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Flexibility in spring arrival of migratory birds at northern latitudes under rapid temperature changes

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Capsule Icelandic migrants have responded to rapidly increasing spring temperatures on the breeding grounds in recent years.
Aims To determine how migrants respond to highly variable spring conditions in their northern breeding areas when they have to cross a barrier on migration.
Methods First arrival dates of common Icelandic migrants between 1988 and 2009 were analysed in the light of climate conditions in the breeding and wintering areas.
Results Most of the 17 species studied showed a tendency to arrive earlier. Six of the 17 species arrived significantly earlier after milder winters and nine arrived significantly earlier in warmer Icelandic springs. Species wintering further south than northern France showed no timing response to spring conditions in Iceland.
Conclusions Migratory birds can respond to high inter-annual variation in spring conditions on the breeding grounds even though they have to face a long journey over a migration barrier. Species that are wintering closer to the breeding grounds or migrating shorter distances in the last leg of the journey seem to be better informed about spring conditions in Iceland and show a more pronounced response to local temperatures.

Many species of birds, and other organisms, have advanced their phenology in recent years (Crick *et al.* 1997, Parmesan & Yohe 2003, Both *et al.* 2005, Tottrup *et al.* 2006, Hubalek & Capek 2008). The fitness benefits of documented phenological changes are often unclear, but species would generally be expected to chase favourable conditions (e.g. optimal timing for breeding) either rapidly through phenotypic plasticity or through an evolutionary response which would require a change in allele frequencies (Visser & Both 2005). These two routes of change are not mutually exclusive as phenotypic plasticity has an evolutionary basis (Nussey *et al.* 2005, Rubolini *et al.* 2007). There is substantial evidence that long-distance migrants have advanced their timing of spring migration less than short-distance migrants in response to climate change (Lehikoinen *et al.* 2004, MacMynowski & Root 2007, Hubalek & Capek 2008), but see Jonsén *et al.* (2006) for opposite effects. Long-distance migrants are thought to be less informed about spring conditions in the breeding grounds than short-distance migrants, resulting in less plastic departure from the wintering grounds and less variation in temporal trends (Both *et al.* 2010, Rubolini *et al.* 2010). This difference may have severe consequences for evolutionary and population processes, through trophic mismatch and differential exposure of the two groups to external conditions on migration and in winter (Balbontín *et al.* 2009, Both *et al.* 2010).

Most studies of changes in the phenology of migration have concerned movements over the landmasses of mainland Europe (and across the Sahara from Africa) and North America (Visser & Both 2005, and references therein). In such cases, birds can migrate gradually in stages, assessing the conditions *en route* to the breeding grounds. However, when birds have to cross barriers, such as large bodies of open water, the trade-off between potential fitness benefits and the decision of whether to migrate or not, becomes more critical. This is especially important at northerly latitudes,

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where conditions upon arrival can be harsh, but less so further south where it is unlikely to hit fatal conditions after crossing a migration barrier. However, studies measuring changes in migration phenology at northern latitudes (north of 60° N) are underrepresented in the literature (Gordo 2007).

Iceland is located in the middle of the North Atlantic ocean and is an important breeding ground for many species of birds, particularly seabirds, wildfowl and shorebirds. During a short period in spring (from late March to early May) the country is invaded by large numbers of migratory birds which have successfully made the crossing from mainland Europe (where most species winter) and in some cases from further away in Africa and the southern oceans. Most of these species are land-birds and for those it is important that they get the timing right to avoid bad conditions on arrival. In occasional springs, arriving migrants hit subzero temperatures with all inland ground and waters frozen. Under such conditions, the cues that individuals have pre-migration that can be used to tune their timing of arrival will be very important. The external cues migrants have, to get the timing of arrival at the breeding grounds right, will include both large-scale phenomena like the North Atlantic Oscillation (NAO), which influences spring condition and preparedness, and smaller-scale weather events (Schaub *et al.* 2004), which give more immediate information about conditions along the migration route. Previous studies of individual Black-tailed Godwits *Limosa limosa islandica* migrating to Iceland have shown that individuals are under the influence of winter conditions as they arrive earlier in years when the NAO Index is higher (Gunnarsson *et al.* 2006). The correlation with conditions on arrival and general prospects for breeding remains unclear for this species and others. The period between assessment of conditions before the sea crossing to Iceland and arrival in Iceland is probably rather short. Satellite-tracked Whooper Swans *Cygnus cygnus* and Greater White-fronted Geese *Anser albifrons* have been shown to cross from the UK in 12–25 hours in favourable conditions (Pennycuick *et al.* 1999, Fox *et al.* 2003). Individually-marked Black-tailed Godwits have similarly been known to cross in one to two days both from the UK and the Netherlands (Gunnarsson *et al.*, unpublished data on re-sightings of marked birds). Black-tailed Godwits migrating to Iceland have shown that individuals can finely tune their arrival dates to the breeding grounds, but this control is most likely a product of close monitoring of conditions during migration (Gunnarsson *et al.* 2004).

The NAO Index is defined as a north–south oscillation in atmospheric pressure between the Iceland low and Azores high (Hurrel & van Loon 1997). By definition, high NAO values coincide with low pressure over Iceland and low values with high pressure over Iceland. With low NAO values, temperature in Iceland can be either high or low depending on the type of the high pressure system. Therefore, the NAO does not generally have a statistically significant influence on temperature in Iceland (Olafsson 1999, Bjornsson & Jonsson 2003, Jonsson *et al.* 2009). Precipitation in Iceland is, on the other hand, slightly related to the NAO and tends to be higher with low NAO values (Bjornsson & Jonsson 2003). The midwinter NAO has been positively correlated with low pressure systems during winter in Iceland (Jonsson *et al.* 2009). These are usually characterized by wet, windy winters. These conditions have been found to negatively affect the breeding parameters of a resident, the Common Eider *Somateria mollissima* (Jonsson *et al.* 2009), but are conversely likely to predict a faster onset of spring as ground-frost can often be reduced after winters with positive NAO values. Migrants that experience milder winters (positive NAO) when wintering in western Europe are likely to be better prepared for migration through improved feeding conditions (Gunnarsson *et al.* 2006).

