Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore

Andrea Kölzsch[1,2,3*], Silke Bauer[1,4], Rob de Boer[1], Larry Griffin[5], David Cabot[6], Klaus-Michael Exo[7], Henk P. van der Jeugd[1,8] and Bart A. Nolet[1,2]

[1]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), 6708 PB Wageningen, The Netherlands; [2]Project Group Movement Ecology, Netherlands Institute of Ecology (NIOO-KNAW), 6708 PB Wageningen, The Netherlands; [3]Department of Migration and Immuno-Ecology, Max Planck Institute for Ornithology, 78315 Radolfzell, Germany; [4]Department of Bird Migration, Swiss Ornithological Institute, 6204 Sempach, Switzerland; [5]WWT Caerlaverock Wetland Centre Eastpark Farm, Dumfries DG1 4RJ, UK; [6]Environmental Consultancy Services, Carrigskeewaun, Carrowniskey, Westport, Co. Mayo Ireland; [7]Institute of Avian Research "Vogelwarte Helgoland", 26386 Wilhelmshaven, Germany; and [8]Vogeltrekstation – Dutch Centre for Avian Migration and Demography (NIOO-KNAW), 6708 PB Wageningen, The Netherlands

Summary

1. Herbivorous birds are hypothesized to migrate in spring along a seasonal gradient of plant profitability towards their breeding grounds (*green wave hypothesis*). For Arctic breeding species in particular, following highly profitable food is important, so that they can replenish resources along the way and arrive in optimal body condition to start breeding early.

2. We compared the timing of migratory movements of Arctic breeding geese on different flyways to examine whether flyways differed in the predictability of spring conditions at stopovers and whether this was reflected in the degree to which birds were following the green wave.

3. Barnacle geese (*Branta leucopsis*) were tracked with solar GPS/ARGOS PTTs from their wintering grounds to breeding sites in Greenland ($N = 7$), Svalbard ($N = 21$) and the Barents Sea ($N = 12$). The numerous stopover sites of all birds were combined into a set of 16 general stopover regions.

4. The predictability of climatic conditions along the flyways was calculated as the correlation and slope between onsets of spring at consecutive stopovers. These values differed between sites, mainly because of the presence or absence of ecological barriers. Goose arrival at stopovers was more closely tied to the local onset of spring when predictability was higher and when geese attempted breeding that year.

5. All birds arrived at early stopovers after the onset of spring and arrived at the breeding grounds before the onset of spring, thus overtaking the green wave. This is in accordance with patterns expected for capital breeders: first, they must come into condition; at intermediate stopovers, arrival with the food quality peak is important to stay in condition, and at the breeding grounds, early arrival is favoured so that hatching of young can coincide with the peak of food quality.

6. Our results suggest that a chain of correlations between climatic conditions at subsequent stopovers enables geese to closely track the green wave. However, the birds' precision of migratory timing seems uninfluenced by ecological barriers, indicating partly fixed migration schedules. These might become non-optimal due to climate warming and preclude accurate timing of long-distance migrants in the future.

Key-words: barnacle goose, *Branta leucopsis*, capital breeding, climatic barrier, GDD jerk, green wave hypothesis, migration flyway, onset of spring

Introduction

Many animal species migrate between a breeding site and an overwintering region in response to seasonal changes. As migrants often cover large distances during their travels, much energy is needed to successfully reach their destination. Hence timing and space use during migration are crucial for survival and reproduction (Drent *et al.* 2003; Sherrill-Mix, James & Myers 2008). This particularly holds true for spring migration, where the timing of arrival and body condition on arrival at the breeding sites are major correlates of fitness (Prop, Black & Shimmings 2003; Drent *et al.* 2006). However, both timing of arrival and arrival body condition are highly dependent upon migration speed and the circumstances experienced during migration, which are mainly determined by conditions at intermediate stopover sites (Nolet & Drent 1998; Holdo, Holt & Fryxell 2009). Most migratory animals, and in particular those using active movement (e.g. flapping flight in birds), use several stopover sites along their routes to replenish body stores in preparation for the next migratory leg (Hedenström & Alerstam 1997).

Ideally, migrants time their arrival at stopover sites such that local conditions facilitate swift and safe refuelling, and thus, a timely migratory progression (Drent *et al.* 2003; Alerstam 2011). Recently, several species of migratory animals (including birds, reptiles and mammals) have indeed been shown to tightly follow the seasonal development of resources along their migration route, that is the 'green wave', and thus, match their timing of stopovers with local peak food availability at stopover sites (Drent & Daan 1980; Van Der Graaf *et al.* 2006; Mueller *et al.* 2008; Sherrill-Mix, James & Myers 2008; van Wijk *et al.* 2012; Schindler *et al.* 2013). However, how animals accomplish such accurate timing remains largely unknown. Although we know that migratory animals use cues for the timing of migration, the identity of most cues remains elusive (Bauer *et al.* 2011). Moreover, it is unclear whether relationships exist between potential environmental variables at successive sites that migrants could use, informing and supporting their staging and departure decisions. Depending on species-specific requirements (Piersma 1987), potential stopover sites can be distant from one another and sometimes separated by 'ecological barriers' such as oceans, deserts or mountain ranges.

Several environmental factors could be used as timing cues by migrating animals. Photoperiod, temperature, wind, precipitation patterns and food depletion have been shown to be related to departure decisions of migrants (Alerstam 2011; Bauer *et al.* 2011). Furthermore, spring arrival times of different bird species in Europe were correlated with the North Atlantic Oscillation (NAO) (Hüppop & Hüppop 2003). Possible relationships between such cues in different regions are, however, rarely analysed in combination with migration. On a rather large scale, it has been shown that temperature anomalies of the Eastern Sahel (Africa) and northern Europe were strongly correlated and linked to the timing of migration of trans-Saharan migratory birds at a population level (Saino & Ambrosini 2008). This gives first insights, but might not be of sufficient resolution for understanding effects on individual migration timing.

