

Environmental parameters linked to the last migratory stage of barnacle geese en route to their breeding sites

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The migration timing of birds can be controlled by endogenous parameters. However, little is known about how environmental parameters influence the timing of migration and which have the greatest influence at different stages of migration. In this study we identified the main environmental parameters that correlate with the timing of the last stage of spring migration for the barnacle goose, *Branta leucopsis*. GPS tracking data were registered for 12 barnacle geese (in 2008–2010) on the Russian flyway and 17 (2006–2010) on the Svalbard flyway. A linear mixed-effect model and principal component analysis were used to retrieve statistically significant parameters. Departure date from the last staging site on the Russian flyway was related to daylength, temperature, cloud cover and barometric pressure, and on the Svalbard flyway to a food availability index and daylength. Arrival date at the Russian breeding site was related to cloud cover and barometric pressure en route and the food availability index and temperature at the breeding site. For the Svalbard flyway, temperature and cloud cover en route and the food availability index, wind, temperature and cloud cover at the breeding site were significantly related to arrival date at the breeding site. Our study highlights the importance of environmental parameters including food, weather and daylength for the last stage of goose spring migration. We found different priorities in selecting the environmental parameters in migration timing decisions between Svalbard and Russian barnacle geese which fly over sea and over land, respectively. Identifying the key factors that act as cues during the final stages of spring migration is important when assessing the possible effects of climate change on the timing of migration for a highly selective herbivore such as the barnacle goose.

In recent decades much knowledge has been gathered on the innate migration template of birds (i.e. the endogenous control of bird migration; Berthold, Gwinner, & Sonnenschein, 2003; Gwinner, 2012). Genetic factors may be directly involved in the initiation and termination of migratory activity and a migratory

bird's choice of direction (Berthold, 1999). However, there is still little known about how environmental parameters shape the internal template. Obtaining this knowledge is especially important when studying Arctic breeders, since they have a short time window for laying eggs, moulting and raising their offspring to accompany them on the southward migration before winter sets in Madsen et al. (2007). Thus, migratory birds need to respond appropriately to environmental parameters so as to anticipate the best date of arrival at their breeding site. Nowadays, new technologies (e.g. Global Positioning System Platform Transmitting Terminal data loggers) allow detailed analyses of migration strategies

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with respect to environmental parameters of high temporal and spatial resolution (Bairlein, 2008).

Food availability is the most likely environmental parameter to determine the date of arrival of geese at an Arctic breeding site and, therefore, reproductive success. Incubation timing is a trade-off between the benefits of an early or a late arrival at the breeding site. Geese arriving early are constrained by extensive snow cover, which due to low food availability may reduce their energy reserves for breeding. Conversely, the costs of early arrival can be offset by having a longer period of high food quality available for hatchlings, as well as having enough pre-migratory fattening time for the goslings and moulting adults before the onset of winter (Prop & de Vries, 1993).

Seasonal change in daylength is also a broad but reliable environmental parameter that indicates the onset of spring at most latitudes (Lofts & Murton, 1968; Owen, 1980). This is an especially important parameter for the geese if the correlation in temperature among the sites along a flyway is low because they cannot use spring conditions at one site as an indicator of the conditions they might encounter at the next site (Tombre et al., 2008). For instance, Duriez et al. (2009) concluded that pink-footed geese, *Anser brachyrhynchus*, in northern Norway most probably rely on time-related cues; that may be because of the weak correlation between weather conditions in Norway and Svalbard. A similar strategy has been observed for barnacle geese, *Branta leucopsis*, during their migration from the Baltic Sea to the White Sea, because of the low correlation between weather patterns at these two sites (Van der Graaf, 2006).

The major influence of weather conditions on flight speed and timing of migration of avian migrants is well established (Gordo, 2007; Jenni & Schaub, 2003; Pulido, 2007). Wind speed is probably the most important weather-related parameter determining flight speed and flight duration of birds (Erni, Liechti, & Bruderer, 2005; Liechti, 2006; Pulido, 2007). Migrant birds can greatly increase their flight speed by responding appropriately to prevailing wind conditions (Newton, 2008). Using favourable tail winds, Canada geese, *Branta canadensis*, maximize their flight speed and thus minimize migration duration (Wege & Raveling, 1984). Dark-bellied brent geese, *Branta bernicla*, make the final flight towards their summer destination when winds are favourable (Green, Alerstam, Clausen, Drent, & Ebbing, 2002). A long-term investigation of bird migration in Lithuania also showed a complex mix of weather parameters, such as air temperature, barometric pressure, cloudiness, tail winds and precipitation, influence flight conditions (Žalakevičius, 2000, 2002). The same set of weather parameters were found to affect the spring migration timing of tagged Canada geese from Rochester to Manitoba, Canada, in 1973–1975 (Wege & Raveling, 1983). These parameters play an important role in saving energy during flight (by creating optimal aerodynamic flight conditions) and aiding optimal navigation (Žalakevičius, Švažas, Stanevičius, & Vaitkus, 1995). In summary, flight speed is higher under favourable weather conditions, i.e. tail winds, low degree of cloudiness, high temperatures and absence of rain (reviewed by Richardson, 1990).

For most species it is not clear which environmental parameters are used as cues during each stage of migration (Bauer et al., 2011). At each migratory stage, different combinations of environmental parameters might be used for making decisions about migration timing (McNamara, Barta, Klaassen, & Bauer, 2011). For instance, it has been shown that migratory geese used different environmental parameters at southern staging sites to adjust their migration timing from those used close to their breeding grounds (Bauer, Gienapp, & Madsen, 2008; Duriez et al., 2009). For some geese species, such as barnacle geese, it is important to track or even get ahead of the northward advance of spring, the 'green wave',

because they are dependent on a seasonal peak of high-quality forage (Kölzsch et al., 2015; Van der Graaf, 2006). However, the differential effects of time-related cues, such as daylength, or other parameters such as weather or food conditions on the timing of the migration of geese at each migratory step are not fully understood.

Arrival date at the breeding site and the success, or otherwise, of the subsequent breeding event depends not only on environmental parameters at the breeding site, but also those at staging sites (Madsen, 2001; Prop, Black, & Shimmings, 2003). Optimization of fuel accumulation is especially important for Arctic-nesting geese since they are partially capital breeders, meaning that they rely on the amount of fat accumulated and energy stored at their different staging sites for successful breeding (Gauthier, Bêty, & Hobson, 2003). This is in line with the green-wave hypothesis, which predicts that migratory geese 'surf' a wave of forage availability during their spring migration from their temperate staging sites to their Arctic breeding areas. This hypothesis has been successfully tested for the barnacle goose, which is a highly selective herbivore. Using direct field measurements of plant biomass and quality at selected field sites (Van der Graaf, 2006), together with satellite imagery (Shariatinajafabadi et al., 2014), it was shown that the arrival date of barnacle geese at staging sites during their spring migration coincided well with peaks of nutrient biomass.

Consequently, understanding staging ecology, i.e. how birds adjust staging decisions, is crucial to understanding bird migration (Bairlein, 2008). In particular, conditions at the last staging site are expected to play a major role. The geese may be able to predict conditions at their breeding site more accurately from the conditions found at their last staging site, allowing them to move on to their nesting location when it becomes snow free (Hübner, 2006; Owen, 1980; Tombre et al., 2008). Indeed, this is supported by some reports of delay in the migration process of barnacle geese at the last staging site in the White Sea and on the Norwegian coast, before moving on to their breeding sites (Griffin, 2008; Gullestad, Owen, & Nugent, 1984; Van der Graaf, 2006). Moreover, environmental parameters at the last staging site may have a large influence on the departure date of geese on their way towards their breeding site (Bety, Giroux, & Gauthier, 2004). These geese may accumulate considerable body reserves at their last staging sites, which according to the 'deposition rate' hypothesis (Prop et al., 2003) has a direct effect on migration decisions. Environmental parameters at the last stage of migration may, therefore, have important implications for the arrival date of geese at their breeding site. Despite the importance of environmental parameters for the last stage, to our knowledge no study has been done to assess which of the parameters related to time (e.g. daylength), weather and food conditions has a considerable effect on the last migratory stage of geese en route to their breeding site.

This study concentrates on the final stage of barnacle goose migration because of the key role that last staging site might play with regard to arrival date at breeding sites in Russia and the Svalbard archipelago. The two geese populations differ considerably in terms of the distances they must cover, but also in terms of the terrain they fly across: while the Svalbard population mainly migrates across the sea, the Russian population mainly migrates across land.

In agreement with the studies already mentioned, it is assumed that the geese would respond proximately to environmental parameters such as food, daylength and weather to anticipate the most favourable time of arrival at their breeding site, and also to decide when to leave their last staging site. In the present study, we applied a principal component analysis (PCA) approach to summarize these environmental parameters in PCA axes. Next, the axes that were related to the date of departure of geese from their last staging sites and those related to the date of arrival at their

breeding site were investigated. We hypothesized, therefore, that: (1) the PCA axes of the environmental parameters at the last staging site are significantly related to the decision to depart from the last staging site; (2) the PCA axes of the environmental parameters en route are significantly related to migration timing of these geese; (3) the PCA axes of the environmental parameters at the breeding site are significantly related to the date of arrival of geese at their Arctic breeding sites; (4) barnacle geese use environmental parameters at the last staging site to predict conditions at their breeding sites.

METHODS

Study Populations

The Russian population overwinters in the Wadden Sea, along the coast of Denmark, Germany and the Netherlands, until April–May (Ganter et al., 1999). These geese migrate in May–early June toward their breeding grounds via staging sites located in the Baltic Sea (most notably on the Swedish island of Gotland and in western Estonia), the White Sea and on the Kanin Peninsula (Eichhorn, Afanasyev, Drent, & van der Jeugd, 2006; Eichhorn, Drent, Stahl, Leito, & Alerstam, 2009; Madsen, Cracknell, & Fox, 1999). The geese usually spend almost 2 weeks in the White Sea area, or in other areas closer to their breeding sites. Van der Graaf (2006) has suggested that from these areas geese are able to more accurately predict conditions prevailing at their breeding sites, which enables them to start their departure when the breeding site is snow free. After a flight of 3000–3700 km, they arrive in June at their breeding sites along the coast of the Barents Sea, located between 68°N and 73°N, and start nesting immediately upon arrival (Eichhorn et al., 2009; Van der Graaf, 2006). The islands of Novaya Zemlya and Vaygach were traditionally the primary breeding sites for this population, but as the population has rapidly grown so has the distribution of breeding grounds, which now stretch from the Kanin Peninsula in the west to Vaygach and Novaya Zemlya in the east, both on islands (e.g. Kulgoeyev Island) and on the Russian mainland (e.g. the abandoned village of Tobseda (Eichhorn et al., 2009; Madsen et al., 1999); Fig. 1).

The Svalbard population of geese overwinters on the Solway Firth, U.K. From mid-April, birds leave their wintering site and migrate northwards via staging sites located on the coastal islands of either Helgeland (mid-Norway) or Vesterålen (northern Norway), with some birds utilizing both. From mid-May onwards the geese arrive at their breeding ground in Svalbard, after flying some 3100 km (Black, Prop, & Larsson, 2007; Hübner et al., 2010; Madsen et al., 1999). They breed in colonies or loose groups on the Svalbard archipelago, mainly along the west coast of the largest island, Spitsbergen, between 76°35'N and 79°50'N, initiating nesting as soon as snow conditions permit (Hübner, 2006) (Fig. 1). Some barnacle geese visit Vårsolbukta (77°45'N, 14°24'E), on the west coast of Spitsbergen, before embarking on the final migratory leg to their breeding sites. Hübner (2006) observed that the length of stay at Vårsolbukta varies between individuals but it usually decreases as the breeding season progresses. The geese are able to better predict snow conditions at their breeding sites from this 'pre-breeding area' and adjust departure dates accordingly.

