

Climate change and contrasting plasticity in timing of a two-step migration episode of an Arctic-nesting avian herbivore

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Abstract Greenland white-fronted geese *Anser albifrons flavirostris* wintering in Britain and Ireland migrate over the sea for 700–1200 km to stage 3–5 weeks in Iceland in spring, continuing a similar distance over the sea and Greenland Ice Cap to West Greenland breeding grounds. During 1969 to 2012, the geese advanced the mean departure date from Ireland by 15 days, during which time also they attained threshold fat stores earlier as well as departing in fatter condition. Over that period, Iceland spring-staging geese shifted from consuming underground plant storage organs to grazing managed hayfields, which provide fresh grass growth despite sub-zero temperatures, when traditional natural foods are inaccessible in frozen substrates. In 2012 and 2013, geese arrived three weeks earlier to Iceland, in fatter condition and accumulated fat significantly slower than in 1997–1999 and 2007. Although geese accumulated sufficient fat stores earlier in Iceland in 2007, 2012 and 2013, they departed around the same date as in 1997–1999, prolonging spring staging by three weeks. Plasticity in winter departure dates is likely due to improved winter feeding conditions (enabling earlier departure in better condition) and a novel predictable food resource in Iceland. Greenland white-fronted geese attained threshold fat stores in Iceland earlier, but remained rather than departing earlier to Greenland. Despite arriving earlier in Iceland, arrival dates on the breeding areas have not changed since the 1880s, presumably because of relatively constant cool springs and heavy snowfall in West Greenland during recent years [*Current Zoology* 60 (2): 233–242, 2014].

Keywords *Anser albifrons flavirostris*, Climate mismatch, Greenland white-fronted geese, Migration phenology, Vernal migration

Recent effects of climate change are most evident in polar areas, with substantial effects, for example, on the phenology of the spring thaw, biological production, distribution of organisms and ecosystem function at the highest of northern latitudes (e.g. Høye et al., 2007; IPCC, 2007; Post et al., 2009; Ward et al., 2009). Long-distance Arctic migrants are dependent on the timing of the thaw for refuelling depleted energy stores and therefore face particular challenges because of the differential advance in the onset of spring at higher latitudes, an apparent consequence of climate change. Because the advancement of spring is more rapid in the High Arctic than further south (Stone et al., 2002; IPCC,

2007), it might be expected that cues and food availability further south are advancing more slowly than further north. This has the potential to decouple critical trophic relationships in time and space, because long-distance migratory birds rely on the pulse of food availability along the seasonal gradient that has traditionally been available to supply energy and nutrients to support onward migration and eventual investment in reproduction on arrival at distant breeding grounds (Ahola et al., 2004; Fiedler et al. 2004; Both and Visser, 2005). In the case of well-studied long-distance migrant passerines in Europe, this has resulted in the traditional timing of migration failing to coincide with the advancement in

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prey availability, with fitness consequences for some populations (e.g. Both and Visser, 2001; Both et al., 2006) whilst others seem more able to adjust (Weidinger and Kral, 2007; Goodenough et al., 2010).

Many populations of herbivorous geese make annual migrations from their temperate winter quarters to Arctic breeding areas, and rely on the availability of plant storage organs (such as rhizomes and seeds) and spring growth of fresh plant tissue for energy and nutrition, the accessibility of which is largely temperature-dependent (either because snow and ice prevents access to food and/or temperature affects the onset of above ground green growth). An earlier onset of spring at higher latitudes might therefore advance food availability compared to the same mechanisms further south where spring migration is initiated. If spring migration is initiated by proximate factors on winter staging areas (Tombre et al., 2008), the earlier melt in the Arctic nesting areas may mean that traditional migration patterns become inappropriate, with geese arriving increasingly late relative to plant growth phenology at the breeding grounds, causing them to miss the rapid seasonal development during late spring. Such “mismatches” between the rate of change in the initiation of seasonal biological activity and the actual arrival of migrating birds, potentially affects the timing of optimal breeding conditions and has been reported in temperate regions (Pearce-Higgins et al., 2005).