In this paper, we attempt to develop an understanding of the environmental information potentially available to migrant geese. First, we analysed three distinct flyways of an Arctic breeding, long-distance migrant, the barnacle goose (*Branta leucopsis*) with regard to the predictability of meteorological conditions at successive stopover sites. It has been shown that meteorological conditions such as temperature sums (Van Eerden *et al.* 2005) are related to the growth of early-spring nutrient-rich vegetation (i.e. onset of spring), which is an important resource for migrating geese. Here, we tested whether a novel measure of onset of spring (van Wijk *et al.* 2012) is correlated across successive stopover sites.

Secondly, we examined whether the timing of goose migration is related to the predictability of the onset of spring at these sites. We analysed individual tracking data for barnacle geese migrating along the three flyways and related them to the onset of spring at all stopover sites along these geographically distinct routes in different years and to the predictability of meteorological conditions and thus vegetation growth. As distances and landscapes between different pairs of consecutive stopovers vary widely, we can draw general conclusions about the ability of barnacle geese to optimally time their spring migration in relation to spring phenology under a variety of circumstances. It is expected that geese will time their stopover arrival at a subsequent site closer to the local onset of spring if predictability of conditions based on environmental information available at the previous stopover is higher.

Materials and methods

GPS TRACKING DATA

Barnacle geese from three geographically distinct breeding populations – Greenland, Svalbard and the Barents Sea – were caught in their wintering regions and equipped with solar GPS/ARGOS PTTs (30 g or 45 g, Microwave Telemetry Inc., Columbia, MD, USA), attached with harnesses. The geese from these populations were wintering in Ireland, Scotland and the Netherlands, respectively. From 40 individuals (including 7 from Greenland, 21 from Svalbard and 12 from the Barents Sea), we received data for one complete spring migration, with typically 3–7 GPS fixes per day. The tracks were recorded in the years 2006–2011 (Greenland: 4 × 2008, 1 × 2009, 2 × 2010; Svalbard: 2 × 2006, 7 × 2007, 3 × 2008, 3 × 2009, 2 × 2010, 4 × 2011; Barents Sea: 6 × 2008, 6 × 2009). For the Greenland and Svalbard populations, only adult males were tagged, whereas adult females were selected for tagging from the Barents Sea population. These data sets nevertheless yield comparable results, because barnacle geese are monogamous and partners travel together (Prop, Black & Shimmings 2003).

STOPOVER REGIONS

For each GPS track, we determined stopover and breeding sites. Stopover sites were defined as sites where the bird stayed within a radius of 30 km for longer than 48 h, allowing for maximally one outlier position (van Wijk *et al.* 2012). The first stopover site was often close to the wintering area, that is, the geese fuelled there to fatten up for migration. We determined initial stopover sites based on a habitat switch from intensive pastures to high-quality saltmarsh vegetation coupled with less movement prior to migration. However, many birds in our data set were caught and tagged too late to allow for correct determination of the arrival time at the initial stopover sites. Thus, initial sites were excluded from subsequent analyses of arrival time. Breeding (and moulting) sites were determined as the last stopover sites before end of June, where birds stayed within a radius of 30 km for between 7 and 26 days.

For the analyses of environmental (long-distance) predictability, we merged individual stopover sites into larger stopover regions (Fig. 1). These were geographically distinct regions where at least three individuals roosted. For each region, a representative mean position was calculated using the (circular) mean longi-

Fig. 1. Map of stopover sites (small grey dots) that were used by the tracked barnacle geese with indications of climate predictability. Large (orange) dots indicate stopover regions that were used for the climate predictability assessment. Arrows indicate predictability of onset of spring between consecutive stopover regions, using a 30-year data set (1982–2011). Line thickness indicates the phenology correlation coefficients between onset of spring anomalies, maximum line thickness is at $r = 1$. Red, dashed lines indicate negative correlations, line thickness then relates to $-r$. Line colours or greyscale (apart from red) indicates the slope of the linear relationship between consecutive spring anomalies (proportionality index s), black indicating maximum predictability $s = 1$, levels of green/grey indicating predictabilities of $s < 1$ (lighter green/grey indicates smaller slopes), levels of blue/grey indicating predictabilities of $s > 1$ (lighter blue/grey indicates steeper slopes; here, colour intensity is related to $1/s$). For greyscale figures, note that only the arrows originating in the White Sea and Southern Greenland have $s > 1$. See Supporting Information for details of correlation coefficients and proportionality indices. Photograph in top right: a tagged barnacle goose taking off near its catch site in Scotland. Photography by K. Kirk.

tude and latitude of all sites (including all sites for the tracks that showed >1 stop in the same region). If this mean position was climatically very different from the original points ($N = 1$, glacier on Iceland), we randomly shifted it to one of the original positions. Some of the stopover regions were clearly separated by ecological barriers, such as oceans or stretches of other unsuitable landscape. For our analyses, we classified the routes going to southern Iceland, southern Greenland, southern Norway, Svalbard and the White Sea as ecological barriers.

GDD JERKS, TIMING AND PREDICTABILITY

In a previous study (van Wijk *et al.* 2012), a measure to define the onset of spring from temperature data was developed, the so-called GDD jerk, which is the third derivative of daily temperature sums (growing degree days – GDD) and can be understood as the acceleration of temperature. The current paper uses the day of peak acceleration (maximum GDD jerk) as the onset of spring. Daily temperatures were determined (data from European Climate Assessment (ECA) gridded data set and weather station data compiled by NOAA; van Wijk *et al.* 2012) for the mean position of each stopover site and region, and used to calculate the GDD jerks and determine the date of the onset of spring for each site each year. Two data sets were derived.

First, in analysing the predictability of the onset of spring between successive stopover regions, the yearly onset of spring (in Julian days) for each stopover region was calculated for the past 30 years (1982–2011) including their anomalies, that is, their deviation from the 30-year mean. A positive or negative anomaly indicates a year of relatively late or early onset of spring, respectively.