Tracking Barnacle Geese

Barnacle geese were lured to a catching area on their overwintering sites using mixed grain and waterfowl pellets and subsequently captured using cannon nets. Immediately after capture, all birds were freed from the net and transported to a nearby farm where they were temporarily housed in a tent. With the exception

of five geese from the Svalbard population, the geese were then fitted with 30 g solar GPS/ARGOS transmitters (Solar GPS 100 PTT, platform transmitter terminal, Microwave Telemetry, Inc., Columbia, MD, U.S.A.). The five individuals (ID 70618, 70619, 78198, 78378 and 178199) from the Svalbard population were equipped with 45 g transmitters. The transmitters were fitted on the geese using a nylon elasticated harness attached to the back of the birds. The geese did not show any visible signs of problems due to the harness, and they appeared to be in otherwise good condition (Ens et al., 2008). According to Microwave (Microwave Telemetry, 2007), the global positioning accuracy of their GPS equipment is: latitude/longitude ± 18 m; altitude ± 22 m; speed ± 1 km/h; and course $\pm 1^\circ$. The PTTs were programmed to transmit the position of the individual goose four or five times per day for the Russian population, and every 2 h from dawn to dusk for the Svalbard population. The data collected included goose ID, date, time, longitude, latitude, speed, course and altitude. The GPS locations were uploaded to ARGOS satellites every 4 days (ARGOS/CLS, 2011; Ens et al., 2008; Griffin, 2008). Females were tagged from the Russian population, whereas males were tagged from the Svalbard population. As the barnacle goose is a monogamous species and pair bonds persist during migration and for a long period thereafter (Owen, 1980), the data sets were considered to be comparable. We received 26 full data tracks for 12 individuals of the Russian population for 2008–2010 (Appendix Table A1), and 19 full data tracks for 17 individuals of the Svalbard population for 2006–2010 (Appendix Table A2).

Ethical Note

To catch and fix transmitters on Russian barnacle geese, we obtained a licence under the Wild Flora and Fauna Protection Act (Flora en Fauna Wet), number FF75A/2007/056, and approval from the Dutch Ethical Committee, under protocol number CL 0703. A licence to conduct this study in the Natura 2000 area 'Waddenzee' was obtained from the Province of Friesland, number 00692701. In the U.K., permission to fit satellite tags was granted by the British Trust for Ornithology Unconventional Marks Panel.

Last Staging Sites and Breeding Sites

We identified the cluster of successive positions within a radius of 30 km as a 'site' if an individual goose stopped for longer than 48 h; the 30 km radius allows for a maximum of one outlier position (Van Wijk et al., 2012). The last staging site was the long stopping site before reaching the Arctic breeding grounds. For the Russian flyway these were located in either the Baltic Sea area, the White Sea area or the Kanin Peninsula, while for the Svalbard flyway these were located in either Helgeland or Vesterålen, Norway. In total, 26 last staging sites were identified along the Russian flyway for the 12 individual barnacle geese tracked from 2008 to 2010. Of these 26 sites, 15 were located on the Kanin Peninsula, nine in the White Sea area and two in the Baltic Sea area (Fig. 1). Along the Svalbard flyway, 19 last staging sites were identified for the 17 individual barnacle geese tracked from 2006 to 2010 (Fig. 1). Of these 19 sites, 15 were located in Helgeland and four in Vesterålen. The average stopping time at last staging sites for the Russian and Svalbard barnacle geese was 11 and 15 days, respectively (Appendix Figs. A1, A2).

Breeding sites were defined as the final stopping site where birds stayed within a radius of 30 km for between 7 and 26 days before the end of June (Kölzsch et al., 2015). In total, 26 breeding sites were recognized along the Russian flyway for the 12 individual barnacle geese tracked from 2008 to 2010, and 19 breeding sites

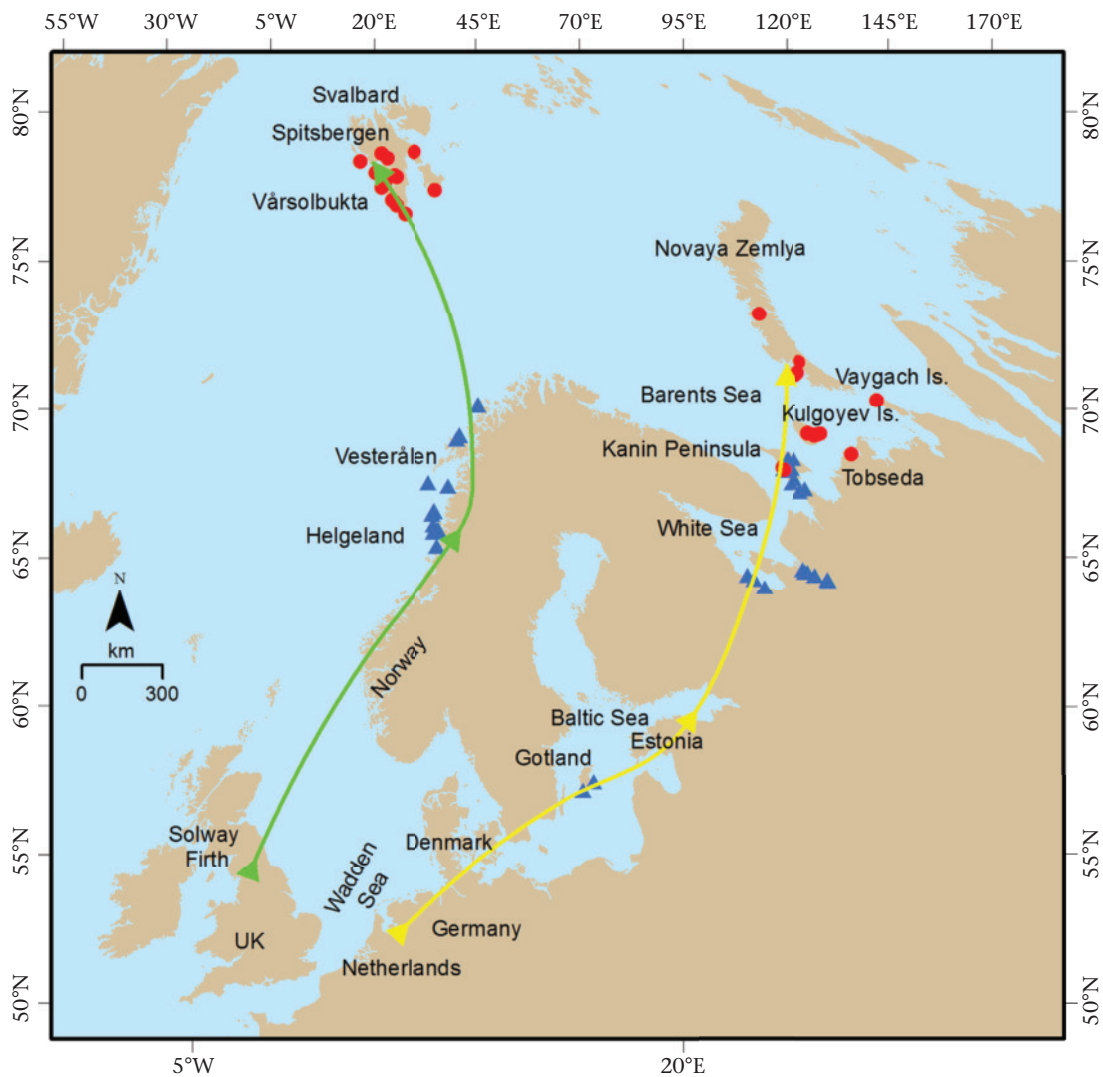


Figure 1. Spring migration routes for two barnacle goose populations from their overwintering grounds to their breeding grounds. Yellow and green arrows indicate the Russian and Svalbard flyways, respectively. Blue triangles denote last staging sites and red circles denote the breeding sites recorded for 12 Russian geese from 2008 to 2010 and 17 Svalbard geese from 2006 to 2010.

along the Svalbard flyway for the 17 individual barnacle geese tracked from 2006 to 2010 (Fig. 1).

Some of the Russian barnacle geese that were tracked for more than 1 year have occupied the same staging site from year to year; this was also the case for their breeding sites. Nevertheless, none of the individual Russian barnacle geese arrived at their last staging sites and breeding sites on the same date as in other years (for more information about the last staging and breeding sites of the two populations, see Appendix Tables A1, A2). Departure date was defined as the date on which each individual left its last staging site and headed for its breeding site, and arrival date was defined as the date on which each individual reached its final destination at the breeding site.

Environmental Parameters

Food availability index

The normalized difference vegetation index (NDVI) is a global vegetation indicator derived by remote sensing and computed as $(\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red})$, where NIR and Red are the amount of near-infrared and red light reflectance, respectively, of terrestrial objects (Huete et al., 2002). This index has led to the creation of

valuable time series describing the status and phenology of vegetation (Atzberger, Richter, Vuolo, Darvishzadeh, & Schlerf, 2011). The NDVI data we used were derived from NASA's MODIS Terra satellite at a 1 km spatial resolution and 16-day temporal resolution for 2006–2010. The 23 NDVI images were interpolated to 365 images for each year using linear regression to get a temporal resolution of 1 day rather than the 16-day composite. In the next step, the images were normalized to cover the range 0–100% (Beck, Wang, Skidmore, & Liu, 2008). The index obtained, the 'green wave index (GWI)', was developed by Shariatinajafabadi et al. (2014). A 0% GWI is used to express the annual minimum NDVI and 100% GWI the annual maximum NDVI for a given pixel. Here we used the 50% GWI (intermediate stage of greenness) as an index of food availability on the arrival date at the breeding sites (Doiron, Legagneux, Gauthier, & Levesque, 2013; Shariati Najafabadi et al., 2015). For the departure date from the last staging sites we used actual GWI values as a food availability index.

Barnacle geese mainly forage on red fescue, *Festuca rubra*, on salt marshes of the Baltic Sea. They also forage on creeping saltmarsh grass, *Puccinellia phryganodes*, and Hoppner's sedge, *Carex subspatheacea*, at the Russian breeding sites. Geese in the Baltic Sea area also forage on agricultural fields, mainly on timothy grass, *Phleum*

pratense (Van der Graaf, Stahl, Klimkowska, Bakker, & Drent, 2006). On Norwegian staging sites the geese mainly forage on salt marshes dominated by red fescue, creeping bentgrass, *Agrostis stolonifera*, and creeping saltmarsh grass and on agricultural land that is mainly being cropped with *Phleum* spp. and *Poa* spp. (Prop & Black, 1998). Therefore, we overlaid the GWI image upon a land cover map, and extracted the GWI values from the pixels that were overlaid with grassland, salt marshes and cropland land cover types in a 15 km radius around each staging and breeding site. European Space Agency (ESA)'s 2009 global land cover map was used to define land cover type, which is the finest possible resolution (300 m) global land cover map from Envisat's Medium Resolution Imaging Spectrometer (<http://www.esa.int>). To ensure the resolution was the same as GWI images, the land cover map was resampled using the nearest-neighbour algorithm to a resolution of 1 km.

Daylength (DL)

Daylength is the time (h) between sunrise and sunset, and for each individual goose in 2006–2010 it was calculated at the last staging site according to the day of the year (departure date from the last staging site) and latitude of the site using the equations proposed by Kirk (1994). The average daylength at the last staging site at the Russian and Svalbard flyways was 21.57 h and 19.96 h, respectively.