In the present study we analysed the changes in timing of spring migration to Iceland for 17 species of common birds between 1988 and 2009 based on first arrivals at an inland site. We analysed the changes in timing of spring arrival to assess if, and how fast, migrants respond to changing conditions when they have to make decisions of when to cross barriers on migration. Data on timing of migration in Iceland is scarce as no formal monitoring occurs (but see Boyd 2003, Boyd & Petersen 2008).

METHODS

Migrant arrivals

Data on the timing of first arrival dates of locally common species were collected in and around the village Laugaras in central southern Iceland (64° 7′ N, 20° 30′ W, Fig. 1). Each day a standardized route of 1 km was walked in the village of Laugaras at four fixed times (around 08:00, 12:00, 13:00 and 18:00 hours) and all first arrivals seen or heard were recorded. During the migration period, nearby farmland and wetlands were also checked from a car once daily (usually between

12:00 and 13:00 hours) for new arrivals. The data set contains first day of spring arrival from 1988 to 2009 for 17 common species that breed in or migrate through the study area. These are four species of Laridae: Arctic Skua *Stercorarius parasiticus*, Arctic Tern *Sterna paradisea*, Black-headed Gull *Larus ridibundus*, and Lesser black-backed Gull *Larus fuscus*; four species of Anatidae: Greylag Goose *Anser anser*, Pink-footed Goose *Anser brachyrhynchus*, Greater White-fronted Goose, and Barnacle Goose *Branta leucopsis*; six species of Charadriiformes: Oystercatcher *Haematopus ostralegus*, European Golden Glover *Pluvialis apricaria*, Black-tailed Godwit *Limosa limosa*, Whimbrel *Numenius phaeopus*, Common Snipe *Gallinago gallinago*, and Common Redshank *Tringa totanus*; and three species of Passeriformes: Redwing *Turdus iliacus*, Meadow Pipit *Anthus pratensis*, and White Wagtail *Motacilla alba*. All are Icelandic breeders except the White-fronted Goose and Barnacle Goose which are High-Arctic breeders that stage in Iceland for a few weeks in spring and autumn. Most of these species winter in western Europe, particularly in the UK, but Whimbrel, Lesser Black-backed Gull and White Wagtail winter in West Africa, Arctic Terns winter in the South Atlantic and Arctic Skuas winter in the central Atlantic ocean (Petersen 1998, G.A. Gudmundsson, pers. comm.). These are about 35% of the common Icelandic migrant species (Petersen 1998). Some less conspicuous, yet fairly common, species in the general area were not included in the analysis as they take more searching to find, or breed out of the monitored area, and thus the timing of first spring arrivals would have been less accurate than for the included species. Missing values for some of the species are because of observer absence during days on which arrival of those species could have occurred and these years were excluded from analysis.

As the study area was inland (40 km from the coast) the data are unlikely to be confounded by the occasional very early arrivals that turn up coastally most years. The data presented here are considered to be very much representative of the major wave of spring arrival of migrants in Iceland. For example, for Black-tailed Godwits, a species whose total arrival period has been monitored in detail since 1999, the first arrivals in our study area are close to the modal values of the