Predictability was calculated for pairs of consecutive stopover regions as (i) the phenology correlation coefficient r, which is the Pearson correlation coefficient of anomalies of onset of spring, indicating the strength of climatic relations and (ii) a proportionality index s, which is the slope of a standardized major axis (SMA) regression between the anomalies. If the proportionality index is positive and close to '1' (identity), then the onset of spring in a stopover region is perfectly proportional to, and thus predictable from, the conditions in the previous region. For positive slopes '>1', the deviation from the average onset of spring is more extreme in site $i + 1$ as compared to site i, that is, the onset of spring would be predicted too early in early years, but too late in late years. For positive slopes '<1', the opposite is true, that is, conditions at site $i + 1$ deviate less from the average than conditions at site i. If slopes are negative, the relationship is negative, that is, an early spring in one region suggests late spring in the following and vice versa. Thus, in addition to the phenology correlation coefficient, which shows the strength of climatic relationships, the proportionality index provides an estimate for the direction of predictability. For our analyses, we selected pairs of consecutive sites or pairs of sites with maximally one stopover in between, as they are biologically most relevant. To obtain an initial overview of the relationships of those predictability measures with route characteristics, we linked them to the three flyways, the presence of ecological barriers, distance between stopovers and distance to the breeding sites using linear regression.

Secondly, the onset of spring for each stopover site in all years during which geese were tracked was compared to the arrival dates of individual birds. If all birds arrived at the onset of spring in an area, then it could be assumed that they had exactly fol-

lowed the 'green wave'. We quantified deviations of arrival from to the onset of spring with the root-mean-square deviation (RMSD). Values of RMSD of <10 days indicate little deviation, 10–15 days moderate and >15 days strong deviation (Duriez *et al.* 2009). RMSD values of the main stopover regions were compared between flyways and set in relation to the phenology correlation coefficient, the proportionality index, the presence of ecological barriers, distance between sites, distance to the breeding areas and two measures of environmental variability: (i) the time interval that the GDD jerk was above 90% of its peak value, indicating how flat/peaked onset of spring was and (ii) the variability (i.e. interquartile range, shown as a boxplot) of onset of spring over the past 30 years (1982–2011), quantifying long-term variability.

Finally, we linked environmental predictability and goose behaviour by relating the deviation of goose arrival from onset of spring to the phenology correlation coefficient and proportionality index. The resulting relationships were then compared between the flyways and examined for additional links to environmental variability (onset of spring peak interval, 30-year onset of spring variability), the presence of ecological barriers, distance between stopover regions, distance to the breeding sites and breeding status, using a linear mixed model. Each goose was classified according to its (initial) breeding status as breeder or non-breeder, if (according to its GPS track) it did or did not stay within a radius of 2 km for at least 7 days in the breeding grounds, allowing for up to one outlier per day (De Boer *et al.* 2014). Thus, those geese that later failed in their breeding attempt were also classified as breeders, as we considered the start of breeding most important in relation to migration timing. We expected that birds that closely followed the green wave during spring migration were more likely to become breeders, or that birds intending to breed aimed at more closely following the onset of spring.

Results

STOPOVER REGIONS

The flyways of the three populations differed considerably not only in the distances covered but also in the geographical characteristics, varying from crossing an ocean or a longer inland stretch to mainly following the coastline (Fig. 1). Migrating *c.* 2300 km to their breeding sites on the coast of Greenland, barnacle geese wintering in Ireland stopped in southern as well as northern Iceland, and on a southern coastal region of east Greenland. Including their first stopover close to the wintering region, they stopped on average 5·3 (±0·2; SE) times at 3·9 (±0·3) stopover regions, and covered *c.* 600 (±220) km between successive regions. Birds of the Svalbard population covered c. 2600 km in total, using two stopover regions along the coast of Norway. They stopped on average 4·2 (±0·3) times at 3·0 (±0·1) successive stopover regions that were each c. 930 (±310) km apart. On the *c.* 3000-km route to their breeding sites in the Barents Sea (Kolguyev Island and Novaya Zemlya), barnacle geese from the population wintering in the Netherlands stopped on average 5·7 (±0·5) times at 4·3 (±0·4) stopover regions that were 535 (±220) km apart. Geese stopped on the

Swedish Baltic islands, the Estonian coast, the White Sea and the Kanin Peninsula, crossing the inland stretch of Karelia in between.

GDD JERKS AND PREDICTABILITY

Onsets of spring for 1982–2011 varied between stopover and breeding sites along the three flyways (see Supporting Information). On initial stopovers, spring started on average as early as 8 March (Ireland), 26 March (Scotland) and 1 April (Central Europe). Breeding sites were more similar in onsets of spring (22 June Northern Greenland, 16 June Svalbard, 20 June Novaya Zemlya). Standard deviations between the years also decreased towards the north, ranging from up to 13 days in central Europe to only 5 days in southern and northern Greenland and at the White Sea.

Phenology correlation coefficients *r* and proportionality indices *s* for pairs of stopover regions within each flyway differed depending on whether or not the sites were separated by ecological barriers (linear regression single-term deletions; *r*: residual sum of squares (RSS) = 0·66, *P* = 0·006; *s*: RSS = 0·99, *P* < 0·001; see Figs 1 and 2, Table 1a and Supporting information): there appeared to be strong correlations between closer pairs of sites and weaker correlations across larger ocean (Ireland – southern Iceland, northern Iceland – southern Greenland, Scotland – southern Norway, northern Norway – Svalbard) or inland crossings (Baltics – White Sea) in all three flyways. Furthermore, predictabilities differed by flyway (*r*: RSS = 0·76, *P* = 0·01, *s*: RSS = 0·57, *P* = 0·05) and distances between stopover
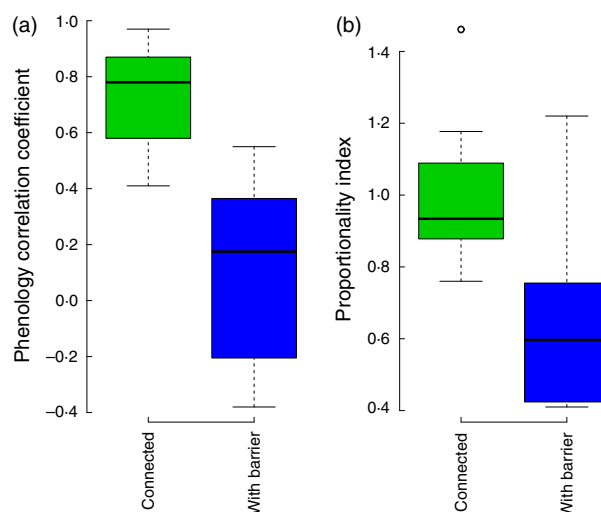

Fig. 2. Boxplots of (a) phenology correlation coefficients and (b) proportionality indices for sites that are climatically connected (green) or separated by ecological barriers (blue). Differences between the respective groups are both significant (Mann–Whitney *U*-tests, *P* = 0·002 and *P* < 0·001). Bold lines indicate the median, boxes the interquartile interval and whiskers the 5 and 95 percentiles.