Weather parameters

In our study we looked at the absolute values of the weather parameters. Although some research shows the significant effect of changes in weather parameters on migration timing (Murphy-Klassen, Underwood, Sealy, Czyrnyj, & Holberton, 2005; Žalakevičius, 2000), this kind of research needs a long-term data set of bird migration which we did not have in our study. As weather parameters we used head wind/tail wind, cross-wind, mean daily air temperature, low-altitude cloud cover, total precipitation and barometric pressure. All weather parameters were obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) European Reanalysis (ERA)-interim data calculated every 6 h (0000, 0600, 1200, 1800 hours UTC); the spatial resolution of the data set is 0.75° latitude by 0.75° longitude from 2006 to 2010 (<http://www.ecmwf.int>). The data closest geographically and temporally to each individual location were extracted. The weather parameters en route for each individual goose were obtained from the GPS points between the last staging and breeding sites while the bird was actively migrating. Since the number of GPS points en route for the Russian barnacle geese varied between two and eight per individual, and for Svalbard barnacle geese between two and 26 per individual, we obtained average values for each of the parameters separately, allowing us to determine the weather parameters for each individual en route. We did not average the weather parameters for the departure date from the last staging site and arrival date at the breeding sites because we only had one GPS point per individual.

Head winds/tail winds and cross-winds (HW/TW & CW). A tail wind is one that blows in the direction of flight. It is expressed as a negative value, while a head wind blows opposite to the direction of flight and is expressed as a positive value. A cross-wind has a perpendicular component to the direction of flight, with positive values showing wind from the right and negative values wind from the left of the line of flight. Head winds/tail winds and cross-winds were determined using the *U*-wind and *V*-wind components (wind speed along the *X*- and *Y*-axes, respectively) that were calculated every 6 h, beginning at 0000 UTC (EPA, 2000; Hord, 2011; Safi et al., 2013).

Head wind/tail wind and cross-winds were obtained from the following equations:

$$\text{Head wind(Tail wind)} = \text{wind speed} \times \cos(\text{wind direction} - \text{runway}) \quad (1)$$

$$\text{Cross - wind} = \text{wind speed} \times \sin(\text{wind direction} - \text{runway}), \quad (2)$$

where runway is the flight direction.

Wind speed was determined from position components:

$$\text{Wind speed} = \sqrt{U^2 + V^2}, \quad (3)$$

where *U* is the wind speed along the *X*-axis and *V* is the wind speed along the *Y*-axis.

Wind direction was obtained from the following equation:

$$D_c = \frac{360}{2\pi} \times \left[\arctan\left(\frac{V}{U}\right) \right], \quad (4)$$

again where *U* is the wind speed along the *X*- and *V* is the wind speed along the *Y*-axis. If *U* > 0, then wind direction would be 270-*D_c*, and if *U* < 0 then wind direction would be 90-*D_c*.

U- and *V*- wind components were extracted from either surface level (10 m above sea level) or different pressure level (1000 hPa, 975 hPa, 950 hPa and 925 hPa) wind direction observations, depending on the altitude of the GPS fix considered. The altitude corresponding to each pressure level was calculated based on its geopotential height, with the closest pressure level to the GPS tag's altitude being used to extract *U*- and *V*-wind components.

Mean daily air temperature (MDAT). Daily air temperatures were obtained for every 6 h beginning at 0000 UTC (0000, 0600, 1200, 1800 UTC) and then averaged to get mean daily air temperature (°C). As for the wind direction, air temperature data were determined from either surface level (2 m above sea level) or pressure level (1000 hPa, 975 hPa, 950 hPa and 925 hPa) readings, depending on the tag's altitude.

Low-altitude cloud cover (LCC). Cloud cover at low altitudes (<2 km above sea level) was determined every 6 h, beginning at 0000 UTC, with values ranging from 0 (no clouds) to 1 (full cloud).

Total precipitation (TP). Total precipitation (mm) refers to any form of water falling from the sky, including snow and rain. Precipitation data were extracted at 3, 6, 9 and 12 h intervals, beginning at 0000 and 1200 UTC. For instance, the total precipitation data at 0600 means the precipitation accumulating between 0000 and 0600. Consequently, to obtain the precipitation accumulating between 0300 and 0600, we subtracted the precipitation at 0300 from the precipitation at 0600. We used the same calculation method to obtain precipitation data for the afternoon and evening; the starting time was 1200.

Barometric pressure (BP). Barometric pressure (atmospheric pressure) is the pressure exerted by the weight of air on the earth's surface at a specific place and time, and it is determined using the following equation (Berberan-Santos, Bodunov, & Pogliani, 1997):

$$P_h = P_0 e^{-\frac{mgh}{kT}}, \quad (5)$$

where *P_h* is barometric pressure (kPa) at flight altitude *h* (m), *P₀* is sea level atmospheric pressure (kPa, obtained from ECMWF), *m* is

molar mass of dry air (0.0289644 kg/mol), g is earth surface gravitational acceleration (9.80665 m/s²), h is flight altitude (m), k is the Boltzmann constant ($1.3806488(13) \times 10^{-23}$ J/K) and T is sea level temperature (K) which was obtained from ECMWF. Barometric pressure data at the tag's altitude were obtained for every 6 h, beginning at 0000 UTC.

Statistical Analysis

Principal component analysis (PCA)

PCA was used to reduce the number of parameters to a few uncorrelated factors, and to avoid multicollinearity in the subsequent multiple regressions (De Lucia and Gottfried, 2011). We used a correlation matrix when doing PCA, since it is always more appropriate when the scale or unit of the measurement differs between variables (McGarigal, Cushman, & Stafford, 2000), as is the case for our parameters. PCA was used to create linearly uncorrelated principal components (PCs) out of the original environmental parameters, thereby reducing the number of dimensions in the data. The number of PCs is equivalent to the number of original parameters; however, the first few PCA-axes encompass most of the variation occurring in the data set, so these can be used to represent the original parameters. The relative importance of the environmental parameters to each PC was examined using the principal component loading. The larger the absolute size of the loading, the more significant that variable is in interpreting the PC (McGarigal et al., 2000). Since there are no accepted 'absolute' standards for the cutoffs, we decided to use a cutoff of [0.45] in our study, following the benchmark proposed by Tabachnick and Fidell (2001). The PCA for the last staging sites was calculated using eight continuous environmental parameters that included GWI, daylength, head wind/tail wind, cross-wind, mean daily air temperature, low-altitude cloud cover, total precipitation and barometric pressure. Of the eight environmental parameters, we chose seven, including GWI, head wind/tail wind, cross-wind, mean daily air temperature, low-altitude cloud cover, total precipitation and barometric pressure, for computing the PCA at the breeding sites. Moreover, six weather parameters comprising head wind/tail wind, cross-wind, mean daily air temperature, low-altitude cloud cover, total precipitation and barometric pressure, were used to compute the PCA en route. At the breeding sites we did not consider daylength because of the 24 h daylight regime at that time of year at those latitudes. The environmental parameters en route were extracted only for the active flight period. This is especially important for the Svalbard barnacle goose because it has to make a nonstop flight over the sea. Therefore, the parameters en route comprised only the weather variables and did not include GWI and daylength.

Linear mixed-effects model

We combined the mixed-effect linear regression method and PCA to investigate the relationship between the last stage of barnacle goose spring migration timing and the environmental parameters. Linear mixed-effect modelling was used to avoid pseudoreplication caused by sequential observations of individual geese. The individual identity (ID) and tracking year were considered as random effects, and those principal components with an eigenvalue >1 (Quinn & Keough, 2002) were used as fixed effects. Backward elimination of statistically nonsignificant fixed effects ($P > 0.05$) was used to define a model that adequately described the data, while the random effects were always kept in the model. However, the random effects with zero variance were removed from the model before running the backward elimination (Mathworks, 2013). For the fixed effects, P values were calculated for an F test based on the Satterthwaite approximation, and P values

for random effects were calculated based on the likelihood ratio test. All analyses were performed on the 'lmer' object of the 'lme4' (Bates, Eigen, & Rcpp, 2014) and 'lmerTest' packages (Kuznetsova, Brockhoff, & Christensen, 2014) in R version 3.1.2 (R Core Team., 2014). Pearson correlation (r) was used to measure the positive (delay) or negative (acceleration) impact of the significant PCs on the departure and arrival dates. The proportion of residual variance in the mixed model that was due to the individual barnacle geese and year (i.e. repeatability) was calculated by dividing the proportion of variance explained by the random effect by the total variance (Lessells & Boag, 1987).

Predictability

To check whether the geese are able to rely on certain environmental parameters at their last staging site as indicators for predicting the situation at their breeding areas, we tested the relationship between arrival date at the breeding site with the PCs (eigenvalue >1) of the environmental parameters at the last staging site, and the relationship between departure date from the last staging site with the PCs of environmental parameters at the breeding site using linear mixed-effect analysis. We used Pearson correlation (r) to examine the correlation between environmental parameters at the last staging site and breeding sites.

RESULTS

The results of the PCA are shown in Table 1 for the Russian and Table 2 for the Svalbard populations. The random (ID, year) and fixed effects (selected PCs) were analysed with regard to departure date from the last staging site and arrival date at breeding sites (Tables 3 and 4 for the Russian and Svalbard population, respectively). The key environmental parameters relating to goose migration along the Svalbard and Russian flyways are summarized in Table 5. The results of PCA and linear mixed-effect regression for the last staging site, en route and breeding site are given in more detail below.

For the Svalbard barnacle geese, only two individuals were tracked for more than one year; therefore, we only calculated the repeatability for the Russian population. Our results showed repeatable interindividual and between-year differences in arrival/departure date for the Russian barnacle geese. This showed the percentage of the residual variance in arrival/departure date, not accounted for by the fixed effects (see Appendix Table A3).

Last Staging Site

For the Russian (Table 1) and Svalbard (Table 2) populations, the first three PCs with eigenvalues > 1 accounted for 65.7% and 64.3% of the total variance of environmental parameters at the last staging site, respectively.

The result of linear mixed-effect regression using these three PCs showed that for the Russian population PC1_{ISR} was a significant factor on departure date from the last staging site (Table 3). Pearson correlation showed that departure date was delayed for PC1_{ISR} ($r_{24} = 0.67$). Mean daily air temperature and barometric pressure showed the highest negative and daylength and low-altitude cloud cover the highest positive correlations with PC1_{ISR} scores (factor loadings of MDAT, BP, DL and LCC: $R = -0.89, -0.78, 0.77$ and 0.73 , respectively).

For the Svalbard population, linear mixed-effect regression showed that departure date was significantly influenced by the second PC (Table 4). However, PC1_{ISS}, which contains the largest variance (27.8% of the overall variance), was not selected by the linear mixed-effect regression model. PC2_{ISS} accelerated

($r_{17} = -0.68$) departure dates. GWI and daylength provided the major negative loading on PC2_{IS} (GWI: $R = -0.96$; DL: $R = -0.49$).

En Route

Of the six PCs en route only the first three were used in linear mixed-effect regression; they explained 77.9% and 77.8% of total variation of parameters in PCA en route for the Russian (Table 1) and Svalbard (Table 2) populations, respectively.

Linear mixed-effect regression analysis showed that arrival date at the Russian breeding site was significantly related to the PC2_{ER}

(Table 3). Arrival date was delayed by PC2_{ER} ($r_{24} = 0.27$). Low-altitude cloud cover and barometric pressure provided the major loading on that PC (LCC: $R = 0.81$; BP: $R = -0.78$).

In the regression model, only PC3_{ES} made a significant contribution to arrival date at the Svalbard breeding site (Table 4). Although the information content of the cumulative variance of PC1_{ES} and PC2_{ES} (61%) is higher than that of PC3_{ES} (16.8%), they were not selected as significant factors by the model. PC3_{ES} delayed the arrival date at the breeding site ($r_{17} = 0.48$) and it had positive loadings on mean daily air temperature (MDAT: $R = 0.83$) and low-altitude cloud cover (LCC: $R = 0.53$).

