the estimated effect. Asterisks indicate statistically significant ($P < 0.05$) estimates. The selected model for inference is in boldface. Coefficients for random effects and residual variability are standard deviations.

|	Fixed effect variable								Random effect variable		
	Habitat		Aspect			Habitat*Aspect					
Model	Intercept (Dry)	Wet	Cosine (aspect) "north exposure"	Sine (aspect) "east exposure"	HLI[a]	Wet*Cosine (aspect)	Wet*Sine (aspect)	Habitat*HLI	Transect	AIC$_c$	ΔAIC$_c$
Habitat*aspect	**−1.14 (±0.21)***	**0.98 (±0.22)***	**−0.52 (± 0.23)***	**0.90 (±0.32)***		**0.37 (±0.31)**	**−0.92 (±0.42)***		**0.69**	**218.0**	**0.00**
Habitat+aspect	−1.14 (±0.19)	0.98 (±0.22)*	−0.37 (0.19)*	0.49 (0.25)					0.63	219.1	1.01
Habitat	−1.20 (±0.19)	1.01 (±0.22)*							0.63	221.4	3.41
Habitat+HLI	−1.20 (±0.19)	1.02 (±0.22)*			−0.22 (±0.56)				0.63	223.5	5.50
Habitat*HLI	−1.20 (±0.19)	1.04 (±0.22)			−0.18 (±0.57)			−0.52 (±0.38)	0.64	225.7	7.70

[a]Heat load index.
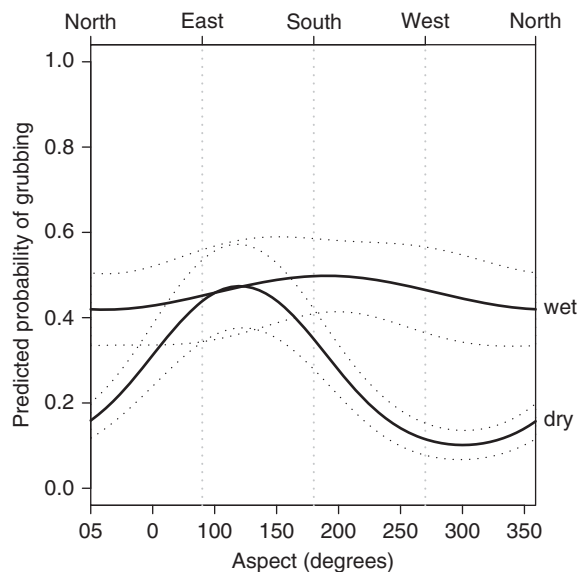
Fig. 4 Predicted probability of pink-footed goose grubbing per 0.25-m² quadrat (solid black line) from the best logistic model on the predictor variable "aspect" for the two major habitat types (wet and dry). Dotted lines show standard errors.

Wet habitats have shown stronger resilience and higher recovery rates than drier habitats (Speed, Woodin et al. 2010). As the dry habitats have a poorer recovery rate, the negative consequences of grubbing may become disproportionately larger. Our findings therefore suggest that patches of dry habitat (which at the time of grubbing are moister in the upper soil horizon owing to permafrost) that become snow-free early may be particularly vulnerable to habitat degradation. Snow cover and spring thawing processes are of substantial significance for the reproductive success of goose populations (Prop & de Vries 1993; Skinner et al. 1998; Bêty et al. 2004; Madsen et al. 2007; Dickey et al. 2008). Early springs allow more pairs to find nest sites which results in higher breeding densities (Madsen et al. 2007; Dickey et al. 2008). Our observations suggest that the timing of snowmelt may also have consequences for the grubbing impact on dry habitat patches. In mid-May 2010, a significant number of pink-footed geese were observed on the snow-free slopes on the side of the valleys while the wet habitat, dominating the valley floor, was still snow-covered (Pedersen & Fuglei, unpubl. data). In years with late snowmelt (as opposed to years when the whole valleys become snow free early), the early snow-free patches of the dry habitat may become "hot-spots" for grubbing. The direct link between weather and grubbing impact as such will need further investigations (but see Hupp et al. 2001). The abundance of productive vegetation commu-

