RESEARCH/REVIEW ARTICLE

Biding time before breeding: flexible use of the Arctic landscape by migratory geese during spring

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Abstract

Many millions of long-distance migrants use pre-breeding staging sites located adjacent to breeding grounds immediately prior to nesting, presumably to improve body condition and thus reproductive success. However, in highly seasonal landscapes such as the High Arctic, early spring feeding opportunities are limited and time to complete the breeding cycle is short. Hence, a more productive strategy may be to initiate breeding as soon as local conditions allow. We used remote sensing satellite imagery combined with field-based methods to demonstrate flexible responses to local environmental conditions by Svalbard pink-footed geese (*Anser brachyrhynchus*), an abundant long-distance migratory herbivore. Satellite imagery revealed greater snow cover at the main nesting area in central Svalbard than at the adjacent pre-breeding staging site when snowmelt was late, with greater numbers of geese using the pre-breeding site. When snowmelt was early, however, snow cover at the main nesting area was lower than in years with late snowmelt and significantly fewer pink-footed geese used the pre-breeding site under such conditions. The response of geese to differing snowmelt conditions demonstrates flexibility in their use of the landscape, suggesting that pre-breeding sites are used primarily as a stop-gap in those years when snowmelt is late and nest sites inaccessible.

Routine feeding at stop-over sites to fuel the energetic demands of migration is the norm for many millions of long-distance migrants undertaking lengthy journeys from wintering grounds to breeding sites (Drent et al. 2006). Moreover, for numerous species, feeding immediately prior to nesting is thought essential for accumulating resources needed for egg production and to improve female body condition and reproductive success (Choinière & Gauthier 1995; Ganter & Cooke 1996; Klaassen et al. 2001). However, in highly seasonal landscapes where summer is short, nesting early in the season may disproportionally enhance reproductive output (Madsen et al. 2007; Meltofte et al. 2008; Anderson et al. 2015) and hence provide a more effective strategy for improving reproductive success.

Geese are the main migratory herbivore species of the highly seasonal Arctic ecosystem (van der Wal 2005) and have been observed feeding at staging areas (pre-breeding sites) prior to nesting (Glahder 1999; Anderson et al. 2012). However, since spring snow conditions in the Arctic are highly variable (Rotschky et al. 2011), with late snowmelt limiting spring feeding opportunities (Anderson et al. 2012), we question whether the extent of snow cover influences the number of birds using such pre-breeding sites.

To investigate this we studied pink-footed geese (*Anser brachyrhynchus*), the main migratory herbivore of Svalbard (Madsen et al. 1999). Since pink-footed geese have spatially discrete pre-breeding sites and nesting areas (Glahder et al. 2006) they are an ideal migratory species

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to use for assessing spatial use of the High Arctic landscape during the key spring period. We hypothesize that, in those years with a high degree of spring snow cover at their breeding sites, larger numbers of pink-footed geese frequent pre-breeding staging grounds. We counted the number of pink-footed geese using the main pre-breeding site in central Svalbard during spring for nine years and determined the extent of snow cover at this pre-breeding site and at the adjacent main pink-footed goose nesting area during spring. This allowed us to examine how the numbers of geese using the main pre-breeding site during spring changed with different snow-cover conditions at that site and at the adjacent nesting area.

Materials and methods

The Svalbard pink-footed goose is an abundant western European migratory species, migrating more than 3000 km from overwintering grounds in Belgium, the Netherlands and Denmark to breed in the High Arctic (Madsen et al. 1999). Two mainland Norwegian stop-over sites are used—Trondheimsfjorden and Vesterålen, the latter the last before the final ca. 1100 km journey to Svalbard (Glahder et al. 2006; Tombre et al. 2008). Geese arrive at pre-breeding staging sites on Svalbard (Glahder et al. 2006), where, like many other Northern Hemisphere goose species (Giroux & Bédard 1987; Kerbes et al. 1990; Carrière et al. 1999), they feed predominantly by grubbing for below-ground plant roots and storage organs early in the season (Fox & Bergersen 2005). Such feeding habits therefore necessitate a relatively snow-free and thawed landscape during spring.

To determine whether the extent of spring snow cover at one of the main pink-footed goose nesting areas in Svalbard influenced the number of geese using the adjacent established pre-breeding site, we determined the amount of spring snow cover in both areas and counted the number of geese using this pre-breeding site during spring for nine years (2004–2012). The nesting area is one of the main breeding grounds for this species (Jepsen et al. 2002) and the pre-breeding site is where the largest concentrations of geese occur in central Svalbard during spring (Glahder et al. 2006). It was impossible to count geese at the breeding area because this species is particularly shy of humans. Upon spotting people, adults flee the nest for distances up to 300 m, resulting in high nest predation levels (Madsen et al. 2009).