Table 1. Results of linear regression and linear mixed models for (a) predictability, (b) timing of the geese in terms of RMSD, (c) variability of onset of spring and (d) timing of the geese in terms of deviation from onset of spring

Full model		Dropped variable	Random effect(s)	AIC_F	AIC_S	RSS, LR	P-value
(a)	$r \sim b + d + d_B + f$	b		−34·21	−28·69	0·66	**0·006**
		d			−36·19	0·37	0·90
		d_B			−34·84	0·41	0·24
		f			−28·98	0·76	**0·01**
	$s \sim b + d + d_B + f$	b		−34·41	−23·50	0·99	**<0·001**
		d			−28·17	0·69	**0·004**
		d_B			−34·48	0·42	0·16
		f			−32·67	0·57	0·06
(b)	$RMSD \sim r + s + b + d + d_B + v_{90} + v_{30} + f$	r		55·52	58·42	291·3	**0·03**
		s			54·16	209·8	0·43
		b			55·27	228·6	0·19
		d			53·85	204·9	0·57
		d_B			61·93	381·6	**0·004**
		v_{90}			57·24	266·0	**0·05**
		v_{30}			53·73	203·0	0·65
		f			61·05	415·7	**0·009**
(c)	$v_{90} \sim d_B + f$	d_B		41·13	60·20	840·4	**<0·001**
		f			38·92	190·8	0·41
	$v_{30} \sim d_B + f$	d_B		30·05	43·72	236·7	**<0·001**
		f			30·54	100·2	0·11
(d)	$Dev_{GDD} \sim r + s + b + d + d_B + v_{90} + v_{30} + f + BS$	r	Y, ID	730·1	728·3	0·22	0·64
		s	Y, ID		736·5	8·41	**0·004**
		b	Y, ID		729·7	1·66	0·20
		d	Y, ID		728·5	0·43	0·51
		d_B	Y, ID		729·6	1·51	0·22
		v_{90}	Y, ID		742·6	14·49	**<0·001**
		v_{30}	Y, ID		728·1	0·02	0·89
		f	Y, ID		741·7	15·65	**<0·001**
		BS	Y, ID		735·3	7·22	**0·007**

Variables are indicated as: r – phenology correlation coefficient, s – proportionality index, b – ecological barrier, d – distance between sites, d_B – distance to breeding grounds, v_{90} – width of 90% peak of onset of spring, v_{30} – variability of onset of spring during 30 years, RMSD – root mean square deviation, Dev_{GDD} – deviation from onset of spring, BS – breeding status, ID – individual goose, Y – year of included goose track, f – flyway. Reported values are results of single-term deletions, AIC_F are the Akaike Information Criteria of the full model, AIC_S those of the model with the selected variable dropped. Higher AIC values indicate variables that should be kept in the model. For linear regressions, residual sums of squares (RSS) are reported, for the linear mixed model (d), find likelihood ratios (LR). P-values are of χ^2-tests. Significant results are marked in bold.

sites were related to the proportionality index (RSS = 0·69, P = 0·004), but not the phenology correlation coefficient. Thus, distance between sites seems to be linked to the direction of predictability rather than the strength of the correlations.

On the Greenland route, the onsets of spring (phenology) were strongly correlated between pairs of sites involving land crossings, that is southern and northern Iceland (r = 0·85), and southern and northern Greenland (r = 0·50), with proportionality indices close to '1' (i.e. high predictability; Fig. 1). Between the two Greenland sites, the proportionality index was larger than '1' (s = 1·46), indicating increased anomaly in the northerly site. For those steps of migration involving sea crossings, phenology correlation coefficients were very small, for example between Ireland and southern Iceland (r = −0·10) and between northern Iceland and southern Greenland (r = −0·33). Hence, based on this measure, there was no apparent predictability of spring conditions between these sites, separated by oceans.

On the Svalbard route, all consecutive pairs of stopover regions showed high phenology correlation coefficients (0·45 < r < 0·81; Fig. 1), even across larger stretches of ocean. The proportionality index was, however, closest to '1' for the land crossing from southern to northern Norway (s = 0·85), and low for the ocean crossing from northern Norway to Svalbard (s = 0·48).

Stopover regions on the migration route to the Barents Sea revealed two interrelated regions, separated by a link with low predictability (Fig. 1). Phenology between Central Europe, Sweden and the Baltics was highly correlated with strong positive predictability (0·78 < r < 0·97, 0·76 < s < 0·90). All sites on the Arctic coast (White Sea, Kanin Peninsula, Pechora/Kolguyev, Novaya Zemlya) showed high phenology correlation coefficients with proportionality indices close to '1' (0·41 < r < 0·93, 0·88 < s < 1·46). For some pairs of Arctic sites, proportionality indices were above '1' indicating an increased anomaly when progressing towards the breeding sites. Correlation and predictability in the intermediate zone,

between the Baltics and the White Sea, were present, but weak ($r = 0.39$, $s = 0.48$).