In spring, the Greenland white-fronted geese *Anser albifrons flavirostris* that winter in Britain and Ireland fly over the sea for 700–1200 km to stage and refuel depleted fat stores for 3–5 weeks in Iceland before migrating a similar distance over the sea and the Greenland Ice Cap to breeding areas in West Greenland (Fox et al., 2003, 2012a; Stroud¹ et al., 2012). The advancement of the spring season has generally been more dramatic in the Arctic than further south (Stone et al., 2002; Parmesan and Yohe, 2003), although this may not be the case along the migratory corridor of the Greenland white-fronted goose. Earlier analyses suggested that temperatures on the wintering areas have increased by 0.3–0.4°C per decade during 1978 to 2007, advancing the date of 500 degree-days above freezing by some 18 days between 1985 and 2007, potentially affecting grass growth (Fox and Walsh, 2012). Geese departed their Irish winter quarters on average 15 days

earlier in 2012 than in 1969 having attained the necessary fat stores earlier than in previous years (Fox and Walsh, 2012). Icelandic temperatures at critical midway staging areas have shown no significant change over this period, creating a potential mismatch between the energy needs of the geese and food availability along the migratory route as a result of geese arriving “too early” to staging areas, where a “late” spring could potentially result in a lack of food for earlier arriving birds (Fox et al., 2012a). However, during the same period, spring-staging Greenland white-fronted geese in Iceland have shifted from consuming below-ground plant storage organs to grazing managed hayfields created in the 1950s (Fox et al., 2012a). These fields provide fresh grass lamina growth despite sub-zero temperatures, when traditional natural foods are physically inaccessible to staging geese due to frozen substrates (Fox et al., 2012a). Hence, advanced departure from the wintering grounds over the last 44 years have allowed the geese to arrive earlier in Iceland without penalty to foraging due to novel opportunities afforded by managed grasslands there (Fox et al., 2012a). Furthermore, there has been no significant change in May temperatures in West Greenland, such that there has been no obvious incentive to depart from the Iceland staging areas earlier to the breeding grounds (Fox et al., 2012a).

In this analysis, we test for the differences in rate of fat accumulation (measured by field scores of abdominal profiles) at midway staging areas in Iceland during five springs from 1997 to 2013 to see how earlier arrival in 2012 and 2013 affected fat accumulation rates. Greenland white-fronted geese appear to depart the winter quarters having attained threshold fat stores (Fox and Walsh, 2012). As geese have attained this threshold earlier in winter, so they have also departed earlier. Consequently, we also investigate the relationship between fat accumulation and departure date for Greenland, to determine whether a similar relationship exists as a result of the earlier arrival in Iceland. Finally, we combine long term monitoring of goose departure dates from the wintering grounds, with historical and recent field observations of departures from Iceland and arrivals in west Greenland to assess how these changes have affected the phenology of the spring migration of the population since the 1880s.

¹ Stroud DA, Fox AD, Urquhart C, Francis IS, 2012. International Single Species Action Plan for the Conservation of the Greenland White-fronted Goose *Anser albifrons flavirostris*, 2012–2022. AEWA Technical Report. Bonn, Germany. Accessible at: http://www.unep-awea.org/meetings/en/mop5_docs/pdf/mop5_27_draft_ssap_gwfg.pdf (Last accessed 22 May 2013).

1 Materials and Methods

1.1 Meteorological data

Mean monthly daily air temperature data for 1973 to 2013 were extracted from the meteorological stations at Cork Airport, Ireland (51°51' N, 8°29' W, http://www.tutiempo.net/en/Climate/Cork_Airport/39550.htm) for March, at Stykkisholmur, Iceland (65°5' N, 22°44' W, <http://www.tutiempo.net/en/Climate/Stykkisholmur/40130.htm>) for April and Kangerlussuaq, West Greenland (67°1' N, 50°42' W, http://www.tutiempo.net/en/Climate/Sdr_Stroemfjord/42310.htm) for May as proxy measures of spring temperatures for the wintering range, Icelandic spring staging areas and breeding grounds, respectively. These were subject to simple linear regression analysis to test for significant changes over time and to test for correlations between Cork and Stykkisholmur and Stykkisholmur and Kangerlussuaq to see if geese could use the prevailing temperature at each site to predict temperatures at the next migration arrival point during spring.

1.2 Study sites and capture of geese

One of us (AJW) recorded abdominal profile index scores (APIs, see below) of wintering Greenland white-fronted geese up until the point of departure at their single most important wintering area at Wexford Slobs in SE Ireland (52°22' N, 6°24' W, see Fox et al., 1998, 2012b). We also studied spring staging Greenland white-fronted geese at their single most important staging area in Iceland at the Agricultural University of Iceland farm at Hvanneyri, Borgarfjörður, west Iceland (64°34' N, 21°46' W, see Fox et al., 1999, 2012a). Geese at this site use wetlands and the new growth of grass in managed hayfields to build condition for onward migration to breeding areas in Greenland. Resightings of individually collar-marked geese have shown that many birds wintering at Wexford regularly stage at Hvanneyri in spring (Fox et al., 2002). Greenland white-fronted geese were caught using cannon-nets on sites baited with barley at Hvanneyri. Although adults and first-year birds were caught together, we only consider older than first-year birds here because sample sizes of young birds were small in all years and variable between seasons. First-year birds are smaller than adults and therefore add unnecessary variance to the date/mass relationship. We caught 106 male and 93 female adult geese on 23 dates between 9 April and 5 May in the springs of 1999, 2007, 2012 and 2013. Each bird was sexed (by cloacal examination), aged (by plumage characteristics) and the API determined (see below),

before being weighed and measured prior to release.