Table 1

Eigenvalues and variances of the first three principal components (eigenvalue > 1) of the PCA conducted on the environmental parameters matrix, with corresponding factor loadings of the parameters for the last staging site (PC_{ISR}), en route (PC_{ER}) and breeding site (PC_{BR}) of the Russian barnacle goose population

Environmental parameters	Last staging site			En route			Breeding site		
	PC1 _{ISR}	PC2 _{ISR}	PC3 _{ISR}	PC1 _{ER}	PC2 _{ER}	PC3 _{ER}	PC1 _{BR}	PC2 _{BR}	PC3 _{BR}
GWI	-0.31	-0.75	-0.29	nc	nc	nc	-0.38	0.83	0.14
DL	0.77	-0.13	-0.09	nc	nc	nc	nc	nc	nc
HW/TW	-0.05	-0.26	-0.74	-0.46	-0.17	0.72	-0.24	-0.32	-0.76
CW	-0.28	0.34	-0.56	0.46	0.15	0.66	-0.63	-0.13	-0.45
MDAT	-0.89	-0.22	0.14	0.84	-0.38	-0.15	0.50	-0.72	-0.05
LCC	0.73	-0.09	-0.23	-0.37	0.81	-0.08	-0.83	-0.27	0.13
TP	0.18	-0.76	0.30	0.79	0.22	0.14	-0.07	-0.33	0.85
BP	-0.78	0.06	-0.03	-0.37	-0.78	-0.01	0.68	0.40	-0.33
Eigenvalue	2.72	1.41	1.11	2.37	1.24	1.05	1.99	1.65	1.64
Variance explained (%)	34.1	17.6	14.0	39.5	20.8	17.6	28.5	23.7	23.6
Cumulative variance (%)	34.1	51.7	65.7	39.5	60.3	77.9	28.5	52.2	75.8

Loadings >|0.45| are in bold type. GWI: green wave index; DL: daylength; HW/TW: head wind/tail wind; CW: cross-wind; MDAT: mean daily air temperature; LCC: low-altitude cloud cover; TP: total precipitation; BP: barometric pressure; 'nc': parameter that was not considered in the PCA.

Table 2

Eigenvalues and variances of the first three principal components (eigenvalue > 1) of the PCA conducted on the environmental parameters matrix, with corresponding factor loadings of the parameters for the last staging site (PC_{ISS}), en route (PC_{ES}) and breeding site (PC_{BS}) of the Svalbard barnacle goose population

Environmental parameters	Last staging site			En route			Breeding site		
	PC1 _{ISS}	PC2 _{ISS}	PC3 _{ISS}	PC1 _{ES}	PC2 _{ES}	PC3 _{ES}	PC1 _{BS}	PC2 _{BS}	PC3 _{BS}
GWI	-0.04	-0.96	-0.14	nc	nc	nc	-0.70	-0.09	-0.47
DL	0.07	-0.49	0.63	nc	nc	nc	nc	nc	nc
HW/TW	0.60	-0.24	0.37	0.88	0.07	0.08	0.74	0.04	0.05
CW	-0.80	0.05	0.31	-0.13	0.74	-0.08	0.45	-0.33	0.51
MDAT	-0.50	-0.45	-0.67	-0.03	-0.43	0.83	-0.53	0.52	0.57
LCC	0.16	-0.33	0.23	-0.02	0.72	0.53	-0.78	-0.14	0.40
TP	0.61	-0.15	-0.34	-0.90	0.10	0.15	-0.28	-0.65	-0.14
BP	-0.76	-0.14	0.25	0.88	0.15	0.10	0.06	0.77	-0.27
Eigenvalue	2.22	1.58	1.33	2.37	1.28	1.01	2.21	1.43	1.06
Variance explained (%)	27.8	19.8	16.7	39.6	21.4	16.8	31.6	20.5	15.2
Cumulative variance (%)	27.8	47.6	64.3	39.6	61.0	77.8	31.6	52.1	67.3

Loadings >|0.45| are in bold type. GWI: green wave index; DL: daylength; HW/TW: head wind/tail wind; CW: cross-wind; MDAT: mean daily air temperature; LCC: low-altitude cloud cover; TP: total precipitation; BP: barometric pressure; 'nc': parameter that was not considered in the PCA.

Table 3

Results of the mixed model after running backward elimination to remove nonsignificant fixed effects (principal components of the environmental parameters) on departure date from last staging sites and arrival date at breeding sites for 12 GPS-tagged Russian barnacle geese (2008–2010)

Migration timing	Random effect	Variance	χ^2	P	Fixed effect	Sum of squares error	F	P
Departure from last staging site	ID	8.06	2.38	0.12	PC1 _{ISR}	202.08	20.98	<0.001
	Year	2.99	0.94	0.33	PC2 _{ISR}	11.33	1.02	0.32
	Residual	11.67			PC3 _{ISR}	4.05	0.34	0.56
Arrival at breeding site	ID	4.32	0.73	0.39	PC1 _{ER}	27.69	2.20	0.15
	Year	18.50	4.53	0.03	PC2 _{ER}	49.32	4.61	<0.05
	Residual	12.76			PC3 _{ER}	6.11	0.47	0.49
	Year	12.81	5.77	0.01	PC1 _{BR}	28.57	2.27	0.14
	Residual	13.05			PC2 _{BR}	221.47	16.89	<0.001
					PC3 _{BR}	1.72	0.13	0.71

Random effects with zero variance were removed from the models before running backward elimination. PC_{ISR}: PCs obtained from eight environmental parameters at the last staging sites; PC_{ER}: PCs obtained from six environmental parameters en route; PC_{BR}: PCs obtained from seven environmental parameters at breeding sites.

Table 4
Results of the mixed model after running backward elimination to remove nonsignificant fixed effects (principal components of the environmental parameters) on departure date from last staging sites and arrival date at breeding sites for 17 GPS-tagged Svalbard barnacle geese (2006–2010)

Migration timing	Random effect	Variance	χ^2	<i>P</i>	Fixed effect	Sum of squares error	<i>F</i>	<i>P</i>	
Departure from last staging site	Year	40.50	2.91	0.08	PC1 _{lS}	0.009	0.004	0.98	
	Residual	26.98			PC2 _{lS}	965.36	36.86	<0.001	
					PC3 _{lS}	68.50	2.66	0.12	
Arrival at breeding site	ID	26.73	0.06	0.80	PC1 _{eS}	35.66	0.38	0.56	
	Year	60.04	1.28	0.25	PC2 _{eS}	70.89	0.82	0.38	
	Residual	92.61				PC3 _{eS}	659.47	6.09	<0.05
						PC1 _{bS}	24.61	5674964.58	<0.001
	Residual	0.00				PC2 _{bS}	0.00	0.17	0.68
						PC3 _{bS}	0.45	105775.06	<0.001

Random effects with zero variance were removed from the models before running backward elimination. PC_{lS}: PCs obtained from eight environmental parameters at the last staging sites; PC_{eR}: PCs obtained from six environmental parameters en route; PC_{bR}: PCs obtained from seven environmental parameters at breeding sites.

Table 5
A summary of the significant principal components ($P < 0.05$) relating to migration timing at the last staging site, en route and breeding site in the Russian and Svalbard flyways

Flyway	Migration timing	PCs ($P < 0.05$)	Environmental parameters							
			GWI	DL	HW/TW	CW	MDAT	LCC	TP	BP
Russian	Departure from last staging site	PC1 _{lS} R		+				–	+	–
	Arrival at breeding site	PC2 _{eR}	nc	nc					+	–
		PC2 _{bR}	+	nc			–			
Svalbard	Departure from last staging site	PC2 _{lS} S	+	+						
	Arrival at breeding site	PC3 _{eS}	nc	nc			+		+	
		PC1 _{bS}	+	nc	–		+		+	

GWI: green wave index; DL: daylength; HW/TW: head wind/tail wind; CW: cross-wind; MDAT: mean daily air temperature; LCC: low-altitude cloud cover; TP: total precipitation; BP: barometric pressure; '+': parameters with high loading values on the significant PCs that delayed migration timing; '–': parameters with high loading values on the significant PCs that accelerated the migration timing; 'nc': parameter that was not considered in the PCA. Delayed ('+') or accelerated ('–') effect on migration timing is based on the correlation of the significant PCs with migration timing and the sign of loading values on those PCs.

Breeding Site

The first three PCs accounted for 75.8% and 67.3% of the total variation in the matrix of environmental parameters at the Russian (Table 1) and Svalbard (Table 2) breeding sites, respectively. These PCs were used in the linear mixed-effect regression analysis to determine the most significant PCs for arrival date at the breeding site.

The results of this analysis indicated a significant relationship between arrival date at the Russian breeding site and PC2_{bR} (Table 3). Arrival date was delayed by PC2_{bR} ($r_{24} = 0.68$). It was positively loaded on GWI ($R = 0.83$) and negatively on mean daily air temperature ($R = -0.72$).

For the Svalbard population there was a significant relationship between PC1_{bS} and PC3_{bS} with arrival date at the Svalbard breeding site (Table 4). Although PC3_{bS} was significantly related to arrival date, the correlation between them was extremely low ($r_{17} = -0.06$). Therefore, we did not interpret the result for this PC. PC1_{bS} accelerated the arrival at the Svalbard breeding site ($r_{17} = -0.51$). GWI and low-altitude cloud cover showed highly negative correlations with PC1_{bS} (factor loading of GWI and LCC: $R = -0.70$ and -0.78 , respectively), and head wind/tail wind showed a highly positive correlation with this PC (factor loading of HW/TW: $R = 0.74$). PC1_{bS} had a lower negative correlation with mean daily air temperature ($R = -0.53$).

Predictability

Departure date from the last staging site along the Russian flyway was significantly related to, and delayed ($r_{24} = 0.44$) by, PC2_{bR}. However, for the Svalbard population there was no significant relationship between departure date from the last staging site and the PCs of the environmental parameters at the breeding sites (Table 6).

The results of linear mixed-effect regression indicated that for both populations the same PCs of the environmental parameters at the last staging site were related to departure date from that site (Tables 3 and 4), as well as arrival date at the breeding sites (Table 7). The only exception was PC3_{lS}S that was significantly related to arrival date at the breeding site, but was not related to departure date from the last staging site on the Svalbard flyway. For the Russian population, PC1_{lS}R was significantly related to arrival date at the breeding site (Table 7): the arrival date was delayed with PC1_{lS}R ($r_{24} = 0.51$). Arrival date at the Svalbard breeding site was significantly influenced by PC2_{lS}S and PC3_{lS}S (Table 7). PC2_{lS}S accelerated ($r_{17} = -0.61$) and PC3_{lS}S delayed ($r_{17} = 0.25$) arrival date.

We did not find a significant relationship between weather parameters for the last staging site and breeding sites. We only found a significant relationship between cross-winds at the last staging site and barometric pressure at breeding sites on the Russian flyway, and between mean daily air temperature at the last staging site and barometric pressure at breeding sites on the Svalbard flyway (Table 8).

DISCUSSION

Our results reveal the importance of environmental parameters at the last stage of migration on the date of departure of individual barnacle geese from their last staging site and their arrival date at their breeding sites along two flyways. More precisely, we found that departure date from the last staging site on the Russian flyway was related to daylength, mean daily air temperature, low-altitude cloud cover and barometric pressure (PC1_{lS}R in our analysis) and on the Svalbard flyway to GWI and daylength (PC2_{lS}S). The main en route parameters that were related to arrival date at the breeding sites comprised low-altitude cloud cover and barometric pressure (PC2_{eR}) for the Russian flyway and mean daily air temperature and low-altitude cloud cover (PC3_{eS}) for the Svalbard flyway. From the

Table 6

Results of the mixed model after running backward elimination to remove nonsignificant fixed effects (principal components of the environmental parameters at the breeding site) on departure date from last staging sites for 12 GPS-tagged Russian (2008–2010) and 17 GPS-tagged Svalbard barnacle geese (2006–2010)

Migration timing	Random effect	Variance	χ^2	<i>P</i>	Fixed effect	Sum of squares error	<i>F</i>	<i>P</i>
Departure from the last staging site in the Russian flyway	ID	10.99	1.99	0.15	PC1 _{BR}	41.35	2.66	0.11
	Year	8.67	3.31	0.06	PC2 _{BR}	72.05	4.61	<0.05
	Residual	16.2			PC3 _{BR}	9.72	0.60	0.45
Departure from the last staging site in the Svalbard flyway	ID	87.66	0.66	0.41	PC1 _{BS}	293.35	2.83	0.11
	Year	10.28	0.39	0.53	PC2 _{BS}	119.54	1.15	0.29
	Residual	11.86			PC3 _{BS}	20.01	0.19	0.66

Random effects with zero variance were removed from the models before running backward elimination. PC_{BR}: PCs obtained from seven environmental parameters at the breeding sites in the Russian flyway; PC_{BS}: PCs obtained from seven environmental parameters at the breeding sites in the Svalbard flyway.