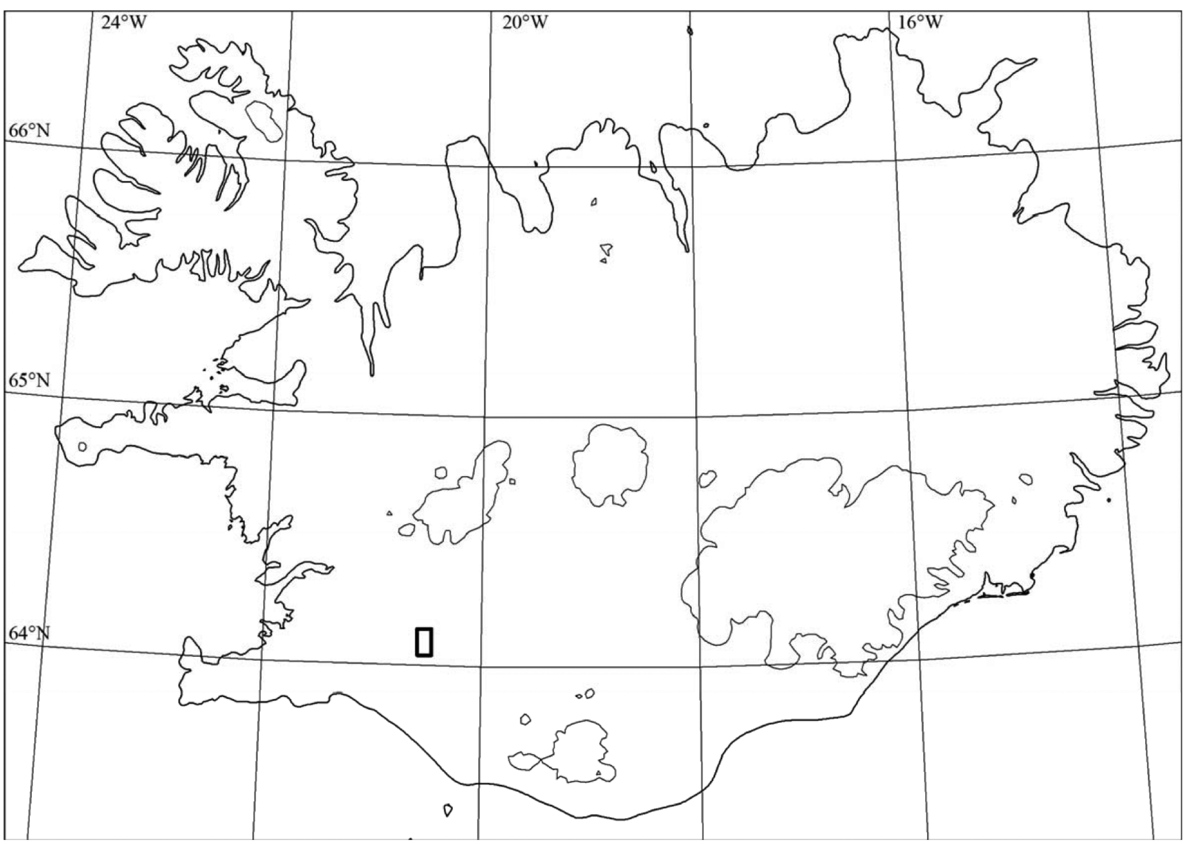

Figure 1. Map of Iceland showing the study area. The village of Laugarás (see Methods) and approximate surveyed nearby farmland and wetlands are shown by a black square.

total arrival curve of birds arriving in the country (Gunnarsson *et al.* 2006).

First arrival dates are generally positively correlated with mean arrival dates, although different parts of migrating populations can respond differently to changing conditions (Sparks *et al.* 2005). For a few of the species, some individuals do winter in Iceland. A few thousand individuals of Black-headed Gulls, Oystercatchers, and Redshanks are resident on the south and southwest coasts (Petersen 1998). Individuals of those species can potentially respond quickly to favourable conditions and move inland to the breeding grounds. These movements would, nevertheless, be linked to changing climate and can be explored in parallel with species, of which all individuals winter abroad. In addition, a few individuals of Common Snipe and Redwing were resident in the study area. These individuals were very few (about 5–10 of each species, authors unpubl. data) and relied on geothermal heat that kept some of the ground in the study area unfrozen year-round. For those two species, first arrival was considered when there was a noticeable influx of individuals outnumbering those that were resident. This spring influx was quite prominent, with several Snipe drumming simultaneously and flocks of Redwing spread around the village of Laugaras.

Climate and weather

To explore whether the timing of spring migration of individual species had changed over time the first arrival dates for each species were regressed over year after first exploring the change in spring temperatures over the study period. We then investigated whether winter conditions influenced timing of spring arrival in Iceland. Data on the NAO were obtained from ftp://ftp.cpc.ncep.noaa.gov/ and the winter NAO (average of January to March NAO values) was entered into the regression models to investigate if winter conditions were related to the variation in timing of arrival. Data on local temperature were obtained from a weather station of the Icelandic meteorological office (www.vedur.is) at Hæll (64° 3.9′ N, 20° 14.5′ W), which is 13 km from the study area. We ran a principal components analysis (PCA) with mean monthly temperature, mean humidity, and mean wind force to explore the relationship between weather factors in April (the month when most species arrived). PC1 explained 63% of the variation in weather. Temperature and humidity loaded positively on PC1, but windforce negatively, characterizing warm, wet and calm springs as opposed to cooler, drier and windier springs. The correlation between temperature and PC1 was very high (Pearson's $r = 0.82$, $n = 18$, $P < 0.001$) and we used temperature as a surrogate for spring conditions in all subsequent analyses. Temperature is arguably very important as it determines directly whether inland waters and grounds are frozen at the time of arrival. For each species the average monthly temperature in the month of arrival of that species was extracted as a measure of the conditions on arrival. For most of the species this was April, but Whimbrel, Arctic Skua, Arctic Tern and White Wagtail arrived in May. Predictors (temperature and NAO) were entered separately into the regression models as they related to different potential causes of changes in arrival (temperature to breeding ground conditions, but NAO to winter conditions) and sample size (number of years) was too small to allow for a multivariate model.

To investigate the relationship between migration distance and the timing of arrival, migration distances (approximate mid-point of winter range) were extracted from the relevant literature and from experts (as much of Icelandic ringing data are unpublished) (Petersen 1998, G.A. Gudmundsson, pers. comm.). To see how long- and short-distance migrants responded to local conditions, Pearson's correlation between spring arrival time and spring temperature was regressed on (log) migration distance.

RESULTS

General trend

Within the period of study, 1988 to 2009, spring temperature (April mean) increased rapidly in the study area, on average by around 4°C (Fig. 2). The annual variation was high; mean April temperatures ranged from about −1 to 6°C. The longer-term April mean temperature from when temperature recording began in the area (1961) changed very little, however, and the average was 2.3°C (± 1.5 sd) (correlation between year and temperature: $r = 0.024$, $P = 0.874$). Most of the species under study (16 of 17) showed a tendency towards earlier arrival during the study period (Table 1, Figs 3–6). The average advancement of arrival for all 17 species was –0.43 days/year (± 0.32 sd). The advance in arrival was significant for Black-headed Gull, Common Snipe, Black-tailed Godwit, all four goose species and White Wagtail (Table 1). The average advancement for the nine species which showed significant trends was –0.66 days/year (± 0.33 sd).

Table 1. Change in the timing of spring arrival of some common Icelandic migrants between 1988 and 2009. Results of a regression analysis of timing of arrival (ordinal date) on year are shown.