1.3 Correlation between abdominal profile scores and goose body mass

Owen (1981) first described the field method of scoring goose abdominal profiles as a non-consumptive method of assessing fat deposits accumulated by individuals. It has been demonstrated that fat stored in the abdomen is a reliable index of general fat stores accumulated throughout the body of geese (Thomas et al., 1983; Madsen and Klaassen, 2006), and that the level of abdominal fat storage can be assessed using a predetermined visual scoring system. In Greenland white-fronted geese, there is a positive correlation between this measure and overall body mass (Fox, 2003). To validate this in Iceland, we present data on body mass determination of individuals caught by cannon nets at Hvanneyri (for details see below). In all years, abdominal profiles were scored in the field using a 0–5 score by a small number of observers who cross-validated their scores to ensure consistency (Owen, 1981, modified according to Boyd et al., 1999). Daily samples of geese were taken, from a mix of small, medium and large flocks to ensure independent assessments. Although we cannot exclude bias in the abdominal profile data between marked individuals and the population as a whole, we consider it unlikely, since 3%–8% of the global population of Greenland white-fronted geese have been counted at Hvanneyri during spring migration, excluding the effects of turnover in numbers known to occur from observations of marked individuals (Fox et al., 1999).

1.4 Changes in mean abdominal profile scores on departure from winter quarters

APIs were scored in the field at Wexford in all years to determine the degree of fat stores accumulated by wintering birds by the date at which 50% of the wintering population had departed in spring, to see if there had been an advance in this measure over time (See Fig. 2 in Fox et al., 2012b). There were no significant differences between samples from collared and random samples of uncollared geese at Wexford in spring (ADF unpubl. data). Scores were derived from an average of 290 geese per winter (range 41–906 during 1985–2012), spread evenly through each season. Third degree polynomial regression models were fitted to abdominal profile score data using date as the independent variable, because changes in body mass and abdominal profile scores show predictable, but nonlinear, changes through the course of the winter, and relatively stable mass, followed by increased rates of accumulation in spring (Fox, 2003). We solved each annual model to generate a mean

API score for the date of departure. No value was available for 2013, so this value was generated from the relationship between year and departure API based on all other years from 1985–2012 inclusive (Fig. 2, although this has little influence on the overall pattern).

1.5 Changes in abdominal profiles in Iceland through the staging period

Experienced observers undertook daily field determinations of the APIs of large samples of marked and unmarked geese (mean 54, range 1–285 per day) in the fields at Hvanneyri every day in the springs of 1997, 1998, 1999, 2007, 2012 and 2013 (Boyd et al. 1999). Because this is an ordinal score, a daily average score was subjected to analysis of covariance (ANCOVA) using PROC GLM in SAS v.9.3 to test for differences in year and date. Because of high annual survival rate and site fidelity, annual mean estimates of abdominal profile scores are not statistically independent within or between years in Ireland or Iceland.

1.6 Departure dates of geese from Iceland

There are no regular observations of goose departures from Iceland except for the six study years at Hvanneyri, when daily counts were undertaken between one and six times per day to determine local abundance and timing of departure (see methods in Fox et al., 1999). For the purposes of this analysis, these counts are presented as a proportion of the total counts until the date when geese had departed the site.

1.7 Compilation of data relating to arrival of geese in West Greenland

We tested for changes in mean spring (May) temperatures during the period 1973–2013 (the years for which there are meteorological data available and for which departure data exist from Wexford) extracted from the meteorological station at Kangerlussuaq, the only Greenlandic weather station within the main breeding range of white-fronted geese that has provided monthly records of temperature and precipitation records. It is the only station in the interior lowlands of west Greenland and typifies the highly continental climate that predominates in the core breeding range of the population and from which the majority of the Islay-wintering Greenland white-fronted geese derive (Boyd, 1958; Fox et al., 1983). In the absence of constant and regular observations in West Greenland to determine arrival phenology, we compile data from a variety of sources. Lite-

ature sources include the accounts of Salomonsen (1950, 1967), Fox and Stroud (1988) and Mitchell et al. (2011)² which provide observational data relating to the start and end of spring migration within West Greenland. In addition, the precise dates of arrival of individuals since 1998 are available from the deployment of telemetry devices to 11 Greenland white-fronted geese at Wexford in winter 1997/8 (Fox et al., 2003), to three geese at Loch Ken, southwest Scotland (54°59' N 4°00' W) in 2007/8 and two in 2009/10 and three geese at Loch Ken and three at Wexford in 2011/12. For each individual, we present the date of arrival as the first positional fix in West Greenland.

