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Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes

Martin Stervander, Åke Lindström, Niclas Jonzén and Arne Andersson

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We studied long-term trends and the yearly variation in mean spring passage time in 36 passerine bird species trapped at Ottenby Bird Observatory in south-eastern Sweden. Between the years 1952–2002, data were available for 22–45 years depending on species. Most long-distance migrant species passed progressively earlier over the study period (range: 2.5 days earlier to 0.7 days later per 10 years, with an average of 0.9 days earlier per 10 years). The annual variation in timing of migration in most species, regardless of migration distance, correlated negatively with the winter index of the North Atlantic Oscillation (NAO), a large-scale climate phenomenon influencing the climate in the North Atlantic region. Birds passed earlier after mild and humid winters, corresponding to the high phase of the NAO. This corroborates the pattern found at a nearby migration site with a comparable dataset (Helgoland, 600 km WSW of Ottenby). However, short/medium-distance migrant species at Ottenby, in contrast to the situation at Helgoland, have shown no general trend of earlier passage in recent years. This was probably a consequence of the shorter study period at Ottenby, which included only the last 22–32 years (41 years at Helgoland), when the NAO showed no significant trend. At the species-specific level, the long-term trends in passage time were similar at the two sites, and there was some congruence to the extent that a given species was affected by NAO. Long-distance migrants wintering south and south-east of the breeding grounds showed some of the strongest changes in long-term trends (passing progressively earlier) at Ottenby, and for some of these species passage time varied negatively with NAO. Obviously, and contrary to previous suggestions, variations in NAO also influence birds migrating through eastern Europe, although the direct or indirect mechanisms through which this is achieved are unknown.

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The timing of various seasonal activities for plants and animals varies with climate (Forchhammer et al. 1998, Post and Stenseth 1999, Ottersen et al. 2001, Walther et al. 2002).

Climate affects migratory birds in many ways, directly such as in the timing of spring arrival (Mason 1995, Sokolov et al. 1998, Tryjanowski et al. 2002, Hüppop and Hüppop 2003, Vähätalo et al. 2004), the start of breeding (Crick et al. 1997, Sokolov and Payevsky 1998, Crick and Sparks 1999, Przybylo et al. 2000, Both and Visser 2001) and the timing of autumn migration (Jenni and Kéry 2003), as well as more indirectly at the population level (Jonzén et al. 2002). Variations in the timing of such life-history events are likely to influence important aspects of the ecology of birds, such as optimal timing of both breeding (Both and Visser 2001) and migratory stopover (Nolet and Drent 1998), in relation to available resources. The timing of

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life-history events is not only of interest for basic research but can also have ramifications for demography and, hence, population viability. It is therefore important to describe and analyse these patterns as well as their causes and consequences.

The climate in western Europe is dictated to a great extent by a large-scale climate phenomenon known as the North Atlantic Oscillation (NAO; Hurrell et al. 2001, 2003). The winter NAO index, in which high values are associated with mild, moist winters, and low values with cold, dry winters, has been found to explain a high degree of the variation in annual events in nature, such as the spring passage/arrival date of various migrant bird species (Forchhammer et al. 1998, 2002, Hüppop and Hüppop 2003, Boyd 2003, Vähätalo et al. 2004).

Hüppop and Hüppop (2003) analysed mean spring passage (msp) times of 24 species of migrants trapped in 1960–2000 on the German island Helgoland in the North Sea, serving as migratory stopover site. They found that both long-distance migrants (birds wintering in tropical areas) and short/medium-distance migrants (birds wintering in central or southern Europe, or around the Mediterranean) passed progressively earlier over the last 40 years, with the annual variation in most species being correlated to NAO. In years when winter and early spring in northern and western Europe were mild and humid, corresponding to the high phase of the NAO, the migrants passed earlier, whereas in years when winter and early spring were cold and dry, the migrants passed later. Since the long-distance migrants migrate later in spring (April–June) than the period over which the winter NAO index is measured (December–March), Hüppop and Hüppop (2003) suggested that the NAO during winter prepares the environment for spring migrating birds, especially through the influence on seasonal timing of food availability.