	Species	Migration distance (km)	R^2	*P*	Yearly change in timing of arrival (days)	se
Larids	Arctic Skua	6000	0.159	0.082	−0.399	± 0.225
	Lesser Black-backed Gull	3300	0.007	0.724	−0.082	± 0.283
	Black-headed Gull	1200	0.508	**0.0002**	−0.713	± 0.216
	Arctic Tern	15000	0.140	0.114	0.375	± 0.141
Waders	Golden Plover	2000	0.183	**0.047**	−0.427	± 0.242
	Oystercatcher	1500	0.165	0.060	−0.407	± 0.215
	Common Snipe	1500	0.408	**0.001**	−0.639	± 0.188
	Redshank	1800	0.132	0.097	−0.363	± 0.202
	Black-tailed Godwit	2000	0.654	**0.0001**	−0.809	± 0.090
	Whimbrel	6000	0.025	0.482	−0.158	± 0.143
Geese	Pink-footed Goose	1500	0.609	**0.0001**	−0.782	± 0.166
	Greylag Goose	1600	0.520	**0.0002**	−0.721	± 0.128
	White-fronted Goose	1500	0.559	**0.0001**	−0.748	± 0.146
	Barnacle Goose	1200	0.445	**0.001**	−0.667	± 0.130
Passerines	Redwing	2000	0.026	0.474	−0.161	± 0.306
	Meadow Pipit	2500	0.048	0.328	−0.219	± 0.181
	White Wagtail	5000	0.219	**0.028**	−0.468	± 0.224

Significance levels below 0.05 are highlighted in bold; yearly change in timing of arrival is presented as standardized beta values; approximate migration distance (to centre of winter range) is also given.

Relationship with weather

Nine of the 17 species under study; Black-headed Gull, European Golden Plover, Oystercatcher, Common Snipe, Black-tailed Godwit and all the goose species, arrived significantly earlier in warmer springs and 13 of 17 species showed a negative relationship with temperature (Table 2).

The midwinter NAO values decreased slightly during the study period, although not significantly so ($R^2 = 0.18$, $P = 0.076$, $y = -0.3387x + 679.66$). There was a significant negative correlation between mean April temperature at Hæll and the winter NAO values ($r = -0.542$, $n = 22$, $P = 0.009$) suggesting that, during the

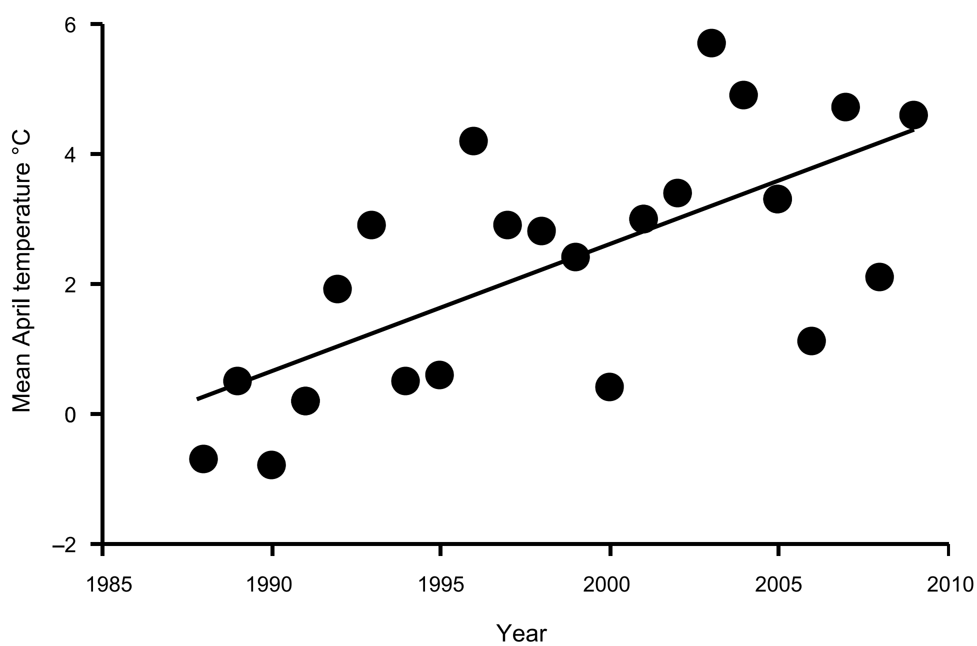

Figure 2. Changes in mean April (the month where majority of the species under study arrive) temperature in the study area from 1988 to 2009. $R^2 = 0.443$, $y = 0.1928x - 382.96$, $P < 0.001$).