GDD JERKS AND MIGRATION TIMING

Generally, arrivals at stopover and breeding sites showed intermediate fits with the onset of spring (RMSD = 18.20 ± 2.08 days (SE), Fig. 3a–n). Better fits (lower RMSD) were related to higher phenology correlation coefficients (Table 1b; linear regression single-term deletion, RSS = 291.3, $P = 0.03$), shorter distance to the breeding site (RSS = 381.6, $P = 0.004$), shorter onset of spring peak interval (RSS = 266.0, $P = 0.05$) and the flyway (RSS = 415.7, $P = 0.009$), indicating that geese made use of predictability between sites and that this differed between flyways. Their timing improved closer to the breeding sites and with tighter timing of peak food availability. The latter is opposite to what is expected by chance, namely that wider peak intervals would coincide with more accurate timing, which is not the case here. Distance between stopovers, the presence of ecological barriers and the 30-year variability of onset of spring did not seem to have had an influence on the general migration timing of barnacle geese (Table 1b), not even if excluding predictability (not shown).

The 90% interval widths of onset of spring peaks did not vary between flyways, but became narrower when approaching the breeding sites (Table 1c; linear regression single-term deletion, RSS = 840.4, $P < 0.001$). A similar spatial pattern appeared for the variability in onsets of spring over the last 30 years: onset of spring at early stopover sites was highly variable, while they became more confined towards the Arctic breeding sites (linear regression single-term deletion, RSS = 236.7, $P < 0.001$). Also this measure of variability did not differ among the flyways. Notably, average (within-year) onset of spring 90% interval widths was related to (between-year) variability of the onset of spring (Spearman's rho = 0.81, $P < 0.001$).

For the Greenland flyway, the onset of spring at the stopover sites on Iceland (Fig. 3c,d) showed rather large 30-year variability (18 and 19 days) and wide 90% peak intervals (27 and 38 days). In southern Iceland, the geese arrived after the onset of spring (RMSD = 21.2 days). In contrast, arrival on stopovers in northern Iceland fitted well to the onset of spring (RMSD = 11.3 days). The 30-year variability (7 and 8 days) and 90% peak onset of spring interval widths (11 and 13 days) were much smaller for the stopovers on Greenland (Fig. 2a,b). Goose arrival at Greenland stopovers was less strongly linked to the onset of spring with birds mostly arriving well before the onset of spring at the breeding sites (RMSD = 25.6 and 24.9 days). Dates of arrival to Greenland sites varied little between years and individuals (16 May–31 May).

Migration tracks of geese from the Svalbard population covered more years (2006–2011) and therefore showed a higher variability in arrival dates. In the two Norwegian stopover regions (Fig. 3f,g), variability of onset of spring over 30 years (10 and 12 days), 90% peak interval (31 and 25 days) and the fit of onset of spring with goose arrival (RMSD = 16.8 and 24.4 days) were intermediate. At those stopovers, goose arrival dates (21 April–27 May and 4 May–23 June) were rather variable. Northern Norway was only used by the tagged geese in 2008, and both Norwegian sites were skipped completely by the tagged cohort in 2011. The 90% onset of spring peak interval (15 days) and 30-year variability (5 days) were narrower on Svalbard (Fig. 3e), and geese arrived moderately close to the onset of spring (RMSD = 18.2 days). Notably, in the exceptionally early spring of 2006, goose arrival coincided very closely with spring onset (RMSD = 3.1 days).

For the Barents Sea population, the first two stopover sites (Sweden, Baltics; Fig. 3m,n) showed high variability (18 and 14 days) and wide peak intervals (32 and 29 days), probably explaining the mismatch between the onset of spring and goose arrival (RMSD = 27.0 days both). There, all birds arrived after the onset of spring. After the long-distance move to the White Sea, all geese matched the onset of spring, with one of the lowest RMSD = 5.9 days of the whole data set (Fig. 2l). The 30-year variability in onset of spring (7 days) was small, and the 90% peak interval (21 days) was relatively narrow. In the following three sites (Kanin Peninsula, Pechora/Kolguyev and Novaya Zemlya; Fig. 2h–k), peak intervals became narrower (15–19 days) and 30-year variability stayed low (7–11 days). Barnacle goose arrival at these sites overlapped relatively well with onset of spring (RMSD 7.9–16.0), but some birds arrived up to 24 days before it.

PREDICTABILITY AND MIGRATION TIMING

We found a negative relationship between phenology correlation coefficients and deviation of goose arrival with regard to the onset of spring (linear regression, $P < 0.001$, $R^2_{adj} = 0.07$, not shown), indicating that birds arrived closer to the onset of spring when there was a stronger relationship between climatic conditions in current and previous stopover regions. However, spread was high, and, as exemplified by the R^2_{adj}, not much variation was explained by the model. Analysis of predictability in terms of the proportionality index gave clearer results, revealing a quadratic relation between predictability and timing of goose arrival in relation to the green wave (Fig. 4; nonlinear least squares, $P < 0.001$ for all three parameters). Results indicated that at a high predictability (between 0.8 and 1), geese arrived at stopover sites closer to the onset of spring, although much variability still remained.