To determine the numbers of pink-footed geese using the pre-breeding site, geese were counted from their arrival in mid-May until the beginning of the nesting period three weeks later, from 2004 to 2012. Counts covered an area of 10 km $\times$ 1 km and lay within an area predicted as having a high likelihood of use by feeding geese (Speed et al. 2009). Observations were restricted to distances of 1 km or less to avoid potential errors due to haze shimmer associated with greater distances. As this shy species is easily disturbed (Madsen et al. 2009), counts were made from a vehicle with the aid of binoculars and telescope at intervals of one, two or three days. We covered the survey area as quickly as feasible, ensuring the highest degree of accuracy possible. However, because of the scattered spatial distribution of geese across such a large area we are unable to provide precise numbers; our counts therefore provide an index of use of the pre-breeding staging site by pink-footed geese. We used the median value from the three highest recorded counts of geese conducted in a single year. The confounding variables of total population size and numbers of adults of breeding age (population estimates taken from two years prior to our spring goose counts to allow for probable age of first breeding) were also considered in our assessment. Population estimates were made on the basis of synchronized total population counts and counts of the proportion of juveniles in goose flocks conducted during autumn staging in Denmark and the Netherlands (Madsen et al. 2014).

Cloud-free MODIS satellite images (spectral bands 1 [620–670 nm] and 2 [841–876 nm], pixel resolution 250 m $\times$ 250 m) were used to determine snow cover during the pre-breeding period in May at the nesting area and the adjacent pre-breeding site. For each year (2004–2012) we used MODIS satellite images of the nesting area from 25 to 31 May (one image per year, nine in total). No atmospheric correction was required and the MODIS Swath Reprojection Tool (www.lpdaac.usgs.gov/tools/modis_reprojection_tool_swath) was used to geo-reference images. Sub-sets from each satellite image were extracted for snow-cover analysis. The extracted areas covered the extent of the colony (see Anderson et al. 2015) and parts of the tundra previously identified as having a high likelihood (60–100%) of utilization by pink-footed geese for feeding (Speed et al. 2009). With each of the nine sub-set images, visual training points and a standard maximum likelihood classification were used to produce a two class (snow or no snow) standard confusion matrix (using no fewer than 100 pixels to define each class). This assigned a snow class to each pixel in the sub-set image, allowing a snow-cover percentage to be estimated.

To exemplify the extreme differences in spring snow cover that geese encounter on arrival in Svalbard in different years, data was extracted from two satellite images representative of early (2010) and late (2008) snowmelt years. It was impossible to obtain suitable cloud-free images from the same date in different years, so images taken on 23 May and 25 May—as close as possible to the date of the peak daily goose count at the pre-breeding site (23 May)—were used. Images were processed as described above, generating an estimation of the percentage distribution of snow cover under both early and late snowmelt conditions for both the pre-breeding site and the breeding area.

All spatial analyses were carried out in ArcGIS 10.1 (© ESRI Inc. 1999–2010) and statistical analyses using R software, version 3.0.1 (R Development Core Team 2013). To ensure that our estimations of spring snow cover were not unduly influenced by the date of image capture, we calculated the Pearson's correlation coefficient between spring snow cover and day of year. This allowed us to explore if snow cover was lower on later dates due to extra time being available for snowmelt. A generalized linear model with negative binomial distribution and log link function was used to determine the relationship between the numbers of pink-footed geese using the pre-breeding site and (i) spring snow cover at the nesting area, and (ii) the number of adults of breeding age. We calculated the variance inflation factors (VIFs) of our predictor variables (snow, goose population size and population size of adult geese) to explore possible multicollinearity and used the Pearson chi-squared test to assess goodness-of-fit of the final model.

Results

There was no correlation between date of MODIS satellite image capture (day of year) and snow-cover estimate ($r = -0.14$, $n = 9$, $p = 0.71$), suggesting that snow cover was influenced more by annual variation in snow depth and melt than image acquisition date. In our model, the VIF for goose population size was large (11.4) so it was removed from our analysis, with the VIFs for the remaining predictors = 1.00. Pearson's chi-squared test indicated that the model including snow cover and size of the breeding population provided a good fit ($p = 0.24$).