Table 7

Results of the mixed model after running backward elimination to remove nonsignificant fixed effects (principal components of the environmental parameters at the last staging site) on arrival date at the breeding sites for 12 GPS-tagged Russian (2008–2010) and 17 GPS-tagged Svalbard barnacle geese (2006–2010)

Migration timing	Random effect	Variance	χ^2	<i>P</i>	Fixed effect	Sum of squares error	<i>F</i>	<i>P</i>
Arrival at the Russian breeding site	ID	11.07	4.60	0.03	PC1 _{SR}	51.18	5.55	<0.05
	Year	22.90	6.84	0.00	PC2 _{SR}	2.59	0.29	0.59
	Residual	8.86			PC3 _{SR}	10.16	1.22	0.28
Arrival at the Svalbard breeding site	ID	113	5.01	0.02	PC1 _{SS}	0.00	1.91	0.66
	Residual	0.00			PC2 _{SS}	23.66	6439393.91	<0.001
					PC3 _{SS}	3.16	861660.46	<0.001

Random effects with zero variance were removed from the models before running backward elimination. PC_{SR}: PCs obtained from eight environmental parameters at the last staging sites in the Russian flyway; PC_{SS}: PCs obtained from eight environmental parameters at the last staging sites in the Svalbard flyway.

Table 8

Correlation matrix displaying Pearson correlation coefficients of the environmental parameters at the last staging site and breeding sites

Flyway	Last staging site	Breeding site							
		GW	HW/TW	CW	MDAT	LCC	TP	BP	
Russia	GW	–0.14	–0.02	0.10	0.28	0.13	–0.10	–0.03	
	HW/TW	–0.06	–0.27	–0.15	–0.09	–0.02	0.15	–0.02	
	CW	–0.26	0.20	0.27	0.16	0.36	0.15	–0.39*	
	MDAT	–0.33	0.09	0.07	0.12	–0.05	0.02	–0.02	
	LCC	0.35	0.29	–0.02	–0.11	–0.004	–0.19	0.11	
	TP	0.07	–0.29	0.06	0.11	–0.05	–0.11	0.26	
	BP	–0.18	–0.04	0.00	0.14	–0.06	–0.18	0.05	
Svalbard	GW	0.25	–0.36	–0.20	–0.03	0.04	0.03	–0.27	
	HW/TW	0.20	–0.04	–0.40	0.30	0.33	0.26	–0.10	
	CW	0.09	–0.01	0.03	0.05	–0.21	–0.29	–0.06	
	MDAT	–0.12	–0.13	0.19	–0.24	0.12	–0.10	–0.47*	
	LCC	0.30	–0.16	–0.21	0.22	0.10	0.00	0.14	
	TP	0.14	–0.17	–0.11	–0.16	0.01	0.30	0.06	
	BP	0.03	0.18	0.06	–0.07	–0.08	–0.37	–0.10	

GW: green wave index; HW/TW: head wind/tail wind; CW: cross-wind; MDAT: mean daily air temperature; LCC: low-altitude cloud cover; TP: total precipitation; BP: barometric pressure. Asterisk indicates significance of correlation: **P* < 0.05.

parameters at the breeding sites we found GWI and mean daily air temperature (PC2_{BR}) to be important for the arrival date at Russian breeding sites, and GWI, head wind/tail wind, mean daily air temperature and low-altitude cloud cover (PC1_{BS}) for the arrival date at Svalbard breeding sites.

Last Staging Site

Considering the correlation of daylength, mean daily air temperature, low-altitude cloud cover and barometric pressure with PC1_{SR}, along with the fact that PC1_{SR} delayed departure date, we can say the Russian geese departed from their last staging site earlier when barometric pressure and mean daily air temperature were higher, but daylength and cloudiness were lower. Reliance on daylength towards the end of the journey and departure on a fixed date were also found to be important for the spring migration of pink-footed geese (Duriez et al., 2009). Furthermore, it seems visibility could be an important parameter affecting departure, since

high temperatures and high barometric pressures are associated with clear skies (Kaiser, 2000). For northern wheatears, *Oenanthe oenanthe*, the majority of stays during spring migration coincided with an almost completely overcast sky: the cloud cover was significantly greater for birds that remained at sites than for birds that departed (Dierschke & Delingat, 2001).

Our results showed that PC2_{SR} and PC3_{SR} were not significant factors affecting departure date. PC2_{SR} was mainly related to GWI and precipitation. This result is in contrast to what we expected, because based on the deposition rate hypothesis we expected that GWI would be related to departure dates of the Russian barnacle geese. The reason for this unexpected result might be related to the fuel expenditure during the flight between the last staging site and their breeding sites. Some of the Russian barnacle geese made a short stop of 2–4 days between their last staging site and their breeding site, which may have given them enough time to refuel. In other words, instead of making one long flight with a large fuel load, they made shorter flights with smaller fuel loads, which

reduces total energy costs for the migration and increases energy savings (Green et al., 2002). The Russian geese may also build up their energy reserves beforehand by staying longer in the White Sea area or along the Baltic coast. Even though many bird species take action to avoid rain (Hume, 1986), our results did not show much effect of rainfall on the geese.

Since PC3_{ISR} was mainly related to wind conditions, we conclude that wind conditions at the last staging site have no prominent effect on departure decisions of Russian barnacle geese. Kölzsch et al. (2016) observed that the selection of supportive winds was stronger in autumn than spring because the general wind conditions were favourable between western Europe and the Russian Arctic during spring. However, our conclusion is in contrast with other studies, which have emphasized the importance of wind conditions on migration timing (e.g. Erni et al., 2005; Pulido, 2007).

Departure date from the last staging site on the Svalbard flyway was not related to the PC1_{IS}, although it accounted for the largest variance of the data. PC1_{IS} was mainly related to wind, temperature, precipitation and barometric pressure. As we observed for the Russian barnacle geese, rainfall did not have much effect on departure date for the Svalbard barnacle geese.

Our results highlighted the impact of GWI and daylength (PC2_{IS}) on departure decision making by the Svalbard barnacle geese. However, GWI may play the major role because it had a higher loading on PC2_{IS} than daylength. Bauer, Madsen, and Klaassen (2006) also found that food quantity and quality had a crucial impact on departure and staging decisions at the last stage of migration for Arctic-breeding migratory geese. Our result is in line with the deposition rate hypothesis, which suggests that deteriorating foraging conditions trigger migration. Prop et al. (2003) came to a similar conclusion about the decision making by barnacle geese for leaving their last staging sites in Norway. Moreover, Duriez et al. (2009) suggested that using daylength to make departure decisions from northern Norway is the best strategy for the geese since there is a weak correlation between weather conditions in Norway and Svalbard.

En Route

Considering the relation of PC2_{ER} to arrival date, and the correlation of the parameters with high loading on this PC (i.e. barometric pressure and cloudiness), we may conclude that higher barometric pressure and less cloudiness en route along the Russian flyway were related to earlier arrival at the final destination. However, less cloudiness may be just an indirect effect of higher barometric pressure (Kaiser, 2000). This supports the hypothesis that visibility is an important parameter in the orientation of migrating birds (Åkesson & Bäckman, 1999).

We found that wind conditions (head wind/tail wind and cross-wind) en route were not related to the migration timing of the individual Russian and Svalbard geese, which is opposite to previous studies (Erni et al., 2005; Liechti, 2006; Pulido, 2007). Wind parameters en route at the Russian flyway had high loading on PC3_{ER}, but this PC was not selected by the model. Also, arrival date at Svalbard breeding sites was not related to PC1_{ES} and PC2_{ES}, although this first PC accounted for 61% of the total variance in the data. As Table 2 shows, wind parameters had the highest correlation with PC1_{ES} and PC2_{ES}.

The flight altitude of the geese en route might be why wind parameters were not related to arrival date. For the Russian and Svalbard geese, 60% and 50% of flights were at altitudes less than 5 m above sea level, respectively. As Finn, Carlsson, Kelly, and Davenport (2012) noted, birds fly close to water surfaces for two reasons: (1) to avoid head winds and (2) to take advantage of ground effects. They found that the wind speeds decline at heights

below 4 m, so birds might be expected to fly lower when flying in head wind. Moreover, birds that fly close enough to water surface may also benefit energetically by using the ground effect (Finn et al., 2012). Ground effects can be caused by an interaction between the bird's wings and the ground or water surface that increases lift, thus minimizing power needed to stay aloft and maximizing range (De la Cueva & Blake, 1993). In other words, lower wind speeds plus ground effects can minimize energy expenditure during flight (Finn et al., 2012).

However, the effect of wind on the Svalbard geese may be less, because they could compensate for unfavourable wind conditions en route by changing flight altitude and choosing the best flight direction. On the other hand, for reasons of safety, the Russian barnacle geese may not be able to fly low over land, so they could not totally compensate for unfavourable wind conditions by changing flight altitude. This could be why about 90% of their low flights were over sea, and 78% of the high flights were over land.

Precipitation also had a high loading on PC1_{ES}. Like departure date from the last staging site, rainfall en route was not related to migration timing and therefore did not delay or accelerate arrival date at breeding sites. Our results show that arrival date at the Svalbard breeding sites was related to PC3_{ES}, and this was loaded on mean daily air temperature and cloud cover. We found that lower temperatures and less cloudiness en route were related to geese arriving earlier at their Svalbard breeding sites.

Breeding Site

Our results indicated that PC2_{BR} was mainly related to arrival date at Russian breeding sites and this was highly loaded by GWI and temperature. These two parameters had the highest correlation with PC2_{BR} among the first three PCs of the environmental parameters at the breeding site (Table 1). The arrival date is such that the growth of goslings is synchronized with high levels of food availability (Owen, 1980). Using ground data, Van der Graaf et al. (2006) and Van Der Jeugd et al. (2009) found that barnacle geese arrive at their Russian breeding sites before the peak in nutrient biomass. So the geese may follow the early settling strategy that allows the goslings to benefit from high-quality food and have enough time for pre-migratory fattening (Prop & de Vries, 1993).

Moreover, temperature at the breeding site may have indirect effects on arrival date, via its influence on food availability. Indeed, arrival date and timing of nesting of these geese is highly constrained by the food availability, which is dependent on the degree of snow cover (Fox, Francis, & Bergersen, 2006; Madsen et al., 2007; Prop & de Vries, 1993). In other words, food availability is related to the rate of snow melt, which starts when the air temperature rises above 0° C (Kostin & Mooij, 1995). As a consequence, birds arriving early have to graze on low-quality feed and must wait until more nutritious plant resources become available. However, the costs of early arrival can be offset by a better survival rate for goslings hatching early in the season, because they benefit from the longest availability of high-quality food (Prop & de Vries, 1993). Therefore, the temporal variability of food at the breeding site affects the costs and benefits of arrival date in terms of food acquisition (Fox et al., 2006). Because of this, there is a possibility that, over time, Arctic-nesting geese that arrive too late with respect to rapid seasonal developments (as a consequence of climate change and global warming) will miss the optimal breeding conditions.