2 Results

2.1 Trends in temperature in Ireland, Iceland and Greenland

During 1973–2013, there were no significant changes in mean monthly daily temperature measurements from Cork Airport (Ireland on the wintering grounds in March, $r = 0.02$, $F_{1,39} = 0.96$, $P = 0.34$), Stykkisholmur (Iceland on the midway staging areas in April, $r = 0.03$, $F_{1,39} = 1.10$, $P = 0.30$) or Kangerlussuaq (Greenland on the breeding grounds in May, $r = 0.06$, $F_{1,39} = 2.24$, $P = 0.14$). There was no significant correlation between April temperatures at Stykkisholmur and March temperatures at Cork ($r = 0.0006$, $F_{1,39} = 0.02$, $P = 0.88$) nor between May temperatures in Kangerlussuaq and April temperatures at Stykkisholmur ($r = 0.01$, $F_{1,39} = 0.47$, $P = 0.50$). Hence, temperatures in Ireland prior to departure for Iceland were very poor predictors of temperatures there as were temperatures in Iceland prior to departure for Greenland of temperatures on the breeding grounds on arrival there.

2.2 Correlation between abdominal profile scores and goose body mass

There was a significant relationship between API scores and total body mass (Fig. 1; adult males: $\text{Mass} = 280.6\text{API} + 2386$, $r = 0.55$, $F_{1,94} = 40.9$, $P < 0.0001$; adult females: $\text{Mass} = 196.9\text{API} + 2310$, $r = 0.42$, $F_{1,83} = 17.5$, $P < 0.0001$). Slopes and intercepts for male and female regressions fell within the 95% confidence interval estimates and were not significantly different (F tests, $P < 0.05$), providing evidence that increases in API scores in the field represent an increase in body mass; there were no major differences between sexes.

² Mitchell C, Francis IS, Griffin L, Stroud DA, Thomas H et al., 2011. Greenland white-fronted geese: Investigating causes of low reproductive output in Greenland Spring 2010 fieldwork: Report to Scottish Natural Heritage. Slimbridge: Greenland White-fronted Goose Study/Wildfowl and Wetlands Trust Report.

2.3 Changes in winter departure date and mean abdominal profile scores

The date of spring departure from Wexford Slobs of half of the wintering population advanced from 29 April 1969 to 27 March 2012 (see Fox et al., 2012b), although departure date in 2013 was 7 April. The mean API score amongst Wexford geese by the date of departure was greatest in the 1980s, declined in the 1990s, but increased again after 1999 (Fig. 2). Hence between 1997 and 2012, arrival date at Hvanneyri advanced from 17 April to 26 March, the mean API at departure from Wexford also increased from 2.3 to 3.4 and the mean API on arrival at Hvanneyri from 1.4 to 2.1 (Fig. 3).

2.4 Changes in abdominal profiles in Iceland through the staging period

The mean daily APIs increased with time in all years (Fig. 4; ANCOVA $r = 0.96$, $F_{11,124} = 107.3$ $P < 0.0001$), but there was a significant date*year interaction term ($F_5 = 34.3$ $P < 0.0001$) so years differed in the slope of the relationship between date and API score. A comparison between the slopes showed that the years 1997, 1998, 1999 and 2007 were not significantly different from each other, but all years differed from 2012 and 2013 which did not differ from each other and had significantly less steep slopes than the earlier years (F -tests, $P < 0.05$).

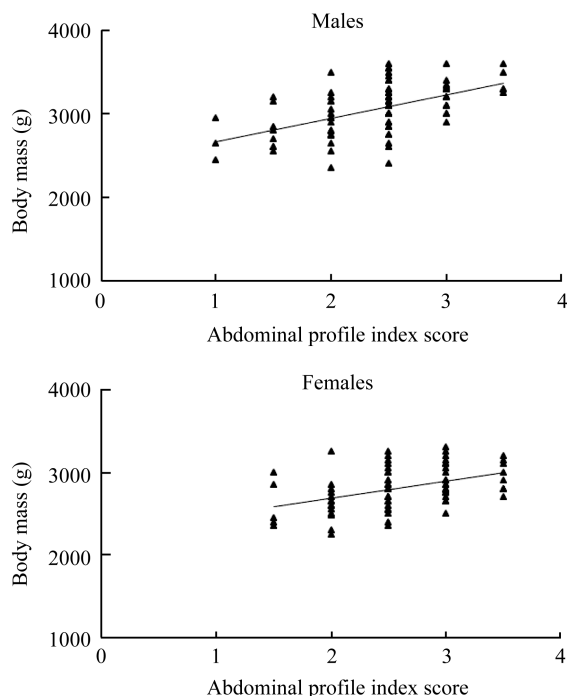


Fig. 1 Relationship between abdominal profile index and body mass in adult male (upper) and female (lower) Greenland white-fronted geese caught at Hvanneyri, West Iceland during the springs of 1997–2013

See text for details of regression models.