At least twice as many geese used the pre-breeding site in those years when spring snow cover at the adjacent main nesting area was high ($z = 3.18$, $p = 0.002$; Fig. 1, Table 1). This pattern of landscape use by pink-footed geese was not influenced by the size of the breeding population ($z = 0.87$, $p = 0.38$; Table 1). MODIS satellite images of central Svalbard captured during spring showed clear differences in snow-cover extent (Fig. 2b, d), with ample dark shaded areas, indicating the absence of, or very low, snow cover when snowmelt was early (Fig. 2d). Furthermore, the pre-breeding site experienced 13–28% less snow cover than the adjacent main nesting area (Fig. 2c, e).

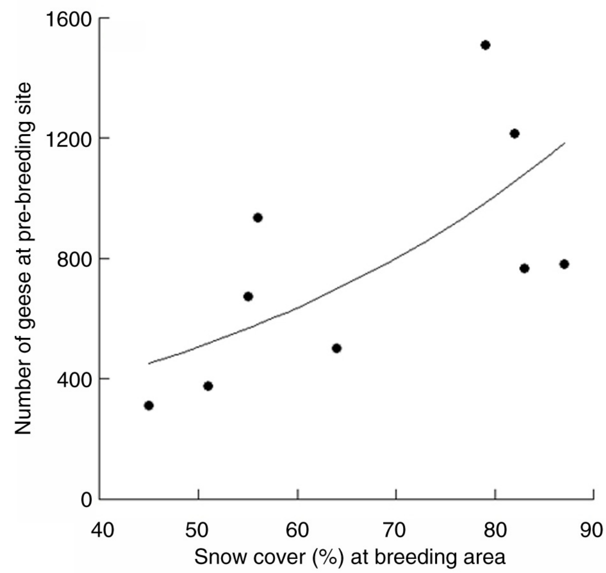

Fig. 1 Number of pink-footed geese using an established pre-breeding site during May and spring snow-cover extent at the adjacent main nesting area.

Discussion

Large differences in the numbers of pink-footed geese (median counts: 312–1510 individuals) using the main pre-breeding site in central Svalbard were observed over nine years. Since the High Arctic landscape is often extensively snow covered in spring, with little live above-ground plant growth and frozen ground restricting access to below-ground biomass (Anderson et al. 2012), it seems unlikely that this pre-breeding site was used principally for routine feeding alone. Indeed, since pink-footed geese can begin egg-laying within one week of arrival on Svalbard, or even earlier when snowmelt allows (Glahder et al. 2006; Madsen et al. 2007), this suggests that feeding to provide nutrients for egg production is not essential at this time. Furthermore, carcass analysis has shown that follicular development begins in northern Norway, with female geese already carrying developed follicles on arrival in Svalbard (Madsen, unpubl. data), thereby negating the need for a period of rapid follicle development in Svalbard. We suggest that geese use

Table 1 Results of a generalized linear model analysis of numbers of pink-footed geese using the main pre-breeding staging site in central Svalbard during May (2004 to 2012). The interaction between snow and population size of adult geese was tested but not significant ($p > 0.65$).

Predictor	Estimate	Standard error	z	p
Intercept	4.15	1.15	3.60	< 0.001
Snow cover at nesting site	0.024	0.007	3.18	0.002
Population of adult geese	0.00002	0.00002	0.87	0.38