If categorizing sites according to their location in the flyway (colours in Figs 3 and 4), geese seemed to mostly have arrived before the onset of spring when close to the breeding sites (yellow) and after the onset of spring when close to the wintering sites (blue). According to an integrated analysis (linear mixed model, random factors: individual bird and year, Table 1d), however, migration timing was only linked to the proportionality index (linear
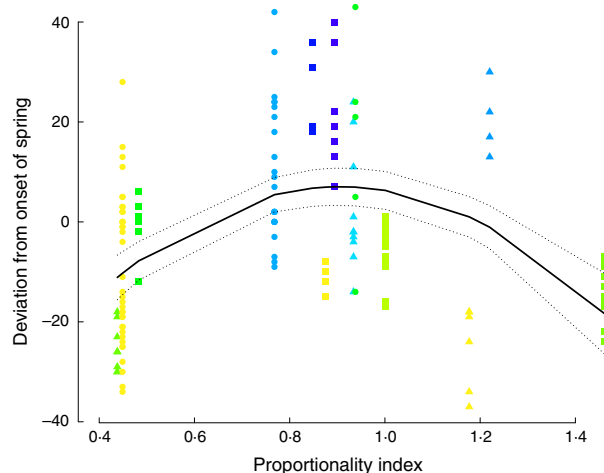
Percentage distance to breeding site
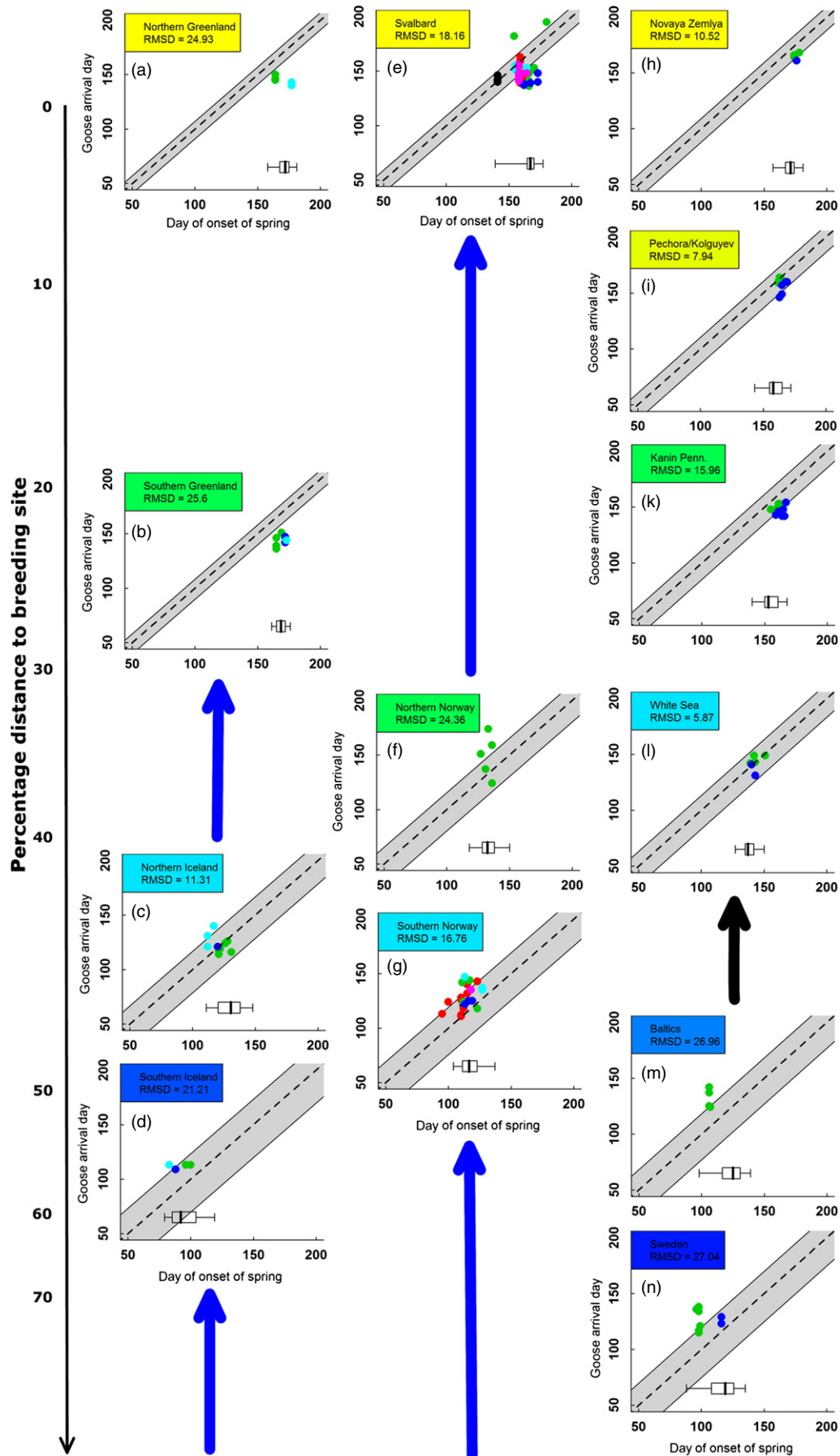
Fig. 4. Relationship of goose arrival timing deviations and proportionality indices (predictability) at stopover regions. Arrival timing deviation (or deviation from onset of spring) is the number of days that a goose arrived before (negative) or after (positive) the date of onset of spring. Symbols indicate populations (square – Barents Sea, circle – Svalbard, triangle – Greenland), colours/greyscales percentage distance to the breeding grounds (see Fig. 3; blue/dark grey – close to the wintering region, yellow/light grey – breeding sites). The solid line is the nonlinear least-squares fit of a quadratic model; dotted lines indicate the 95% confidence band of the fit.

mixed model single-term deletion, LR = 8·41, *P* = 0·004), the width of the peak of onset of spring (LR = 14·49, *P* < 0·001), flyway (LR = 15·65, *P* < 0·001) and breeding status (LR = 7·22, *P* = 0·007). Phenology correlation coefficients, the existence of ecological barriers, distance between sites and to the breeding grounds and 30-year variability of onset of spring did not seem to be influential. This lack of influence of barriers and distance remained also when excluding the two predictability measures from the model (not shown).

The strength and direction of the links between timing, predictability and variability differed by flyway, with geese of the Svalbard flyway on average arriving earliest in relation to the onset of spring and geese of the Barents Sea flyway arriving latest (Tukey contrasts, Greenland – Svalbard = 7·9 days, Barents Sea – Greenland = 7·3 days). General conclusions can, however, be made: goose timing was closer to the onset of spring if the direction of predictability was favourable (proportionality index close to '1')

and the peak of spring restricted to a narrow time window. The timing of barnacle geese that were classified as non-breeders (*N* = 11 individual birds) and breeders (*N* = 28) differed by 5–6 days (Tukey contrast = 5·5 days), breeding birds usually arriving earlier to stopovers en route. Similarly, all birds arrived at the breeding grounds before the onset of spring, but those that subsequently attempted breeding arrived on average 6 days before non-breeders (breeders: average deviation = −15·5 days; non-breeders: average deviation = −10·0 days).