How general are the patterns found at one site to a larger geographical area? NAO has shown a strong positive trend for the last 40–50 years (Hurrell et al. 2003) and, accordingly, many species have been reported to arrive progressively earlier over the corresponding period at sites in north-western and central Europe (Mason 1995, Forchhammer et al. 1998, Sparks et al. 2001, Tryjanowski et al. 2002, Hüppop and Hüppop 2003). However, in other areas, such as northernmost Norway and Iceland, arrival dates have not changed over the past few decades (Barrett 2002, Boyd 2003), and there are also exceptions at the individual species level (e.g. Mason 1995, Hüppop and Hüppop 2003). Even within the same species, different patterns emerge at different sites. For example, whereas the arrival date of pied flycatchers *Ficedula hypoleuca* in the Netherlands did not seem to change during the last decades (Both and Visser 2001), the same species has been reported to arrive on average six days earlier over the last 40 years at Helgoland (Hüppop and Hüppop 2003). It is known that populations from different breeding or wintering areas often migrate in parallel "corridors" (Salomonsen 1955, Alerstam 1990). In such cases, different populations would visit different geographical areas during migration and winter, and therefore may be affected by different weather/climate, which in turn could influence their timing of migration.

Comparisons between sites, at the within- or between-species level, may be difficult because different methods of analysis and data collection have been used. For example, studies using first arrival date cannot necessarily be compared with data on mean arrival date for a particular population (Sparks et al. 2001). Further, the sets of species studied often differ at least partly between sites. At some localities long-term datasets of migrants can be biased by the occurrence of locally breeding populations. In this respect, Hüppop and Hüppop (2003) pointed at the advantage of ringing data from bird observatories situated on small islands, where no or few breeding birds occur. One aim of the present study was therefore to compare trends and patterns in passage time for a number of species at two different sites: our study site Ottenby in Sweden and at Helgoland, situated some 600 km WSW of Ottenby, as studied by Hüppop and Hüppop (2003), where methods of data collection and analysis were almost identical. Given that most migrants in western Europe move towards north-east in spring, these two sites are more or less along the same migration route for many species (Roos 1984, Liljefors et al. 1985, Pettersson et al. 1986, Hüppop and Hüppop 2003).

Forchhammer et al. (2002), Tryjanowski et al. (2002) and Hüppop and Hüppop (2003) suggested that birds which follow a central or easterly route through Europe in spring should be less affected by NAO than those following a westerly route, given that the influence of NAO on local climate should decrease with increasing distance from the Atlantic coast (Visbeck et al. 2001). Unlike the situation at Helgoland (Hüppop and Hüppop 2003), many long-distance migrant species that appear at Ottenby follow a central or easterly route through Europe. We were therefore able to test whether the effects of NAO are different on species with different migratory flyways.

In our analysis of the spring migration phenology of birds at Ottenby we address the following questions: (1) Does our dataset on spring migration confirm the overall picture of earlier spring passage and influence of the NAO? (2) At the species-level, are the trends similar at two nearby sites when the datasets are directly comparable? (3) Are species that follow an easterly route through Europe in spring less affected by NAO, as predicted by Forchhammer et al. (2002), Tryjanowski et al. (2002) and Hüppop and Hüppop (2003)?

Methods

Study area

Ottenby Bird Observatory (56° 12′ N, 16° 24′ E) is situated at the southernmost point of Öland, a 137 km long island ~10 km off the coast of south-eastern Sweden. The trapping area in the observatory garden is 1.2 hectares and contains most of the higher vegetation within the nearest 2 km. It is surrounded by water on three sides and by grazed meadows to the north. The next larger area of high vegetation is a forest 2 km to the north. During the migration period, the garden attracts large numbers of shrub- and woodland birds.