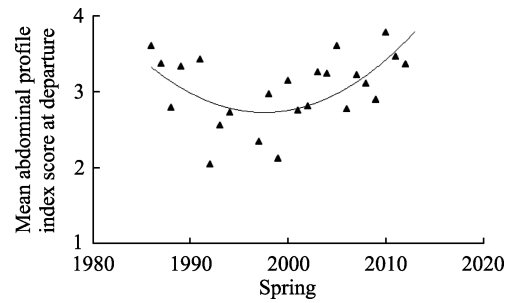


Fig. 2 Mean annual abdominal profile index score at Wexford, Ireland amongst Greenland white-fronted geese at the point of spring departure (of more than 50% of the wintering population) to Iceland 1985–2012

Note that API scores at departure in the late-1980s were as high as in recent years, but those in 1997 and 1999 (featured in this analysis) were particularly low. Fitted regression has formula $API = 0.0045y^2 - 17.8423y + 17822.14$ ($F_{2,23} = 5.62$, $P = 0.011$) where y = year.

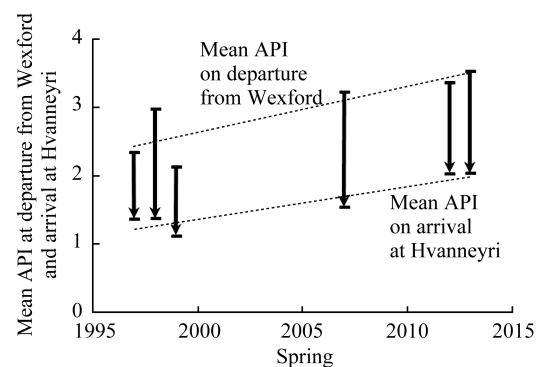


Fig. 3 Difference between mean annual abdominal profile index score at Wexford, Ireland (upper) and those on arrival at Hvanneyri, Iceland amongst Greenland white-fronted geese during spring migration in the springs of 1997, 1998, 1999, 2007, 2012 and 2013

Light dotted lines represent least squares regression models fitted to the two sets of data. Vertical arrows represent the inferred depletion of fat stores during migration from Wexford to Iceland. Note that there were insufficient data from 2013 to generate a departure API which was calculated from the relationship in Fig. 2 for that year.

2.5 Departure dates of geese from Iceland

The departure phenology of geese from Hvanneyri in years 1997, 1998, 1999, 2007, 2012 and 2013, at the point of final departure, varied only between 3 and 9 May (Fig. 5).

2.6 Arrival dates of geese in West Greenland

Mean May temperature showed no significant change in Kangerlussuaq during 1973–2013 (see above) Salomonsen (1950) described arrival dates of Greenland white-fronted geese in West Greenland between 27 April and 16 May during the late-1940s, which changed little in his later account (30 April–16 May) in the mid-1960s (Salomonsen, 1967). Expeditions to Eqaalumiut Nunaat (67°34' N, 50°20' W) described arrivals of geese

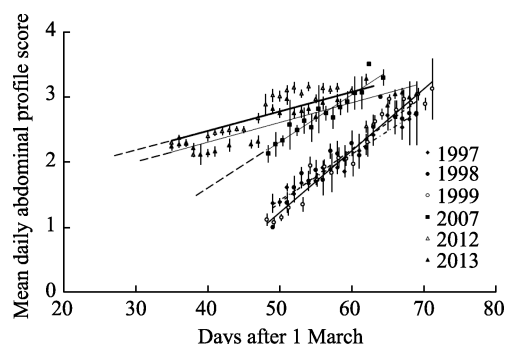


Fig. 4 Relationship between mean daily abdominal profile index (\pm 95% CI) and date amongst Greenland white-fronted geese caught at Hvanneyri, West Iceland during the springs of 1997–1999, 2007 and 2012–2013

See text for details of fitted ANCOVA models which showed significant differences in slopes between years. Hence, individual annual regression models are fitted here for clarity. Note that observations in 1997–1999 started almost immediately after geese arrived, but in 2007 observations started on 17 April (when geese arrived on 7 April) and in 2012 and 2013 on 4 April, even though birds had arrived on 26 and 30 March respectively (shown by the dotted line extensions in those years).