Discussion

Our results indicate that individual barnacle geese on the three flyways were able to predict foraging conditions in subsequent stopover sites during spring migration. Predictability between sites was higher if they were not separated by large stretches of ocean or other unsuitable landscapes ('ecological barriers'). Analysing tracking data in relation to the predictability of onset of spring, we showed that geese generally arrived at stopover sites at the onset of spring if predictability was high. However, they seemed to be uninfluenced by the presence of ecological barriers; rather, deviation of arrival from onset of spring was related to the distance to the breeding site and the width of the food peak. Additionally, geese seemed not to linearly follow the green wave, but to overtake the green wave, arriving after onset of spring at early stopovers and before onset of spring close to the breeding grounds. Nevertheless, timely arrival at stopovers was related to breeding status, suggesting that the timing of migration steps during spring was linked to goose fitness.

PREDICTABILITY ALONG MIGRATION FLYWAYS

We showed that the effect of ecological barriers differed by migratory flyway and was related to distance between stopover regions (linear regression, single-term deletion, RSS = 3·08, *P* < 0·001). However, distance could not explain more of the variability in predictability between stopovers than the simple existence of ecological barriers alone (Table 1a). Ecological barriers should be understood as a combination of geographical structures and complex climatic phenomena such as weather systems and ocean currents. Along the Greenland flyway, we showed very clear effects of two long, ocean crossings on predict-

Fig. 3. Onset of spring dates vs. days of goose arrival (both in Julian days) in the main stopover regions of (a–d) the Greenland flyway, (e–g) the Svalbard flyway and (h–n) the Barents Sea flyway. Dots are data points of stopover sites from GPS-tracked geese, the colour indicates the year (2006 – black, 2007 – red, 2008 – green, 2009 – blue, 2010 – light blue, 2011 – pink). The grey shaded area shows the time interval (confidence interval over 30 years) when GDD jerk was above 90% of the peak value within a given time period, indicating how sharp the peak is at that time. Note that wide peak intervals do not coincide with better fits of goose arrival. The small boxplot gives the variability of the onset of spring in the respective region over the past 30 years. Bold lines in the boxplots indicate the median, boxes the interquartile interval and whiskers the 5 and 95 percentiles. Subplots are aligned according to their proximity to the breeding site, and arrows indicate ecological barriers, oceans (blue) and inland crossings (black). RMSD values provide goodness-of-fit of arrival dates to onset of spring, that is, how well do the geese follow the green wave. Colours/greyscales underlying the legends indicate percentage distance to the breeding site for each flyway and relate to Fig. 4.

ability. The lack of correlation in the onset of spring between Ireland, Iceland and Greenland sites might be linked to a decoupling of different climatic systems (Van Der Graaf 2006): in the case of northern Iceland and southern Greenland likely increased by a cold ocean current. Differences in climatic conditions were also seen between the Baltic and the White Sea regions of the Barents Sea population, here separated by a large stretch of unsuitable forest landscape.

High correlations between other, usually geographically close, pairs of sites might be related to being situated in the same climatic regime (e.g. southern/northern Iceland, southern/northern Greenland, southern/northern Norway, sites along the coast of the Barents Sea). In contrast to our expectations, some sites separated by ocean stretches were still correlated (Scotland – south Norway, north Norway – Svalbard), which might be caused by the connecting ocean currents mediating for the effects of weather systems. The finding that all pairs of successive stopovers in the Svalbard flyway were climatically linked seems contrary to some previous findings (Tombre *et al.* 2008), but not others (Hahn, Loonen & Klaassen 2011).

GOOSE MIGRATION TIMING

On all three flyways, goose arrival at stopover sites coincided well with the onset of spring, even when crossing ecological barriers and even more so at sites where intervals of peak food quality were short. This is in line with the previous findings that the availability of high-quality food is the main driver of the timing of goose migration (Owen 1980; Bauer, Gienapp & Madsen 2008), because many goose populations are at least partly 'capital breeders' (Gauthier, Bety & Hobson 2003; Hahn, Loonen & Klaassen 2011) and need to bring extra reserves to the breeding areas. Our finding that initiation of breeding was more likely after timely migration (or vice versa) supports this hypothesis (Prop, Black & Shimmings 2003; van Wijk *et al.* 2012). However, there might also be other causes of non-breeding, for example divorce or death of the partner (Forslund & Larsson 1991).

Barnacle geese arrived late and stayed longer at early stopover sites. In the framework of capital breeding, this might be caused by a time constraint for building up enough reserves to start migration (Drent & Daan 1980). Another explanation might be that food quality in European stopovers has improved due to intensive agriculture (Jefferies & Drent 2006) and outweighs any penalty for mistimed arrival. Such a penalty might be low due to the long distance remaining to the breeding grounds and high transport costs of any build-up of body reserves for breeding (Piersma 1987; Bauer, Gienapp & Madsen 2008). As also expected for capital breeders, arrival of barnacle geese to the breeding sites was somewhat ahead of the onset of spring, allowing them to start breeding early, under still unfavourable conditions. However, their arrival before the onset of spring may also (or additionally) be explained by

poor predictability due to the narrow peak food availability at northerly breeding sites, competition for nesting sites (Kokko 1999), and/or breeders striving to match peak requirements of their young with peak food availability (Van Der Graaf 2006; Van Der Jeugd *et al.* 2009). Thus, in contrast to previous findings (Van Der Graaf *et al.* 2006), we showed that barnacle geese do not consistently 'surf the green wave', but 'overtake the green wave'.