Russian barnacle geese that arrive earlier at their breeding sites face higher air temperatures. As the results of Smith III and Hayden (1984) showed, spring migration phenology may be related to large-scale atmospheric circulation patterns. High temperatures

may be an indirect effect of other environmental parameters associated with weather systems, such as, for example, barometric pressure and/or favourable winds. During the passage of a low pressure system from the Atlantic, large-scale changes in temperature, pressure and wind conditions occur. The geese may be able to detect these conditions of low pressure systems, which may give them an extra boost on their way towards their destination (Smith III & Hayden, 1984). In other words, the arrival of geese at their Arctic breeding sites is associated with strong southerly winds and these winds at higher latitudes are generally associated with low-pressure systems. The geese fly on the appropriate side of low-pressure systems to obtain a tail wind, thus increasing their flight speeds (Ball, 1983). It has been suggested that migratory birds may be sensitive to changes in weather patterns coinciding with the start of spring and so adjust their spring migration according to weather conditions in central and northern latitudes. Time of arrival at the breeding site could, therefore, be an indicator of spring weather conditions, and any change in arrival date occurring over a long period may be reflecting changes in those conditions (Ball, 1983).

Arrival date at Svalbard breeding sites was mainly related to PC1_{BS}. GWI, low-altitude cloud cover and head wind/tail wind had high component loading values for PC1_{BS}, whereas temperature had a lower loading. With the explanation just given above in mind regarding the relation between food and temperature, we can say PC1_{BS} corresponds to food availability at the breeding site. Moreover, it is likely that PC1_{BS} also reflects the importance of visibility for arrival date at the breeding site, since cloudiness and head winds can both be related to visibility. Cloudiness at the breeding site had a direct effect on arrival date. Moreover, we found that Svalbard geese arrived earlier at their breeding sites with increasing head winds. Since the geese are flying north, head winds (winds coming from the north) near their point of arrival make it likely that the landing site is more sheltered, with possibly better visibility.

Repeatable Interindividual and Between-Year Variation in Migration Timing

We observed interindividual and between-year variability in migration timing for the Russian barnacle geese. This could be because of a trade-off between staying longer at the last staging site to accumulate a larger body store and early arrival at the breeding site to increase the survival rate of the offspring (Prop et al., 2003). Repeatable variation in arrival dates at the breeding site has been observed for other migratory geese such as snow geese, *Anser caerulescens* (Bety et al., 2004). Migration timing of birds may have a genetic basis (Berthold, Bauer, & Westhead, 2001) as was suggested for snow geese (Bety et al., 2004). This genetic basis for migration timing may consequently also explain the inter-individual variation in migration timing for the Russian barnacle geese. Moreover, phenotypic plasticity, which is an environmentally based change in the phenotype, could also explain some of the observed variability in migration timing (Teplitsky, Mills, Alho, Yarrall, & Merilä, 2008).

Predictability

For both geese populations, the same combination of environmental parameters (i.e. the same PCs) at the last staging site were related to both departure date from this site and arrival at the breeding site. Moreover, the same PCs of the environmental parameters at the Russian breeding site that were significantly related to arrival at this site were also related to departure from the last staging site. However, this does not mean that environmental

parameters at the last staging site were indicators for the geese of conditions at their breeding site. This is especially true for Svalbard barnacle geese, since we did not find any significant relationship between the PCs of the environmental parameters at the breeding site and departure from the last staging site. In fact, having the same combination of environmental parameters at the last staging or breeding site relating to date of departure or arrival might be linked to the high correlation between arrival date at the breeding site and departure date from the last staging site for the Russian ($r_{24} = 0.69$, $P < 0.001$) and Svalbard ($r_{17} = 0.87$, $P < 0.001$) populations. Moreover, we did not find a significant relationship between environmental parameters at the last staging sites and breeding sites on both flyways. Tombre et al. (2008) found that successive sites on the Svalbard flyway were not climatically linked, so barnacle geese could not use conditions at one site to predict conditions they might encounter at the next. Moreover, Hahn, Loonen, and Klaassen (2011) have indicated that climatic conditions on Svalbard breeding sites were not predictable from climatic conditions on Norwegian staging sites. They found no correlation between temperature and snow conditions on the departure date of pink-footed geese in May from their mid-Norwegian staging site and conditions actually occurring (in May) on Svalbard breeding sites. They only found a weak correlation between temperature in May on northern Norwegian staging sites and temperature and snow conditions on breeding sites in the Svalbard archipelago. Nevertheless, Kölzsch et al. (2015) believed that individual barnacle geese are able to predict foraging conditions at subsequent staging sites since the dates of spring onset were correlated between consecutive sites.

Lower predictability between the last staging and breeding sites may cause barnacle geese to rely more on time-related cues such as daylength and departure on a fixed date, as suggested by Van der Graaf (2006). Therefore, with climate change and an earlier onset of spring (IPCC, 2007), geese may arrive later at the breeding site with respect to the start of spring there. This could lead to an increase in nesting success due to a longer frost- and snow-free season on the Arctic breeding site (Jensen, Madsen, Johnson, & Tamstorf, 2014; Madsen et al., 2007). On the other hand, the advancement of the growth of forage plants, due to earlier melting of snow, may lead to a mismatch between the gosling's time of hatching and the time of peak plant nutrient content. This could ultimately impact the growth and survival of goslings because they have to ingest feed of lower quality (Gauthier et al., 2013).

Conclusion

Our results showed that the environmental parameters at the last stage of migration have a considerable correlation with arrival date at the breeding site. More knowledge about the parameters and decision rules used by birds during migration is essential to be able to predict the consequences of environmental changes for them (Bauer et al., 2011). Since migratory birds depend on forage of high nutritional quality, they have to follow the advancement of plant phenology. An inappropriate arrival date at the breeding site can be disadvantageous for Arctic-breeding geese (Brown & Brown, 2000; Madsen et al., 2007). Barnacle geese may benefit from using the local environmental conditions to adjust their migration timing; however, they may not be able to predict the situation at their destination from their last staging site. We found weather parameters to have a significant impact on migration timing. For instance, earlier departure from the last staging site or earlier arrival at the breeding site were related to lower cloudiness and therefore higher visibility along the flyway. Some weather parameters could also indirectly be related to migration timing, such as high temperatures and high barometric pressures, which are associated with clear skies.

We observed some differences between the Russian and Svalbard flyways with respect to the effect of environmental parameters on migration timing. For instance, food availability was not an important parameter for departure date from the last staging site for the Russian barnacle geese, whereas it was for the Svalbard geese. The latter, which fly over large stretches of sea, do not have the opportunity to feed, drink or rest as the Russian geese flying over land do. Moreover, the distance between the last staging site and breeding sites is different for each population, which may have an effect on which environmental parameters are used as cues for departure.

Besides environmental parameters such as daylength, weather and food, the physical condition (body fat) of the geese may be an endogenous parameter affecting migration timing. Differences in physical condition may influence arrival date and reproductive success of migratory birds (Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004). Schaub, Jenni, and Bairlein (2008) have shown that some individual birds that put on fat at a higher rate leave their current site earlier than others. However, we had no access to this information and could not incorporate this parameter into our analysis. Integrating environmental parameters (food, weather and daylength) with energy cues could be used to build an optimal migration model so as to be able to more accurately predict migration timing of avian herbivores.

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References

- Åkesson, S., & Bäckman, J. (1999). Orientation in pied flycatchers: The relative importance of magnetic and visual information at dusk. *Animal Behaviour*, 57(4), 819–828.
- ARGOS/CLS. (2011). *Argos user's manual*. <http://www.grouptechnologies.com.au/downloads/apex/apex-argos-mk2-user-manual.pdf>.
- Atzberger, C., Richter, K., Vuolo, F., Darvishzadeh, R. and Schlerf, M. (2011) Why confining to vegetation indices? Exploiting the potential of improved spectral observations using radiative transfer models. In: Proceedings of Remote Sensing for Agriculture, Ecosystems, and Hydrology XIII, 19-21 September 2011, Prague, Czech Republic / ed. by C.M.U. Neale and A. Maltese. Washington: SPIE, 2011. (Proceedings of SPIE; 8174) Article no. 81740Q-1, 16 p.
- Bairlein, F. (2008). The mysteries of bird migration—Still much to be learnt. *British Birds*, 101(2), 68.
- Ball, T. (1983). The migration of geese as an indicator of climate change in the southern Hudson Bay region between 1715 and 1851. *Climatic Change*, 5(1), 85–93.
- Bates, D., Eigen, C., & Rcpp, L. (2014). *Package 'lme4'*. <https://cran.r-project.org/package=lme4>.
- Bauer, S., Gienapp, P., & Madsen, J. (2008). The relevance of environmental conditions for departure decision changes en route in migrating geese. *Ecology*, 89(7), 1953–1960.
- Bauer, S., Madsen, J., & Klaassen, M. (2006). Intake rates, stochasticity, or onset of spring: What aspects of food availability affect spring migration patterns in Pink-footed Geese *Anser brachyrhynchus*? *Ardea*, 94(3), 555–566.
- Bauer, S., Nolet, B. N., Giske, J., Chapman, J. W., Åkesson, S., Hedenström, A., et al. (2011). Cues and decision rules in animal migration. In E. J. Milner-Gulland, J. M. Fryxell, & A. R. E. Sinclair (Eds.), *Animal migration—A synthesis* (pp. 68–87). Oxford, U.K.: Oxford University Press.
- Beck, P. S. A., Wang, T. J., Skidmore, A. K., & Liu, X. H. (2008). Displaying remotely sensed vegetation dynamics along natural gradients for ecological studies. *International Journal of Remote Sensing*, 29(14), 4277–4283.
- Berberan-Santos, M. N., Bodunov, E. N., & Pogliani, L. (1997). On the barometric formula. *American Journal of Physics*, 65(5), 404–412.
- Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich*, 70(1), 1–11.
- Berthold, P., Bauer, H.-G., & Westhead, V. (2001). *Bird migration: A general survey* (Vol. 12). Oxford, U.K.: Oxford University Press.
- Berthold, P., Gwinner, E., & Sonnenschein, E. (Eds.). (2003). *Avian migration*. Berlin, Germany: Springer.
- Bety, J., Giroux, J. F., & Gauthier, G. (2004). Individual variation in timing of migration: Causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology*, 57(1), 1–8.
- Black, J. M., Prop, J., & Larsson, K. (2007). *Wild goose dilemmas*. Groningen, The Netherlands: Branta Press.
- Brown, C. R., & Brown, M. B. (2000). Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behavioral Ecology and Sociobiology*, 47(5), 339–345.
- De la Cueva, H., & Blake, R. (1993). Mechanics and energetics of ground effect in flapping flight. *Contemporary Mathematics*, 141, 421–442.
- De Lucia, F. C., & Gottfried, J. L. (2011). Influence of variable selection on partial least squares discriminant analysis models for explosive residue classification. *Spectrochimica Acta Part B: Atomic Spectroscopy*, 66(2), 122–128.
- Dierschke, V., & Delingat, J. (2001). Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. *Behavioral Ecology and Sociobiology*, 50(6), 535–545.
- Doiron, M., Legagneux, P., Gauthier, G., & Levesque, E. (2013). Broad-scale satellite Normalized Difference Vegetation Index data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation. *Applied Vegetation Science*, 16(2), 343–351.
- Duriez, O., Bauer, S., Destin, A., Madsen, J., Nolet, B. A., Stillman, R. A., et al. (2009). What decision rules might pink-footed geese use to depart on migration? An individual-based model. *Behavioral Ecology*, 20(3), 560–569.
- Eichhorn, G., Afanasyev, V., Drent, R. H., & van der Jeugd, H. P. (2006). Spring stopover routines in Russian Barnacle Geese *Branta leucopsis* tracked by resightings and geolocation. *Ardea*, 94(3), 667–678.
- Eichhorn, G., Drent, R. H., Stahl, J., Leito, A., & Alerstam, T. (2009). Skipping the Baltic: The emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *Journal of Animal Ecology*, 78(1), 63–72.
- Ens, B. J., Bairlein, F., Camphuysen, C. J., de Boer, R., Exo, K. M., Gallego, N., et al. (2008). *Tracking of individual birds*. Report on WP 3230 (bird tracking sensor characterization) and WP 4130 (sensor adaptation and calibration for bird tracking system) of the FlySafe basic activities project: SOVON-onderzoeksrapport 2008/10.SOVON Vogelonderzoek Nederland, Beek-Ubbergen, The Netherlands.
- EPA. (2000). *Meteorological monitoring guidance for regulatory modeling applications*. Washington D.C.: Environmental Protection Agency.
- Erni, B., Liechti, F., & Bruderer, B. (2005). The role of wind in passerine autumn migration between Europe and Africa. *Behavioral Ecology*, 16(4), 732–740.
- Finn, J., Carlsson, J., Kelly, T., & Davenport, J. (2012). Avoidance of head winds or exploitation of ground effect—Why do birds fly low? *Journal of Field Ornithology*, 83(2), 192–202.
- Fox, 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(3), 691.
- Ganter, B., Larsson, K., Syroechkovsky, E. V., Litvin, K. E., Leito, A., & Madsen, J. (1999). Barnacle geese *Branta leucopsis*: Russia/Baltic. In J. Madsen, G. Cracknell, & T. Fox (Eds.), *Goose populations of the western palearctic: A review of status and distribution*. Rond, Denmark: National Environmental Research Institute.
- Gauthier, G., Bety, J., Cadieux, M.-C., Legagneux, P., Doiron, M., Chevallier, C., et al. (2013). Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 368(1624), 20120482.
- Gauthier, G., Bety, J., & Hobson, K. A. (2003). Are greater snow geese capital breeders? New evidence from a stable-isotope model. *Ecology*, 84(12), 3250–3264.

- Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, 35(1), 37.
- Green, M., Alerstam, T., Clausen, P., Drent, R., & Ebbinge, B. S. (2002). Dark-bellied Brent Geese *Branta bernicla bernicla*, as recorded by satellite telemetry, do not minimize flight distance during spring migration. *Ibis*, 144(1), 106–121.
- Griffin, L. R. (2008). Identifying the pre-breeding areas of the Svalbard Barnacle Goose *Branta leucopsis* between mainland Norway and Svalbard: An application of GPS satellite-tracking techniques. *Vogelwelt*, 129, 226–232.
- Gullestad, N., Owen, M., & Nugent, M. (1984). Numbers and distribution of barnacle geese *Branta leucopsis* on Norwegian staging islands and the importance of the staging area to the Svalbard population. *Norsk Polarinstittutt Skrifter*, 181, 57–65.
- Gwinner, E. (2012). *Bird migration: Physiology and ecophysiology*. Berlin, Germany: Springer Science & Business Media.
- Hahn, S., Loonen, M. J., & Klaassen, M. (2011). The reliance on distant resources for egg formation in high Arctic breeding barnacle geese *Branta leucopsis*. *Journal of Avian Biology*, 42(2), 159–168.
- Hord, C. (2011). *Report of the ad-hoc working group on the calculation of cross-wind and tail wind components with particular regard to the inclusion of gusts*. Paper presented at the Aerodrome Meteorological Observation and Forecast Study Group (AMOFSG), Montréal.
- Hübner, C. E. (2006). The importance of pre-breeding areas for the Arctic Barnacle Goose *Branta leucopsis*. *Ardea*, 94(3), 701–713.
- Hübner, C. E., Tombre, I. M., Griffin, L. R., Loonen, M., Shimmings, P., & Jonsdottir, I. S. (2010). The connectivity of spring stopover sites for geese heading to arctic breeding grounds. *Ardea*, 98(2), 145–154.
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83(1–2), 195–213.
- Hume, R. (1986). Reactions of birds to heavy rain. *British Birds*, 79, 326–329.
- IPCC. (2007). *Climate change 2007: Synthesis report. Contribution of Working Groups I, II and III to 534 the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland.
- Jenni, L., & Schaub, M. (2003). Behavioural and physiological reactions to environmental variation in bird migration: a review. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian migration* (pp. 155–171). Berlin, Germany: Springer.
- Jensen, G. H., Madsen, J., Johnson, F. A., & Tamstorf, M. P. (2014). Snow conditions as an estimator of the breeding output in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology*, 37(1), 1–14.
- Kaiser, D. P. (2000). Decreasing cloudiness over China: An updated analysis examining additional variables. *Geophysical Research Letters*, 27(15), 2193–2196.
- Kirk, J. (1994). *Light and photosynthesis in aquatic ecosystems*. London, U.K.: Cambridge University Press.
- Kölzsch, A., Müskens, G., Kruckenberg, H., Glazov, P., Weinzierl, R., Nolet, B., et al. (2016). Towards a new understanding of migration timing: Slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. *Oikos*. Vol. in press. ISSN 1600-0706.
- Kostin, I. O., & Mooij, J. H. (1995). Influence of weather conditions and other factors on the reproductive cycle of red-breasted geese *Branta ruficollis* on the Taymyr Peninsula. *Wildfowl*, 46(46), 45–54.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2014). *Package 'lmerTest'*. <https://cran.r-project.org/package=lmerTest>.
- Lessells, C., & Boag, P. T. (1987). Unrepeatable repeatabilities: A common mistake. *Auk*, 104, 116–121.
- Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, 147(2), 202–211.
- Lofts, B., & Murton, R. K. (1968). Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *Journal of Zoology*, 155(3), 327–394.
- Madsen, J. (2001). Spring migration strategies in Pink-footed Geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. *Ardea*, 89(1), 43–55.
- Madsen, J., Cracknell, G., & Fox, T. (1999). *Goose populations of the Western Palearctic: A review of status and distribution*. Ronde: National Environmental Research Institute.
- Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Riget, F., et al. (2007). Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biology*, 30(11), 1363–1372.
- Mathworks. (2013). *Matlab, the language of technical computing*. Natick, MA: Mathworks, Inc.
- McGarigal, K., Cushman, S., & Stafford, S. (2000). *Multivariate statistics for wildlife and ecology research*. New York: Springer.
- McNamara, J. M., Barta, Z., Klaassen, M., & Bauer, S. (2011). Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, 14(12), 1183–1190.
- Microwave Telemetry. (2007). *Argos/GPS PTT-100 field manual*. Columbia, MD: Microwave Telemetry, Inc.
- Murphy-Klassen, H. M., Underwood, T. J., Sealy, S. G., Czyrnyj, A. A., & Holberton, R. (2005). Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba, in relation to climate change. *Auk*, 122(4), 1130–1148.
- Newton, L. (2008). *The migration ecology of birds*. London, U.K.: Academic Press.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W., & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 271(1534), 59–64.
- Owen, M. (1980). *Wild geese of the world*. London, U.K.: B. T. Batsford Ltd.
- Prop, J., & Black, J. M. (1998). Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. *Skrifter-Norsk Polarinstittutt*, 175–194.
- Prop, J., Black, J. M., & Shimmings, P. (2003). Travel schedules to the high arctic: Barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, 103(2), 403–414.
- Prop, J., & de Vries, J. (1993). Impact of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis*. *Ornis Scandinavica*, 24, 110–121.
- Pulido, F. (2007). Phenotypic changes in spring arrival: Evolution, phenotypic plasticity, effects of weather and condition. *Climate Research*, 35(1–2), 5–23.
- Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. New York: Cambridge University Press.
- R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Richardson, W. (1990). Timing of bird migration in relation to weather: updated review. In E. Gwinner (Ed.), *Bird migration* (pp. 78–101). Berlin, Germany: Springer.
- Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., et al. (2013). Flying with the wind: Scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecology*, 1(4), 10.1186.
- Schaub, M., Jenni, L., & Bairlein, F. (2008). Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behavioral Ecology*, 19(3), 657–666.
- Shariatinajafabadi, M., Wang, T., Skidmore, A. K., Toxopeus, A. G., Kölzsch, A., Nolet, B. A., et al. (2014). Migratory herbivorous waterfowl track satellite-derived green wave index. *PLoS One*, 9(9), e108331.
- Shariati Najafabadi, M., Darvishzadeh, R., Skidmore, A. K., Kölzsch, A., Vrieling, A., Nolet, B. A., et al. (2015). Satellite- versus temperature-derived green wave indices for predicting the timing of spring migration of avian herbivores. *Ecological Indicators*, 58(0), 322–331.
- Smith, T., III, & Hayden, B. (1984). Snow goose migration phenology is related to extratropical storm climate. *International Journal of Biometeorology*, 28(3), 225–233.
- Tabachnick, B. G., & Fidell, L. S. (2001). *Using multivariate statistics*. New York: Harper and Row.
- Teplitsky, C., Mills, J. A., Alho, J. S., Yarrall, J. W., & Merilä, J. (2008). Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences of the United States of America*, 105(36), 13492–13496.
- Tombre, I. M., Høgda, K. A., Madsen, J., Griffin, L. R., Kuijken, E., Shimmings, P., et al. (2008). The onset of spring and timing of migration in two Arctic nesting goose populations: The pink-footed goose *Anser brachyrhynchus* and the barnacle goose *Branta leucopsis*. *Journal of Avian Biology*, 39(6), 691–703.
- Van der Graaf, A. J. (2006). *Geese on a green wave: Flexible migrants in a changing world* (Doctoral thesis). Groningen, The Netherlands: University of Groningen.
- Van der Graaf, A. J., Stahl, J., Klimkowska, A., Bakker, J. P., & Drent, R. H. (2006). Surfing on a green wave – How plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *Ardea*, 94(3), 565–577.
- Van Der Jeugd, H. P., Eichhorn, G., Litvin, K. E., Stahl, J., Larsson, K., Van Der Graaf, A. J., et al. (2009). Keeping up with early springs: Rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology*, 15(5), 1057–1071.
- Van Wijk, R. E., Kölzsch, A., Kruckenberg, H., Ebbinge, B. S., Muskens, G., & Nolet, B. A. (2012). Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos*, 121(5), 655–664.
- Wege, M. L., & Raveling, D. G. (1983). Factors influencing the timing, distance, and path of migrations of Canada geese. *Wilson Bulletin*, 95(2), 209–221.
- Wege, M. L., & Raveling, D. G. (1984). Flight speed and directional responses to wind by migrating Canada geese. *Auk*, 101, 342–348.
- Žalakevičius, M. (2000). *Global climate change, bird migration and bird strike problems*. Paper presented at the 25th IBSC meeting, Amsterdam.
- Žalakevičius, M. (2002). Biophysical impacts of climate change on bird populations and migration in Lithuania. *Geographical Journal*, 57(3), 191–201.
- Žalakevičius, M., Švažas, S., Stanevičius, V., & Vaitkus, G. (1995). Monograph: Bird migration & wintering in Lithuania. *Acta Zoologica Lituanica*, 2(1), 252.