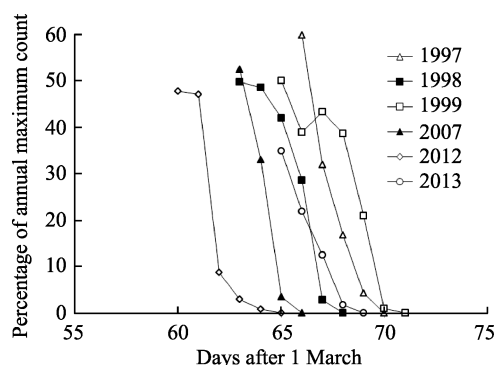


Fig. 5 Departure dates of Greenland white-fronted geese from Hvanneyri, West Iceland during the springs of 1997–1999, 2007 and 2012–2013

For each year the annual count at Hvanneyri is expressed as a percentage of the maximum annual count as an index of departure. Note the variation in departure varied by 6 days (3 May to 9 May) compared to the 23 days (26 March–17 April) variation in arrival date over the same period.

between 4 and 17 May 1979 and 6 and 20 May 1984 (Fox and Stroud, 1988) and to Isunngua ($67^{\circ}05' \text{ N}$, $50^{\circ}33' \text{ W}$) between 1 and 16 May 2010 (Mitchell et al., 2011), summarised in Fig. 6. Telemetry data providing specific dates of arrival for specific birds span the period from 5–21 May 1998 and 3–15 May for 2008 and 2010–2012 combined (Fig. 6). These arrival dates appear to have changed little since the accounts in Schiøler (1925) from the late 19th and early 20th centuries which include 9 May 1880 (Ilimanaq $69^{\circ}05' \text{ N}$, $51^{\circ}07' \text{ W}$), 10 May 1881 and 15 May 1882 (Ilulissat, $69^{\circ}13' \text{ N}$, $51^{\circ}06' \text{ W}$), 23 May 1893 and 12 May 1901 (Godthåbsfjord,

Nuup Kangerlua $60^{\circ}55' \text{ N}$, $48^{\circ}15' \text{ W}$), 27 April 1907 (Nanortalik, $60^{\circ}08' \text{ N}$, $45^{\circ}15' \text{ W}$) and 10 May 1907 (Sisimiut, $66^{\circ}55' \text{ N}$, $53^{\circ}40' \text{ W}$). Likewise Alerstam et al. (1986) reported the main arrivals at Kangerlussuaq during 10–14 May in the early 1980s, although visible migration was recorded until 4 June. Records from East Greenland back to the early 1900s show a similar pattern from early May until early June (e.g. Helms, 1926; Chapman, 1932; Fox and Stroud, 1981), but occurrences there *en route* outside of the normal summer range may be affected by the presence of sick or injured individuals and therefore may not reflect normal periods of passage.

3 Discussion

Greenland white-fronted geese wintering at Wexford advanced their departure on spring migration by an average of 15 days between 1969 and 2012, related to the degree of fat accumulation by a given date, irrespective of temperature on site (which is expected to affect grass growth, Fox and Walsh, 2012). New analysis presented here based on temperature data from Cork Airport suggests that mean March daily air temperatures have not significantly changed there during 1973–2013. Other new analyses presented here showed that fat store accumulation at departure also increased from the late-1990s, after falling from the mid-1980s (Fig. 2). Geese departed Wexford with greater fat stores, almost three weeks earlier in 2012 and 2013 than in 1997–1998 and arrived earlier to Iceland in better condition (Figs. 3, 4).

Although the geese could apparently have accumulated sufficient fat stores earlier in Iceland in 2012 and 2013, the rate of change in API scores was significantly lower than in 1997–1999 and 2007, suggesting accumulation of fat stores was slower, because we can find no reason to suspect optimal fat stores should be lower in those years. Despite the variation in arrival dates from 26 March to 17 April during these years, geese departed for Greenland around the same time in all studied years (range 3–9 May). We speculate that the departure date plasticity from Ireland and Britain is the result of (i) improved feeding conditions on the winter quarters (which may be influenced by climate change affecting grass growth, but this does not significantly contribute to annual variation in departure condition), and (ii) a predictable but novel food resource in Iceland.