Exceptions to the general pattern of timely arrival of geese at highly predictable sites can have different causes. First, the number of years that geese were tracked differed between populations, possibly hampering our ability to find consistent patterns between the flyways. Sample size issues can lead to deflated variability in arrival for the Barents Sea flyway ($N = 2$ years) and inflated variability at sites for the Svalbard flyway ($N = 6$ years). Secondly, the ecological barrier between the Baltic and White Sea seems not to have influenced goose timing; even if predictability was low, the birds arrived very close to the onset of spring. This finding is in line with results (Van Der Graaf 2006) that suggest that geese might have departed at a fixed time (e.g. photoperiod related) from the Baltic States. Thus, they might have used time-related cues if onset of spring had low between-year variability, and other external cues were not available. Thirdly, high predictability did not lead to timely arrival at southern sites on the Barents Sea flyway and stopover sites in northern Norway (birds arrive later than the onset of spring). Birds might be limited to come into condition at initial stopovers (southerly stopovers on the Barents Sea flyway), or improved food availability at a previous site (Jefferies & Drent 2006) outweighs costs of late arrival in subsequent stopovers. Furthermore, disturbance (Madsen 1995), adverse weather conditions or the anticipation of crossing an ecological barrier (Delingat, Bairlein & Hedenstrom 2008) might alter migration timing (e.g. northern Norway).

CUES FOR MIGRATION TIMING

It has been suggested that arrival at intermediate stopover sites is mainly driven by phenology, whereas arrival and departure from southern stopovers and sites close to the breeding grounds are also driven by other factors (Bauer, Gienapp & Madsen 2008). Consequently, at different stages of migration, different cues or combinations of cues might be used for timing (McNamara *et al.* 2011). Indeed, goose migration timing has been explained by a combination of three types of cues (Duriez *et al.* 2009) as follows: (i) time-related cues such as photoperiod (early stopovers), (ii) energetics cues such as the amount of body stores (before barriers) and (iii) environmental cues that include temperature sum, food availability (intermediate stopovers), rainfall, nest site availability, competition, human disturbance, predation and wind (Green 2004; Schaub, Jenni & Bairlein 2008; Alerstam 2011; Bauer *et al.* 2011). Time-related cues are constant and reliable if conditions do not change; environmental cues vary between years

and with conditions that are of importance to the animals' fitness, and energetic cues are easy to assess for the animal, but usually driven by food availability (environmental cue). Environmental and energetic cues relate to the intake rate that has been used as best predictor for timing of stopover in optimal migration theory (Alerstam & Lindström 1990; Alerstam 2011). If no environmental cues are available, that is predictability is low, it has been suggested that animals best migrate on a fixed schedule and use photoperiod as a time-related cue (Weber 1999; Van Der Graaf 2006), which might apply for barnacle goose arrival to the White Sea and Greenland stopovers.

ECOLOGICAL BARRIERS

Ecological barriers can trigger the use of energetic rather than environmental cues and alter stopover duration (Delingat, Bairlein & Hedenström 2008; Schaub, Jenni & Bairlein 2008; Smolinsky *et al.* 2013) and possibly lead to skipping stopovers (Deutschlander & Muheim 2009). Our geese stopped longer before crossing barriers (northern Iceland, southern Norway – from where most birds fly directly to Svalbard – and the Baltic States; see Supporting Information, Table S1), possibly increasing their fuel loads. Similarly, it has been shown that female barnacle geese left Norway with extra fat loads and refuelled directly on arrival at Svalbard (Prop, Black & Shimmings 2003). Coastal regions in Svalbard and stopovers at the White Sea and on the Kanin Peninsular have been found to provide so-called pre-breeding stopovers (Hübner 2006; Van Der Graaf 2006), where geese refill their fat stores before continuing to the breeding grounds. This might be especially important for the barnacle geese that recently started to completely skip stopovers in Norway (Griffin 2008) and the Baltic (Eichhorn *et al.* 2009) and might have no indication of conditions at the breeding grounds when leaving their winter quarters.

HABITAT CHANGES AND ARCTIC AMPLIFICATION

As habitats and the climate change (IPCC 2007), migrants have to deal with changes in environmental conditions, cues and optimal times (Forchhammer, Post & Stenseth 1998; Both & Visser 2001). Because there is evidence for both high variability between individuals and high within-individual (between-years) consistency in migratory timing across species (Battley 2006; Gill *et al.* 2014), bird populations are expected to be able to adapt to changes in climate, namely earlier springs. However, adaptation is expected to take longer for invariant departure times, for example across ecological barriers, compared to departures driven by environmental cues (Van Der Graaf 2006; McNamara *et al.* 2011). This might also have implications for the adaptation to climate change by the three populations of barnacle geese considered here, namely delayed arrival at stopovers during migration. Furthermore, climate change models predict a quicker advance of onset of spring in

northerly sites (IPCC 2007), leading to a greater shift in the best possible timing compared to the cues at more southerly sites and an increased loss of fitness if initial correlation is low (McNamara *et al.* 2011). This so-called Arctic amplification is already indicated by the larger anomalies of onset of spring ($s > 1$) in the Greenland and Arctic Russian sites in our 30-year data set. Thus, Arctic breeding geese might show reduced capacity to predict conditions at more northerly stopovers after crossing ecological barriers, leading to delayed arrival at the breeding grounds in relation to the onset of spring or decreased fuel stores for directly starting breeding, ultimately causing a decrease in fitness.

Data accessibility

The GPS tracking data of all three populations of barnacle geese are uploaded to Movebank (www.movebank.org), each as a separate study:

1. Greenland population: 'Migration timing in barnacle geese (Greenland)', DOI: 10.5441/001/1.5d3f0664.
2. Svalbard population: 'Migration timing in barnacle geese (Svalbard)', DOI: 10.5441/001/1.5k6b1364.
3. Barents Sea population: 'Migration timing in barnacle geese (Barents Sea)', DOI: 10.5441/001/1.ps244r11.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Average and SD of GDD jerk peak days (onset of spring) on the stopover regions of the three populations of barnacle geese.

Tables S2–S7. GDD jerk peak day (onset of spring) anomalies in pairs of stopover regions per flyway.

Figure S1. GDD jerk peak dates (onset of spring) for the stopover regions of the three flyways: (a) Greenland, (b) Svalbard and (c) Barents Sea.

Figure S2. GDD jerks as a function of day of the year in the Greenland flyway.

Figure S3. GDD jerks as a function of day of the year in the Svalbard flyway.

Figure S4. GDD jerks as a function of day of the year in the Barents Sea flyway.