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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, & Ebbinge, 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