In all years, the mean API score tended to dip before the final departure of all geese from Iceland, which we interpret to mean that departure of the heaviest birds occurred prior to final departure. Nevertheless, Greenland

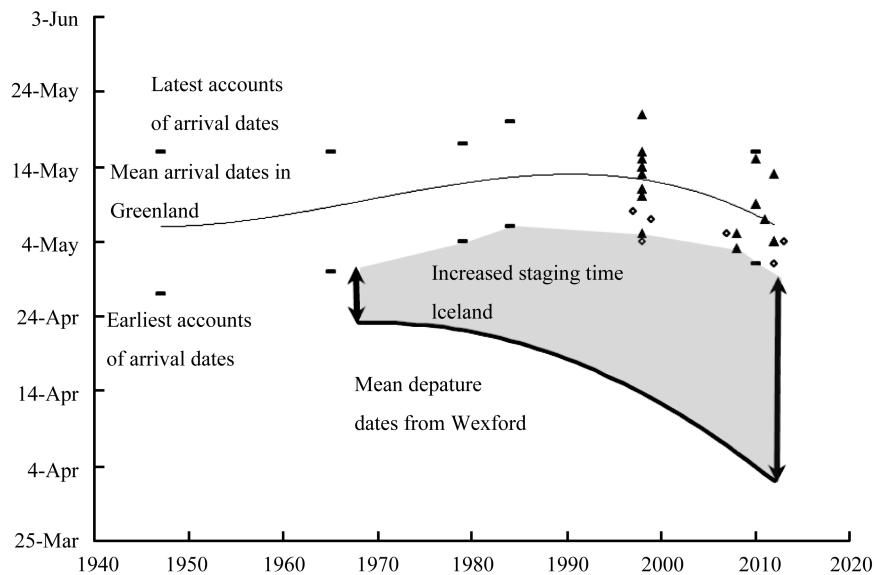


Fig. 6 Schematic representation of changes in staging phenology of Greenland white-fronted geese

Graphic is based on mean departure dates from Wexford Slobbs in Ireland (solid heavy line), observed departure date of 50% of birds from Hvanneyri in Iceland (open diamonds) and extreme arrival times in West Greenland (horizontal bars) based on ground observations of the start and end of arrivals in the late-1940s (Salomonsen, 1950), the mid-1960s (Salomonsen, 1967), expeditions to Eqaqummiut Nunaat in 1979 and 1984 (Fox and Stroud, 1988) and Isunngua in 2010 (Mitchell et al., 2011). In addition, dates of first arrival in West Greenland of satellite tracked individual birds are shown (solid triangles) from 1998 (Fox et al., 2003) and those tracked by telemetry devices by LG and MW in 2008, 2009, 2010 and 2011 (unpublished data). Solid heavy line is the fitted regression of Fox et al. (2012a), fine line is third order polynomial fitted to all observational data simply as a guide to trends. Shaded area imputes the nature of the increase in staging time in Iceland since the late-1960s.

white-fronted geese attained a maximum mean APIs-core of between 2.7 and 3.1 in years 1997–1999 immediately prior to departure. Geese exceeded the upper value by 29 April in 2007, by 21 April in 2012 and by 27 April in 2013. In 2007, geese accumulated fat stores at a similar rate to the three earlier years, but arrived 12 days earlier, and departed for Greenland only 2–4 days earlier in May. In 2012 and 2013, geese arrived 18–22 days earlier than the late-1990s and attained similar fat stores well before the end of April, but left Iceland within 0–4 days of the mean departure date in 1997–1999.

So why do the geese arrive in Iceland in better condition earlier and not accumulate fat stores as rapidly as in former years, which would allow for an earlier departure to Greenland? We propose two potential hypotheses to explain this: (i) constraint, i.e. insufficiency of food during staging in Iceland or (ii) restraint, i.e. the geese work to a predefined schedule (e.g. day length) and have selected to retain a specific departure date (similar to that in the 1880s). In 2012, Iceland experienced one of the warmest springs on record; as a result, hayfield grass biomass was (unusually for this time of year) substantial in late March and the geese had a surfeit of highly palatable above-ground green plant material

(unpubl. data). Unusually, geese spent much time sleeping in 2012 and appeared to have more food than was necessary to eat, as many suitable grass fields were not exploited at all that year. A full energetic and nutritional comparison of feeding ecology of the geese in the 1990s, 2012, and 2013 will form the subject of a future publication. Nevertheless, these observations strongly suggest that geese were not limited in their ability to accumulate fat stores in 2012 due to food constraints. Hence, despite their ability to attain threshold fat stores in Iceland earlier as a result of these changes, Greenland white-fronted geese have simply prolonged their stay in Iceland. We therefore favour the restraint hypothesis, because West Greenland has (i) shown no significant change in May temperatures during 1973–2013 and (ii) been subjected to exceptional snowfall in April and May since the mid-1990s, denying geese access to food on the breeding grounds immediately after the depletion of stores during the flight from Iceland (Boyd and Fox, 2008; Fox et al., submitted).