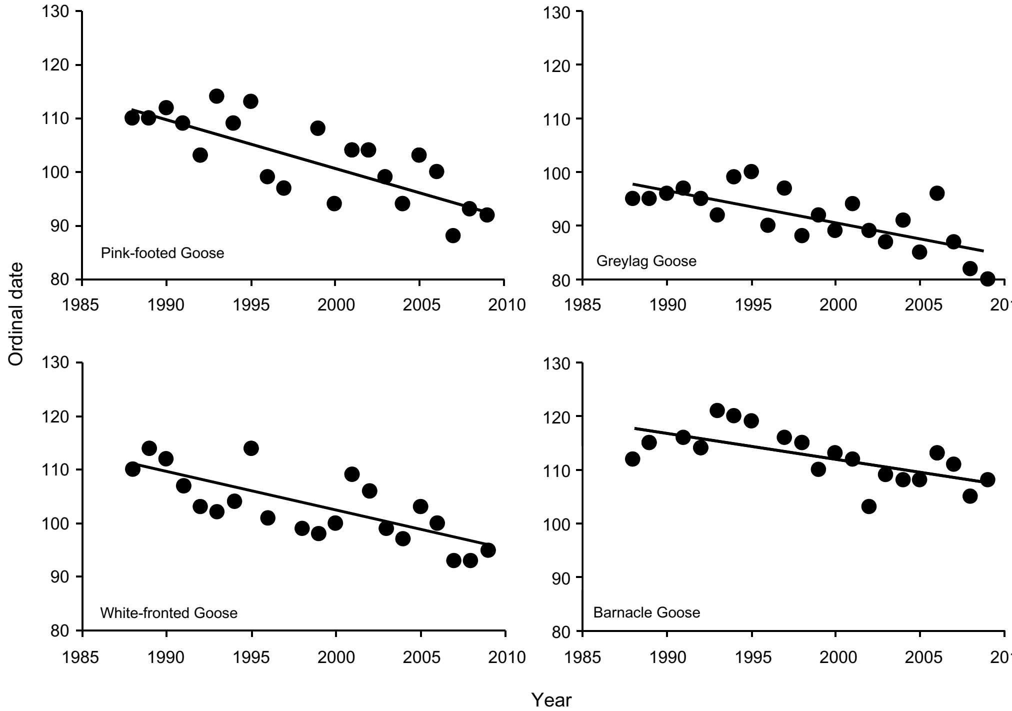

Figure 3. First spring arrival dates of four goose species in southern Iceland from 1988 to 2009. Results of linear regression are in Table 1; equations: Pink-footed Goose, $y = -0.9012x + 1903.8$; Greylag Goose, $y = -0.5963x + 1283.3$; White-fronted Goose, $y = -0.7176x + 1536.9$; Barnacle Goose, $y = -0.4937x + 1099.3$.

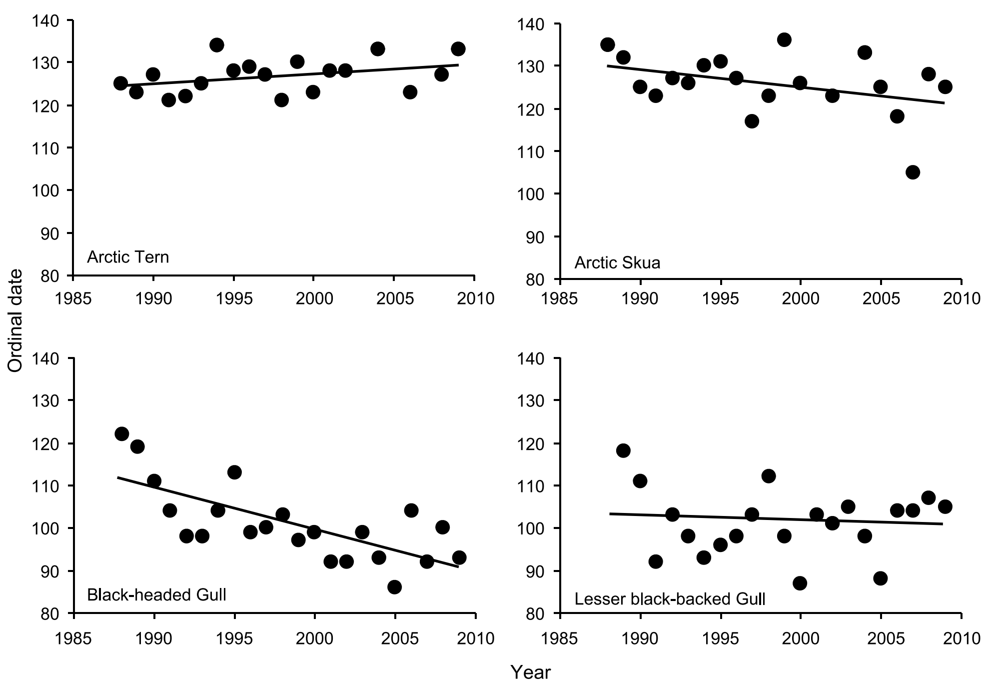

Figure 4. First spring arrival dates of four species of Larids in southern Iceland from 1988 to 2009. Results of linear regression are in Table 1; equations: Arctic Tern, $y = 0.2352x - 343.05$; Black-headed Gull, $y = -0.9825x + 2064.3$; Arctic Skua, $y = -0.4147x + 954.47$; Lesser Black-backed Gull, $y = -0.1013x + 303.64$.