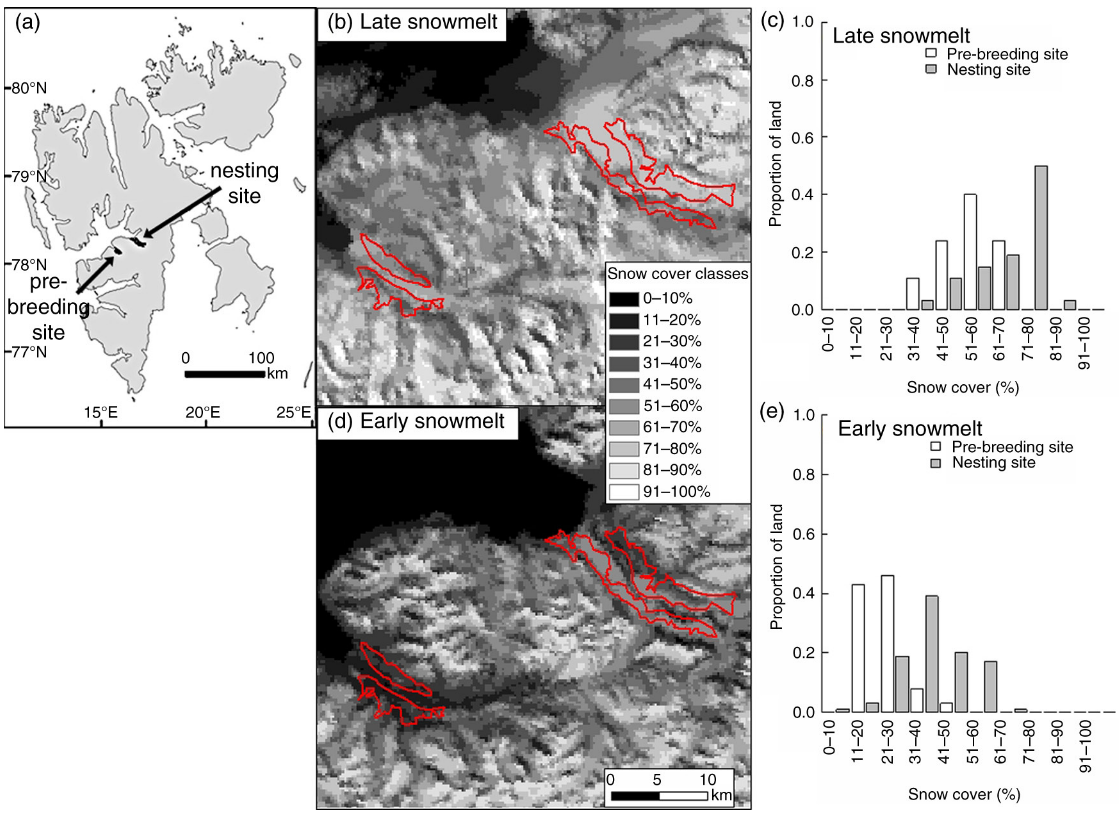

Fig. 2 Snow cover at a pink-footed goose pre-breeding site and adjacent main nesting area in central Svalbard during late May. (a) Svalbard map with locations of the pre-breeding site and nesting area indicated in black, (b) MODIS satellite image of snow cover in central Svalbard when snowmelt was late (2008), and (d) early (2010), (c) proportions of land at the pre-breeding site (white bars) and nesting area (grey bars) covered by snow during spring when snowmelt was late (2008), and (e) early (2010). The pre-breeding site and nesting area are outlined in the satellite images, where visual training points and a standard maximum likelihood classification were used to produce a 10-class standard confusion matrix. This assigned a snow class to each pixel in the image, allowing snow-cover percentages to be estimated.

pre-breeding sites primarily because they are advantageously located close to their nesting areas and provide ideal places at which to wait for the favourable conditions required for nesting as early in the season as possible.

We propose that pink-footed geese responded to favourable snow-cover conditions by moving directly to the nearby nesting area if they observed low snow cover at the pre-breeding site. Indeed, satellite tagged male pink-footed geese spent less time at pre-breeding sites in central Svalbard when snow cover was low (Glahder et al. 2006) and barnacle geese (*Branta leucopsis*) at a different pre-breeding site frequently made short trips to the adjacent nesting area to assess snow-cover conditions and initiate nesting when snowmelt revealed nest sites (Hübner et al. 2010). Furthermore, Anderson et al. (2015) reported that significantly more pink-footed geese attempted to breed in the nesting area detailed in this study when snow cover was low, with early season nesting improving nesting success by 3% per day (Madsen et al. 2007).

Although the Svalbard pink-footed goose population increased rapidly from some 40 000 in the early 2000s to ca. 81 500 in 2012 (Madsen et al. 2014), there was no relationship between the number of geese using the pre-breeding site and size of the breeding population. This suggests that fluctuations in numbers using the pre-breeding area were not due to the increasing size of the goose population. Despite pink-footed geese following an established route during their migration through Norway (Madsen 2001), with their Svalbard arrival fixed to within one week in mid-May (Glahder et al. 2006), the numbers of geese using the pre-breeding site appears highly dependent on snow-cover conditions.

Pink-footed geese responded rapidly to changing snowmelt conditions in the Arctic. Hence, routine pre-breeding staging immediately prior to nesting does not appear essential. We therefore propose that, since geese cannot predict the extent of snow cover at their nesting grounds while staging at distant stop-over sites along the migratory flyway (Tombre et al. 2008), pre-breeding sites are used as

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a stop-gap in years when extensive snow cover limits access to nesting grounds. This allows geese to respond rapidly to changing snowmelt conditions, highlighting the flexible responses shown by this long-distance migratory species to the variable local environmental conditions encountered in a highly seasonal landscape.

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