For long-distance migratory geese, migratory decisions prior to egg-laying are of paramount importance; arrival on the nesting areas in the best possible condition is timed to match optimal conditions for reproduction. The short summer growing season in Arctic re-

gions imposes a strict temporal discipline that requires arriving female geese to heavily invest nutrients and energy in a clutch of eggs and in self-maintenance during incubation and nest defence (Bêty et al., 2004; Madsen et al., 2007) to produce goslings at a time when suitable plant growth is available in sufficient abundance to successfully fledge the most offspring (Sedinger and Raveling, 1986; Prop and de Vries, 1993; van der Jeugd et al., 2009). Elevated spring temperatures on the breeding grounds tend to mean less snow and correlate with greater nesting density, earlier nesting and greater nesting success in the greater snow goose *Chen caerulescens* (Dickey et al., 2008); thus, warming on nesting areas has the potential to make a substantial difference to fitness measures. This does not seem to be the case for Greenland white-fronted geese, which since the mid-1990s have arrived in West Greenland to heavy snow in many recent springs and no evident change in May temperatures, and hence have little incentive to depart Iceland earlier. Indeed, those fit individuals attempting an early passage and meeting heavy snow on arrival in west Greenland would be less likely to restore nutrient and energy stores before nesting than those geese arriving later to less snow cover and milder conditions. If these early migrants were persistently less successful because they were unable to reconstitute optimal body condition to lay a clutch or they laid and failed because of poorer reproductive investment compared to later arriving birds, there would be considerable incentive to modify individual migration timing of these relatively long lived birds, i.e. by maintaining long term stability in arrival date. Iceland is a mid-way staging area between wintering and breeding areas and as such allows some flexibility in decision-making for Greenland white-fronted geese. However, this speculation requires support from the long term study of individual birds, whose migration patterns are currently being followed by direct observations and telemetry. Nevertheless, the timing of the two migration legs needs to best exploit availability of food en route (Rudi Drent's green wave hypothesis, Drent et al., 1978; van der Graaf et al., 2006). Large avian herbivores (as is the case for smaller passerines) spend relatively little time in shorter bursts of migration flight, but invest considerably more time regaining nutrient stores at stopover staging areas (Nolet, 2006; Stutchbury et al., 2009). Therefore, decision-making along the way is likely to reflect ambient weather and food availability to anticipate the most favourable arrival time to the breeding grounds. This seems to be the case for the pink-footed

goose *Anser brachyrhynchus* that travels to Svalbard from Denmark via staging areas in Norway, and responds to day-length and temperature to make decisions about onward migration although the relative importance of these two factors changed during the course of migration (Bauer et al., 2008). In contrast, light-bellied brent geese *Branta bernicla hrota* make their migration from Danish wintering sites to Svalbard and northeast Greenland in one trip over the ocean (Clausen and Bustnes, 1998; Clausen et al., 2003; Clausen and Clausen, 2013). They therefore cannot adjust their migration strategy in response to prevailing environmental conditions en route, but make a "leap in the dark" based largely on day length, for which there may be a fitness penalty, as falling reproductive success in this population mirrors the increasing mismatch in timing of optimal conditions for breeding (Clausen and Clausen, 2013). It may be the case that responses to climate and other environmental change will be highly species-specific (e.g. Tombre et al., 2008) and dependent on the ability of species to adapt to environmental change subject to the nature and duration of the stopovers involved along the vernal migration route. Long-distance migrants with fewer stopovers are likely to be less able to modify migration patterns than shorter distance migrants with more staging sites.

We therefore consider the responses of long-distance migratory avian herbivores to be highly species- and population-specific, dependent on the biogeographical nature of their migration routes, the number and nature of stopovers and the effects of climate change along these corridors. Despite the two-stage migration of the Greenland white-fronted goose, this population has shown considerable plasticity in its response to environmental change and ability to acquire energy stores earlier, by departing for spring staging areas earlier and with greater fat stores from the winter quarters. In contrast, attaining greater fat stores earlier in the spring in Iceland has not precipitated advancements in departure dates (even though temperatures have not changed on staging areas in Iceland), perhaps because the breeding grounds in West Greenland have shown no warming in spring since the 1970s. However, despite this flexibility, the Greenland white-fronted goose continues to endure a period of low reproductive success related to spring and summer conditions in West Greenland (Fox et al., submitted); it is likely that if the geese were not able to show such adaptation to changing conditions during vernal migration, the fitness consequences for the population could be worse. Miller-Rushing et al. (2010) ar-

gued that there is urgent need to understand the consequences of phenological changes in migration and energy acquisition for the demography and population dynamics of species. We contend that with further environmental change expected in the immediate future, continued monitoring of the Greenland white-fronted goose and its phenological responses is necessary to understand species that bridge Arctic and temperate climates throughout their annual cycle.

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