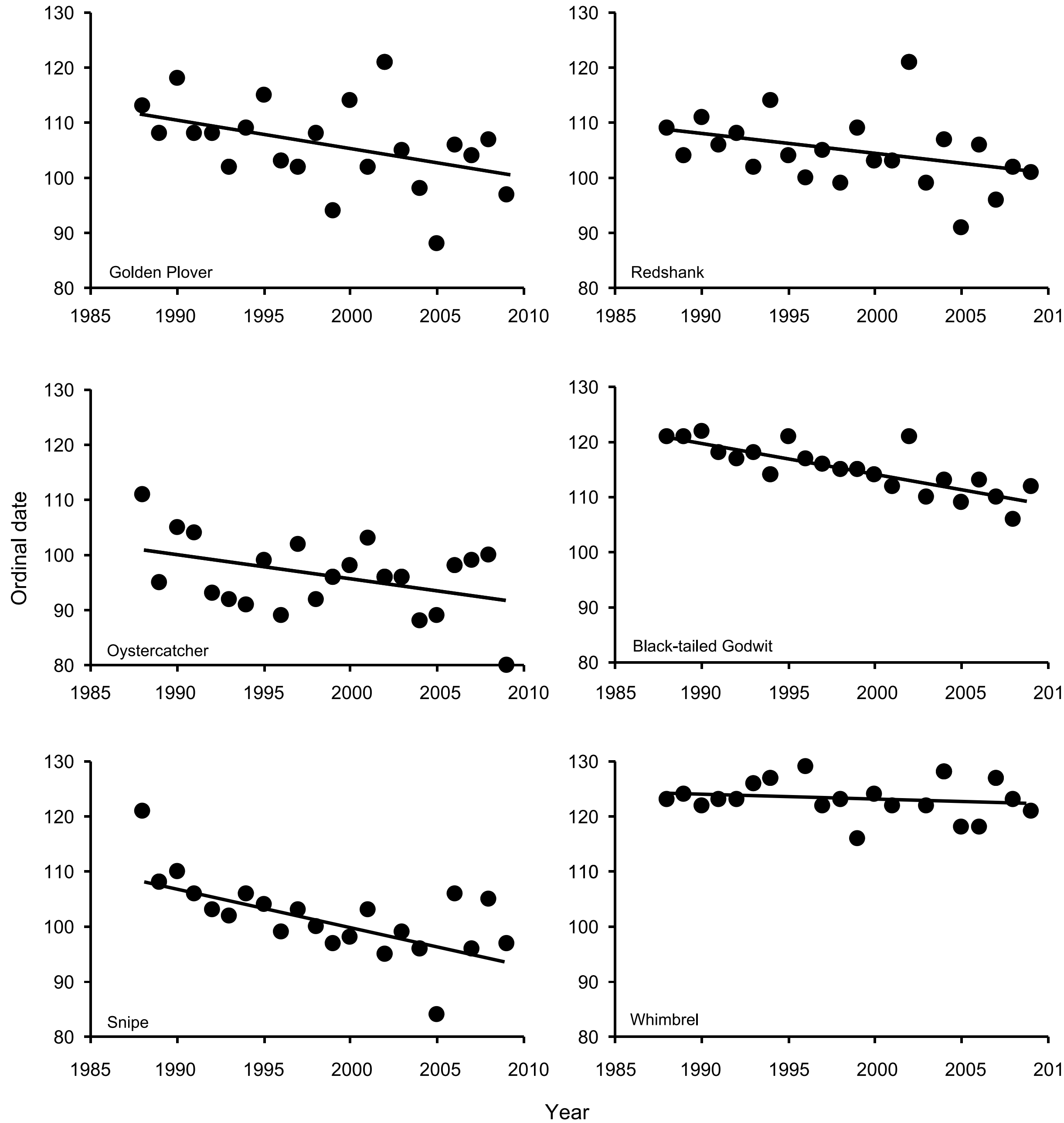

Figure 5. First spring arrival dates of six species of waders in southern Iceland from 1988 to 2009. Results of linear regression are in Table 1; equations: Golden Plover, $y = -0.5104x + 1126$; Oystercatcher, $y = -0.428x + 951.55$; Snipe, $y = -0.6979x + 1496.5$; Redshank, $y = -0.3523x + 808.7$; Black-tailed Godwit, $y = -0.5528x + 1220$; Whimbrel, $y = -0.1028x + 329.29$.

study period, when wintering conditions were harsher in Europe, migrants could expect better conditions on arrival in southern Iceland. Black-headed Gull, Golden Plover, Black-tailed Godwit, Pink-footed Goose, White-fronted Goose and Barnacle Goose showed a significant tendency to arrive earlier after milder winters (positive NAO values) and 15 of 17 species showed a positive relationship with the NAO (Table 2).

Migration distance and timing of arrival

Even though the sample size was too small to control for taxonomic bias, overall there was a

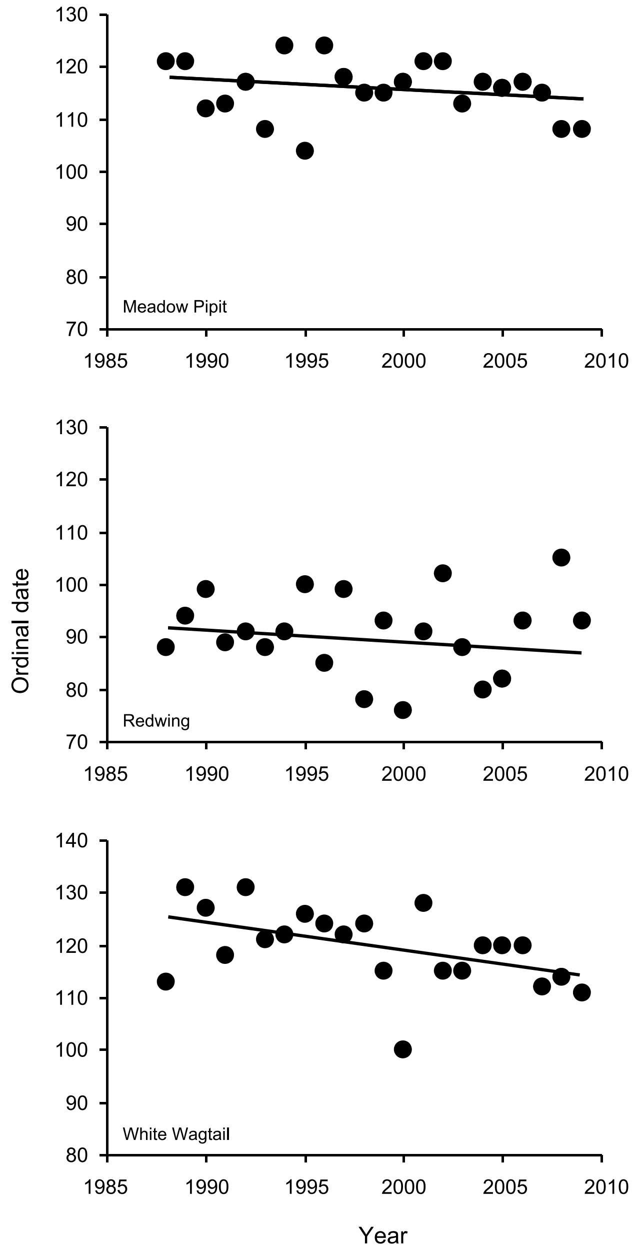

Figure 6. First spring arrival dates of three species of passerines in southern Iceland from 1988 to 2009. Results of linear regression are in Table 1; equations: Meadow Pipit, $y = -0.1813x + 477.92$; Redwing, $y = -0.223x + 535.42$; White Wagtail, $y = -0.5302x + 1179.1$.

significant trend for longer-distance migrants to arrive later in Iceland (linear regression of mean arrival day [ordinal date] during the study period on [log] migration distance: $R^2 = 0.563$, $n = 17$, $P < 0.001$) and to show less response to local spring temperature in Iceland (Fig. 7). Correlation coefficients between arrival and spring temperature for each species were regressed on (log) migration distance ($R^2 = 0.832$, $n = 17$, $P < 0.0001$). Considering the migration distance of the species, which showed a significant correlation between spring temperature and arrival (Table 2, Fig. 7), species that are wintering further away from Iceland than approximately 2300 km (further south than northern France) did not seem to show a phenological response to spring temperatures in Iceland.