nities is expected to impact the viability of herbivore populations (Ward et al. 2005). In Svalbard, degradation of the tundra vegetation, caused by grubbing, may therefore result in reduced population sizes of the endemic tundra herbivores—the Svalbard rock ptarmigan (*Lagopus muta hyperborea*) and the Svalbard reindeer (*Rangifer tarandus plathyrynchus*)—and have cascading effects on the rest of the ecosystem. Since Speed et al. (2009) conducted the first studies on the impact of goose grubbing on the tundra vegetation in Svalbard in 2006, the population of pink-footed geese has increased from 56 000 to 80 000 individuals (Madsen, unpubl. data; Madsen & Williams 2012). This increase in population size suggests that the grubbing intensity may have increased substantially over the same period. We argue that there is a need for continued monitoring of the impact of grubbing due to its potential for causing widespread degradation of the tundra vegetation (Speed et al. 2009; Speed, Woodin et al. 2010). We also note that a change towards a warmer climate has been a significant contributor to the increase in the pink-footed goose population over the last decade (Madsen & Williams 2012), an increase which therefore is likely to continue (Jensen et al. 2008). The potential implications of extensive grubbing for the functioning of the entire tundra ecosystem (Ims et al. 2008; Post et al. 2009) add weight to a call for a responsible monitoring of the processes involved. The recently launched International Flyway Management Plan recommends management actions controlling the pink-footed goose population size, and its implementation is focused (Madsen & Williams 2012). In a European management context, this dynamic and adaptive plan is unique. It sets a long-term population size at 60 000 individuals. This emphasizes the need for monitoring the expanding pink-footed goose population and its impact on the tundra ecosystem.

Acknowledgements

References

Abraham K.F., Jefferies R.L. & Alisauskas R.T. 2005. The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology 11*, 841–855.

Bates D., Maechler M. & Bolker B. 2012. *lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0.* Accessed on the internet at http://CRAN.R-project.org/package=lme4 on August 2012.

Batschelet E. 1981. *Circular statistics in biology.* London: Academic Press.

Bauer S., Van Dinther M., Hogda K.A., Klaassen M. & Madsen J. 2008. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. *Journal of Animal Ecology 77*, 654–660.

Bazely D.R. & Jefferies R.L. 1997. Trophic interactions in Arctic ecosystems and the occurrence of a terrestrial trophic cascade. In S.J. Woodin & M. Marquiss (eds.): *Ecology of Arctic environments.* Pp. 183–297. Oxford: Blackwell.

Bêty J., Giroux J.-F. & Gauthier G. 2004. Individual variation in the timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology 57*, 1–8.

Burnham K.P. & Anderson D.R. 2004. Multimodel inference—understanding AIC and BIC in model selection. *Sociological Methods & Research 33*, 261–304.

Dickey M.-H., Gauthier G. & Cadieux M.-C. 2008. Climatic effects on the breeding phenology and reproductive success of an Arctic-nesting goose species. *Global Change Biology 14*, 1973–1985.

Elvebakk A. 2005. A vegetation map of Svalbard on the scale 1: 3.5 mill. *Phytocoenologia 35*, 951–967.

Fox A.D., Ebbinge B.S., Mitchell C., Heinicke T., Aarvak T., Colhoun K., Clausen P., Dereliev S., Faragó S., Koffijberg K., Kruckenberg H., Loonen M.J.J.E., Madsen J., Mooij J., Musil P., Nilsson L., Phil S. & van der Jeugd H. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. *Ornis Svecica 20*, 115–127.

Fox A.D., Eide N.E., Bergersen E. & Madsen J. 2009. Resource partitioning in sympatric Arctic-breeding geese: summer habitat use, spatial and dietary overlap of barnacle and pink-footed geese in Svalbard. *Ibis 151*, 122–133.

Fox A.D., Madsen J., Boyd H., Kuijken E., Norriss D.W., Tombre I.M. & Stroud D.A. 2005. Effects of agricultural change on abundance, fitness components and distribution of two Arctic-nesting goose populations. *Global Change Biology 11*, 881–893.

Fox T.A., Francis I.S. & Bergersen E. 2006. Diet and habitat use of Svalbard pink-footed geese *Anser brachyrhynchus* during arrival and pre-breeding periods in Adventdalen. *Ardea 94*, 691–699.

Gornall J.L., Woodin S.J., Jonsdottir I.S. & van der Wal R. 2009. Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. *Oecologia 161*, 747–758.

Handa I.T., Harmsen R. & Jefferies R.L. 2002. Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. *Journal of Ecology 90*, 86–99.

Hupp J.W., Zacheis A.B., Anthony R.M., Robertson D.G., Ericson W.P. & Palcios K.C. 2001. Snow cover and snow goose *Anser caerulescens caerulescens* distribution during spring migration. *Wildlife Biology 7(2)*, 65–75.

Ims R.A. & Fuglei E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience 55*, 311–322.

Ims R.A., Henden J.A. & Killengreen S.T. 2008. Collapsing population cycles. *Trends in Ecology & Evolution 23*, 79–86.

Jefferies R.L., Jano A.P. & Abraham K.F. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology 94*, 234–242.

Jefferies R.L., Rockwell R.F. & Abraham K.F. 2003. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands—a continuing saga. *Environmental Reviews 11*, 193–232.

Jefferies R.L. & Rockwell R.L. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science 5*, 7–16.

Jensen R.A., Madsen J., O'Connell M., Wisz M.S., Tommervik H. & Mehlum F. 2008. Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Change Biology 14*, 1–10.

Johansen B.E., Karlsen S.R. & Tommervik H. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM plus data. *Polar Record 48*, 47–63.

Kerbes R.H., Kotanen P.M. & Jefferies R.L. 1990. Destruction of wetland habitats by lesser snow geese—a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology 27*, 242–258.