Appendix

Table A1

Tag ID, year of tracking, last staging site, departure date from the last staging site, breeding site, arrival date at the breeding site and the number of received positions from the last staging to breeding site for the tracked barnacle geese from the Russian population

Bird ID	Tracking year	Last staging site	Departure from last staging site	Breeding site	Arrival at breeding site	No. of received positions from last staging to breeding site
78041	2008	Kanin Peninsula	7 Jun 2008	Novaya Zemlya	12 Jun 2008	7
78043	2008	Kanin Peninsula	7 Jun 2008	Kulgoyev Is.	11 Jun 2008	3
78044	2008	Kanin Peninsula	5 Jun 2008	Vaygach Is.	19 Jun 2008	6
78045	2008	Kanin Peninsula	10 Jun 2008	Novaya Zemlya	14 Jun 2008	5
78046	2008	Kanin Peninsula	6 Jun 2008	Kulgoyev Is.	7 Jun 2008	3
78047	2008	White Sea	3 Jun 2008	Novaya Zemlya	14 Jun 2008	10
78033	2009	White Sea	26 May 2009	Kanin Peninsula	28 May 2009	3
78034	2009	Kanin Peninsula	8 Jun 2009	Kulgoyev Is.	9 Jun 2009	5
78035	2009	Baltic Sea	19 May 2009	Kanin Peninsula	4 Jun 2009	9
78036	2009	Kanin Peninsula	7 Jun 2009	Novaya Zemlya	10 Jun 2009	8
78037	2009	White Sea	25 May 2009	Tobseda	6 Jun 2009	6
78039	2009	Kanin Peninsula	8 Jun 2009	Kulgoyev Is.	9 Jun 2009	4
78041	2009	Kanin Peninsula	8 Jun 2009	Novaya Zemlya	10 Jun 2009	4
78043	2009	White Sea	29 May 2009	Kulgoyev Is.	6 Jun 2009	4
78044	2009	Kanin Peninsula	26 May 2009	Vaygach Is.	11 Jun 2009	5
78046	2009	Kanin Peninsula	2 Jun 2009	Kulgoyev Is.	3 Jun 2009	3
78047	2009	White Sea	31 May 2009	Novaya Zemlya	6 Jun 2009	4
78033	2010	White Sea	28 May 2010	Kanin Peninsula	30 May 2010	5
78034	2010	Kanin Peninsula	3 Jun 2010	Kulgoyev Is.	4 Jun 2010	3
78035	2010	Baltic Sea	21 May 2010	Kanin Peninsula	24 May 2010	10
78036	2010	White Sea	30 May 2010	Novaya Zemlya	4 Jun 2010	9
78039	2010	Kanin Peninsula	2 Jun 2010	Kulgoyev Is.	3 Jun 2010	3
78041	2010	Kanin Peninsula	5 Jun 2010	Novaya Zemlya	8 Jun 2010	6
78043	2010	White Sea	29 May 2010	Kulgoyev Is.	30 May 2010	5
78044	2010	White Sea	29 May 2010	Vaygach Is.	3 Jun 2010	9
78047	2010	Kanin Peninsula	11 Jun 2010	Novaya Zemlya	12 Jun 2010	4

Table A2

Tag ID, year of tracking, last staging site, departure date from the last staging site, breeding site, arrival date at the breeding site and the number of received positions from the last staging to breeding site for the tracked barnacle geese from the Svalbard population

Bird ID	Tracking year	Last staging site	Departure from last staging site	Breeding site	Arrival at breeding site	No. of received positions from last staging to breeding site
64685	2006	Helgeland	18 May 2006	Spitsbergen	20 May 2006	14
64687	2006	Helgeland	18 May 2006	Spitsbergen	26 May 2006	15
64687	2007	Helgeland	18 May 2007	Spitsbergen	1 Jun 2007	20
70564	2007	Helgeland	25 May 2007	Spitsbergen	28 May 2007	16
70565	2007	Helgeland	14 May 2007	Spitsbergen	24 May 2007	18
70566	2007	Helgeland	25 May 2007	Spitsbergen	27 May 2007	16
70567	2007	Helgeland	18 May 2007	Spitsbergen	12 Jun 2007	20
70618	2007	Helgeland	17 May 2007	Spitsbergen	19 May 2007	12
70619	2007	Helgeland	17 May 2007	Spitsbergen	19 May 2007	14
170563	2007	Helgeland	17 May 2007	Spitsbergen	22 May 2007	16
78198	2008	Vesterålen	28 Jun 2008	Edgeøya	13 July 2008	10
78378	2008	Vesterålen	15 May 2008	Spitsbergen	15 May 2008	10
178199	2008	Vesterålen	19 May 2008	Spitsbergen	1 Jun 2008	12
78378	2009	Vesterålen	18 May 2009	Spitsbergen	20 May 2009	11
86824	2009	Helgeland	14 May 2009	Spitsbergen	19 May 2009	28
86828	2009	Helgeland	15 May 2009	Spitsbergen	20 May 2009	22
186827	2009	Helgeland	16 May 2009	Spitsbergen	16 May 2009	22
33953	2010	Helgeland	1 Jun 2010	Spitsbergen	2 Jun 2010	11
33954	2010	Helgeland	27 May 2010	Spitsbergen	4 Jun 2010	27

Table A3

The repeatability in arrival/departure date between different individuals and tracking year for the Russian barnacle geese

Population	Model	Random effect	Repeatability (%)
Russian barnacle geese	Departure from last staging site based on the PCs of the environmental parameters at the last staging site	ID	35
		Year	13
	Departure from last staging site based on the PCs of the environmental parameters at the breeding site	ID	31
		Year	24
	Arrival at the breeding site based on the PCs of the environmental parameters at the last staging site	ID	26
		Year	53
	Arrival at the breeding site based on the PCs of the environmental parameters en route	ID	12
		Year	52
	Arrival at the breeding site based on the PCs of the environmental parameters at the breeding site	ID	0
		Year	49

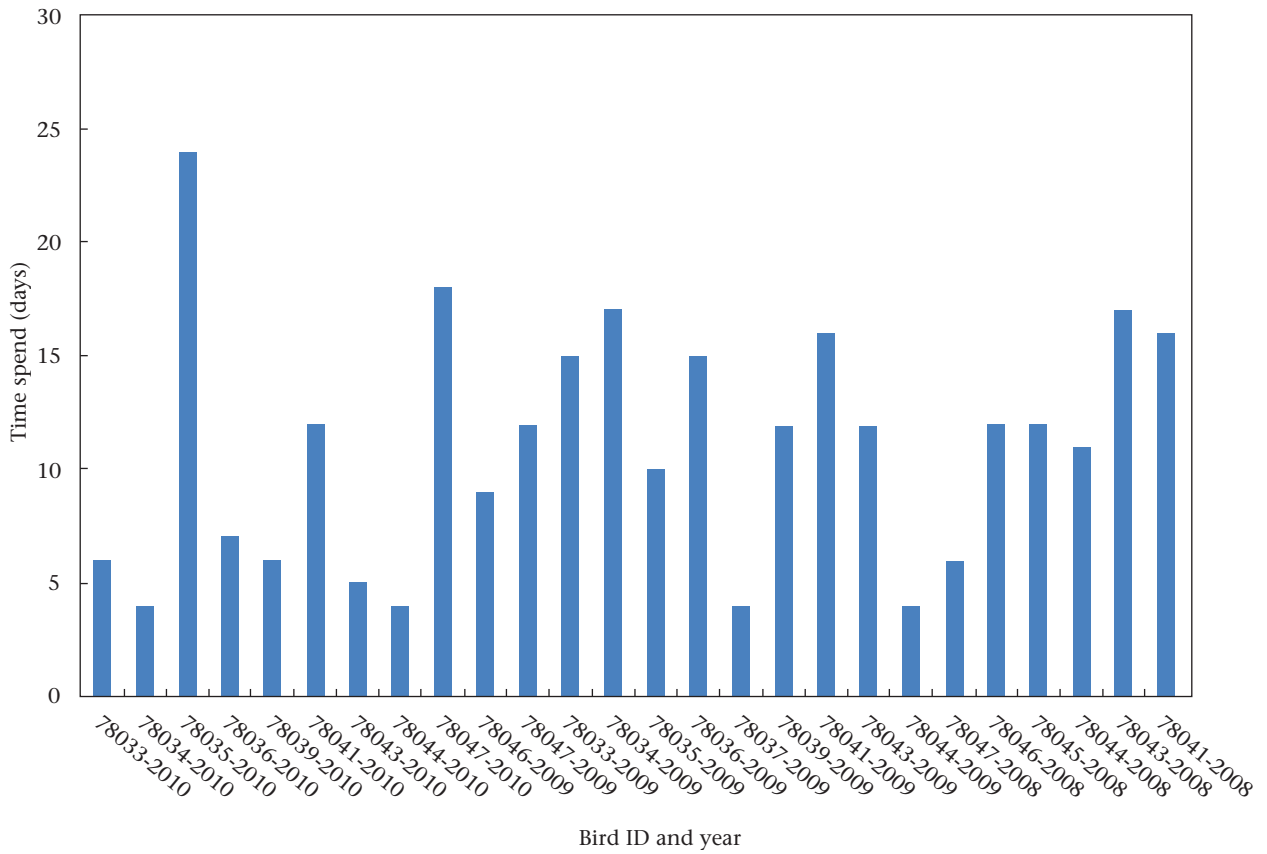


Figure A1. Duration of stay at the last staging site for 12 Russian barnacle geese from 2008 to 2010.

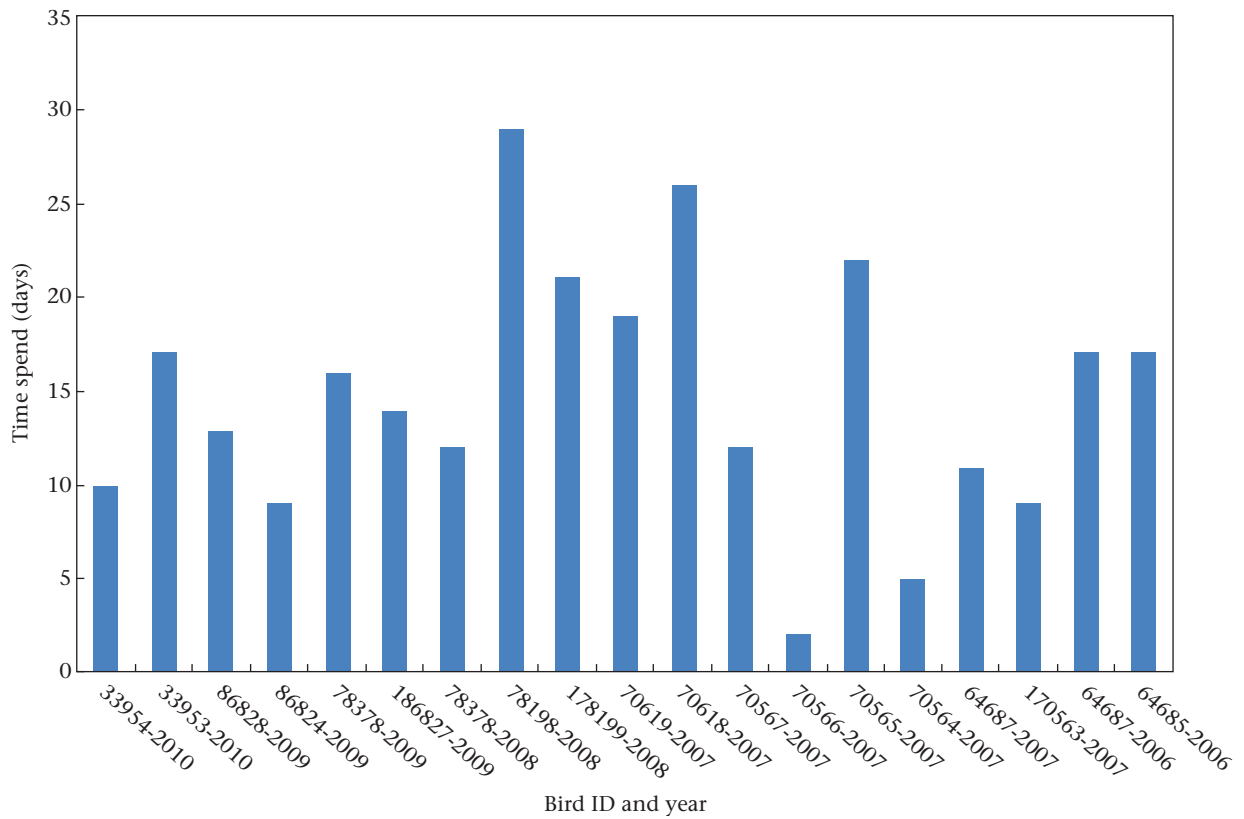


Figure A2. Duration of stay at the last staging site for 17 Svalbard barnacle geese from 2006 to 2010.