Table 2. Relationship between the timing of migration and climate variables from 1988 to 2009. Regression statistics are shown for the winter (mean of January–March) North Atlantic Oscillation (NAO) and the mean temperature in the study area in the month when a given species arrived most frequently.

		NAO				Mean temperature in arrival month			
Species		R^2	P	ß	se	R^2	P	ß	se
Larids	Arctic Skua	0.036	0.424	0.189	± 6.35	0.087	0.220	0.295	± 1.81
	Lesser Black-backed Gull	0.045	0.337	0.212	± 6.55	0.001	0.873	0.037	± 0.98
	Black-headed Gull	0.334	**0.005**	0.578	± 6.37	0.546	**0.0001**	−0.739	± 0.72
	Arctic Tern	0.049	0.364	−0.221	± 3.56	0.165	0.095	0.406	± 0.98
Waders	Golden Plover	0.311	**0.007**	0.558	± 5.61	0.299	**0.008**	−0.547	± 0.77
	Oystercatcher	0.075	0.218	0.273	± 5.73	0.336	**0.005**	−0.579	± 0.66
	Common Snipe	0.150	0.075	0.387	± 5.70	0.475	**0.001**	−0.684	± 0.61
	Redshank	0.109	0.134	0.330	± 5.18	0.165	0.061	−0.406	± 0.68
	Black-tailed Godwit	0.331	**0.005**	0.575	± 3.16	0.302	**0.008**	−0.549	± 0.44
	Whimbrel	0.099	0.155	0.314	± 3.49	0.019	0.551	0.139	± 1.11
Geese	Pink-footed Goose	0.222	**0.031**	0.471	± 5.92	0.371	**0.003**	−0.609	± 0.73
	Greylag Goose	0.167	0.059	0.409	± 4.27	0.392	**0.002**	−0.626	± 0.50
	White-fronted Goose	0.269	**0.016**	0.519	± 4.81	0.412	**0.002**	−0.642	± 0.58
	Barnacle Goose	0.244	**0.027**	0.499	± 4.10	0.240	**0.029**	−0.489	± 0.55
Passerines	Redwing	0.075	0.218	0.273	± 7.55	0.096	0.161	−0.309	± 1.02
	Meadow Pipit	0.028	0.457	−0.167	± 4.61	0.002	0.842	−0.045	± 0.64
	White Wagtail	0.030	0.444	0.172	± 6.31	0.053	0.314	−0.231	± 1.85

Significance levels < 0.05 are highlighted in bold. Beta levels are standardized values.

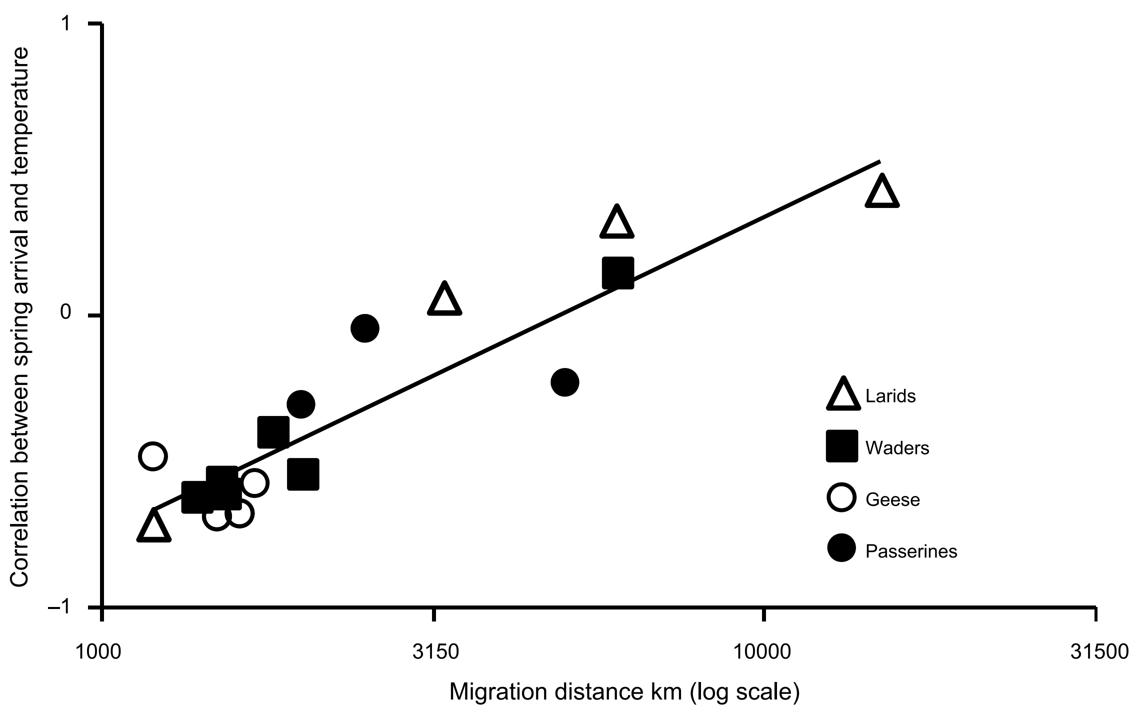

Figure 7. Relationship between migration distance (log km to centre of winter range) and the correlation between spring arrival time and spring temperature in Iceland ($R^2 = 0.831$, $y = 1.091x - 4.0233$, $P < 0.001$). The sample size is too small to correct for taxonomic bias, but different taxonomic groups are noted with separate symbols.