Kéry M., Madsen J. & Lebreton J.D. 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology 75*, 1172–1181.

Madsen J., Cracknell G. & Fox A.D. (eds.) 1999. *Goose populations of the western Palearctic. A review of status and distribution. Wetlands International Publication 48.* Wageningen: Wetlands International.

Madsen J., Tamstorf M., Klaassen M., Eide N.E., Glahder C., Riget F., Nyegaard H. & Cottaar F. 2007. Effects of snow cover on the timing and success of reproduction in High-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology 30*, 1363–1372.

Madsen J. & Williams J.H. 2012. *International species management plan for the Svalbard population of the pink-footed goose Anser brachyrhynchus.* Aarhus: Aarhus University.

Milakovic B., Carleton T.J. & Jefferies R.L. 2001. Changes in midge (Diptera: Chironomidae) populations of sub-Arctic supratidal vernal ponds in response to goose foraging. *Ecoscience 8*, 58–67.

Milakovic B. & Jefferies R.L. 2003. The effects of goose herbivory and loss of vegetation on ground beetle and

spider assemblages in an Arctic supratidal marsh. *Ecoscience* 10, 57–65.

Parker K.C. 1988. Environmental relationships and vegetation associates of columnar cacti in the northern Sonoran desert. *Vegetatio 78*, 125–140.

Pierce E.P. 1997. Sex roles in the monogamous purple sandpiper *Calidris maritima* in Svalbard. *Ibis 139*, 159–169.

Post E., Forchhammer M.C., Bret-Harte M.S., Callaghan T.V., Christensen T.R., Elberling B., Fox A.D., Gilg O., Hik D.S., Hoye T.T., Ims R.A., Jeppesen E., Klein D.R., Madsen J., McGuire A.D., Rysgaard S., Schindler D.E., Stirling I., Tamstorf M.P., Tyler N.C.R., van der Wal R., Welker J., Wookey P.A., Schmidt N.M. & Aastrup P. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science 325*, 1355–1358.

Prop J. & de Vries J. 1993. Impacts of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis*. *Ornis Scandinavica 24*, 110–121.

R Core Team 2012. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rockwell R.F., Witte C.R., Jefferies R.L. & Weatherhead P.J. 2003. Response of nesting savannah sparrows to 25 years of habitat change in a snow goose colony. *Ecoscience 10*, 33–37.

Sjogersten S., van der Wal R. & Woodin S.J. 2008. Habitat type determines herbivory controls over CO_2 fluxes in a warmer Arctic. *Ecology 89*, 2103–2116.

Sjogersten S., van der Wal R. & Woodin S.J. 2012. Impacts of grazing and climate warming on C pools and decomposition rates in Arctic environments. *Ecosystems 15*, 349–362.

Skinner W.R., Jefferies R.L., Carleton T.J., Rockwell R.F. & Abraham K.F. 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. *Global Change Biology 4*, 3–16.

Speed J.D.M., Cooper E.J., Jonsdottir I.S., van der Wal R. & Woodin S.J. 2010. Plant community properties predict vegetation resilience to herbivore disturbance in the Arctic. *Journal of Ecology 98*, 1002–1013.

Speed J.D.M., Woodin S.J., Tommervik H., Tamstorf M.P. & van der Wal R. 2009. Predicting habitat utilization and extent of ecosystem disturbance by an increasing herbivore population. *Ecosystems 12*, 349–359.

Speed J.D.M., Woodin S.J., Tommervik H. & van der Wal R. 2010. Extrapolating herbivore-induced carbon loss across an Arctic landscape. *Polar Biology 33*, 789–797.

van der Wal R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos 114*, 177–186.

van der Wal R., Sjogersten S., Woodin S.J., Cooper E.J., Jonsdottir I.S., Kuijper D., Fox A.D. & Huiskes A.D. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology 13*, 539–545.

Walker D.A. 1996. Disturbance and recovery of Arctic Alaskan vegetation. In J.F. Reynolds & J.D. Tenhunen (eds.): *Landscape function and disturbance in Arctic tundra*. Pp. 35–71. Berlin: Springer.

Walker N.A., Henry H.A.L., Wilson D.J. & Jefferies R.L. 2003. The dynamics of nitrogen movement in an Arctic salt marsh in response to goose herbivory: a parameterized model with alternate stable states. *Journal of Ecology 91*, 637–650.

Ward D.H., Reed A., Sedinger J.S., Black J.M., Derksen D.V. & Castelli P.M. 2005. North American brant: effects of changes in habitat and climate on population dynamics. *Global Change Biology 11*, 869–880.

Wisz M.S., Tamstorf M.P., Madsen J. & Jespersen M. 2008. Where might the western Svalbard tundra be vulnerable to pink-footed goose (*Anser brachyrhynchus*) population expansion? Clues from species distribution models. *Diversity and Distributions 14*, 26–37.