DISCUSSION

During the study period spring temperatures in the study area in southern Iceland increased rapidly and much faster than the longer-term trend from 1961, which was largely static. This provides an opportunity to explore how flexibly migrant birds are able to respond to such high interannual variation in climate. Indeed, many of the species showed rapid significant advancement in the timing of arrival to Iceland and most showed a tendency to arrive earlier (Figs 3–6). There was similarly an overall trend for many species to arrive earlier after milder winters (positive NAO). This is despite the fact that winter conditions are negatively correlated with conditions on arrival in the northern breeding areas. In fact, the migrants seemed both to respond positively to favourable winter conditions and arrive earlier in warmer springs. So how do these birds resolve this contrasting information? It is likely that the explanation has to do with the process of migration itself. Warmer springs in Iceland are most often accompanied by southerly winds (Boyd & Petersen 2006). For most Icelandic migrants these will be tailwinds which will make the crossing over the North Atlantic both energetically cheaper and less risky. So even though a migrant is in a poorer condition after a harsher winter, the condition may still be good enough to make use of the favourable southerly winds that characterize warm springs in Iceland. When crossing inhospitable barriers on migration, a favourable tailwind will be of great importance (Gudmundsson 1993). Studies comparing spring departure condition of Icelandic/Greenland breeding Wheatears *Oenanthe oenanthe* (sea crossing of 1000–2500 km) and Scandinavian Wheatears (sea crossing of 50–500 km), from Helgoland in the North Sea, have shown that the former depart almost exclusively under favourable wind assistance, whereas the latter are indiscriminate (Dierschke & Delingat 2001). A migrant departing from the British Isles or mainland Europe for Iceland in spring will face a decision of whether to catch the current tailwind or to wait an unknown period for the next period of favourable conditions, risking negative fitness consequences. Hence, the negative effects of poor winter condition (as measured by the NAO) on timing of arrival may be overridden by this effect in most years.

Most studies of changes in timing of migration have taken place over landmasses where migrants can travel gradually, assessing conditions on the way. In our case, birds have to cross the North Atlantic from the British Isles or mainland Europe or Africa, which could be expected to result in conservative departure decisions masking any links between climate and timing of migration. This seemed to be the case in a recent study by Tombre *et al.* (2008). In that study, Barnacle Geese, migrating from the Solway Firth in Britain to northern Norway (about 1500 km) showed no relationship between timing of migration and advancement of spring (a climate surrogate, measured by the Normalized Difference Vegetation Index), whereas Pink-footed Geese that migrated gradually from Belgium to northern Norway showed a clear relationship with the onset of spring (Tombre *et al.* 2008). Most of the Barnacle Geese migrating to Iceland also winter in the Solway Firth and migrate a comparable distance to Iceland. Yet, they show a strong tendency to migrate earlier in warmer springs, as do the other species of geese also wintering in the northern part of the British Isles. This discrepancy might possibly be related to the difference in spring conditions in southern Iceland and northern Norway or the differences between cues about conditions at the destination that the geese can obtain pre-departure. A study exploring the phenology of spring migration of several species to northern Norway in 1980–2000 did not find general advancement of spring arrival, but mean spring temperatures changed little during the period (Barrett 2002). Barnacle Geese travelling to Iceland can generally expect milder spring conditions on arrival than they can in northern Norway, but they will also have experienced continuous warming for several years, which may facilitate a plastic response.

As found in several other studies (Lehikoinen *et al.* 2004, Both *et al.* 2005, MacMynowski & Root 2007, Hubalek & Capek 2008), long-distance migrants in this study showed very little or no tendency to arrive earlier through the period or in relation to climate variables. However, it should be borne in mind that this relationship is based on few species and taxonomic bias is not corrected for. The distribution of migration distances of the larids and waders in this study was considerable and both fell into the same pattern, whereas geese and passerines showed much less variation in migration distances (Fig. 7). Only species migrating about 2300 km or less showed a phenological response to annual variation in conditions. Birds that are wintering further away are likely to be less able to assess conditions for the sea crossing to Iceland and for prospects on arrival, making their departure less flexible. A recent study on Black-tailed Godwits migrating to Iceland lends some support to this and shows how this contrast can operate within populations (Alvés *et al.* forthcoming). Godwits winter across western Europe from Britain to Iberia and span a range of distances of about 1000–3000 km from Iceland (Gunnarsson *et al.* 2006). Spring migration is rather synchronous despite this fact and is achieved because individuals wintering furthest south start their migration before their northern counterparts. As a result, birds wintering at the southern end of the range can take advantage of favourable migration conditions and departure cues at the northern end of the range, and early springs in Iceland, as do northern winterers (Alvés *et al.* forthcoming). For species which winter over such broad ranges this mechanism may well be common within populations if optimal timing on the breeding grounds has strong fitness consequences. However, for most of the long-distance migrant species in this study, most individuals winter further away (>2300 km), which is likely to explain why they do not show a response to annual variation in conditions within the time period studied here.

In conclusion, Icelandic, short-distance migrants show flexibility in their spring arrival in relation to changeable climate conditions, where as long-distance migrants do not. The fact that migrants have to cross a large body of open ocean – a migration barrier – does not mask the correlation between spring conditions and timing of migration. It is likely that pre-migrating birds can reliably assess conditions in Iceland before embarking on the sea crossing.

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