Birds have been caught at Ottenby in funnel traps of Helgoland-type (Bub 1991) since the first year of trapping in 1946, and mist nets have been used since 1959. Since 1980 the number of nets and traps, their position and use in spring have been strictly standardised. A total net length of 90 metres as well as two funnel traps are used. The fact that only funnel traps were used during the early years might have influenced the number of birds trapped. However, we see no reason why this should affect *when* in spring a bird is trapped. We therefore used trapping data for all years as a basis for calculating the mean spring passage (msp) time.

Origin of birds trapped

Birds have annually been ringed in spring since 1948. Up to 2002, more than 231,000 birds of 140 species were ringed during the spring migration. The majority of birds trapped are passerines on migration to their breeding grounds in Sweden, Finland, western Russia, and the Baltic states (Liljefors et al. 1985). Among short/medium-distance migrants, the vast majority in spring arrive from the south-west, since the birds winter mainly in western and south-western Europe or around the Mediterranean (Pettersson et al. 1986). In contrast, among long-distance migrants, roughly equal proportions (one third) of the common species in spring arrive from the south-east, the south and the south-west. They arrive from wintering grounds in tropical Africa or in a few cases Asia (Pettersson et al. 1986). We defined the main migration direction for each species. The northern subspecies of willow warbler *Phylloscopus trochilus acredula* migrates towards the south-east whereas the southern subspecies *Phylloscopus t. trochilus* migrates towards the south-west (Hedenström and Pettersson 1987). Since both subspecies are trapped at Ottenby, but not always distinguishable when handled in ringing, we considered the willow warbler a south migrant.

Data analysis

The start of spring trapping varied considerably in 1952–1979, whereas from 1980 onwards, the spring trapping started on March 15. In 1948–1951, spring trapping was carried out only sporadically. In order to make use of a maximal number of years for each species, we defined three different periods of analysis. Years when ringing was carried out from March 15 to June 15 are defined as early coverage years (early: 24 years comprising 1971 and 1980–2002). In principle, this period covers the complete spring migration of all species analysed (Enquist and Pettersson 1986). For medium coverage years, ringing carried out from April 1 to June 15 was analysed (medium: 35 years comprising 1961, 1965, 1969, and 1971–2002). This period allows analyses of all but the earliest short/medium-distance migrants. For late coverage years, ringing carried out from April 13 to June 15 was analysed (late: 45 years comprising 1952–1953, 1955, 1958–1959, 1961–1965, and 1968–2002). During this period, all long-distance migrant species except the white wagtail *Motacilla a. alba* (analysed as medium) pass Ottenby (Enquist and Pettersson 1986), although a very small number of the latest individuals in some species may pass even after June 15.

In some short/medium-distance migrants, small numbers appear in the March 15–31 period, whereas the main migration period clearly falls in April. For some species it was therefore not obvious whether they should be analysed as early or medium. Vähätalo et al. (2004) reported that, based on combined ringing and observation data from two Finnish bird observatories 1970–1999, the strongest effect of NAO is generally found in the migration phase containing the earliest 5% of the migrants. Combining all years when trapping started on March 15, we calculated the proportion of birds trapped before April 1. Detailed analyses showed that the mean msp time (mmsp time), trends and significance levels for species of which less than 5% of the spring total was trapped in the March 15–31 period were very similar when analysed as early and medium respectively. We therefore chose to analyse these species as medium.

Since an important part of our analysis is the comparison with data from Helgoland, we followed the protocol of analysis used by Hüppop and Hüppop (2003) as closely as possible. Therefore, we only selected species where a minimum of five birds were ringed in at least 75% of the years analysed. Within the selected species, years were excluded when less than five birds were ringed. Msp times were calculated as the arithmetic means of the ringing totals in the given years (Hüppop and Hüppop 2003).

Some differences between the datasets from Ottenby and Helgoland remain. The Helgoland dataset covers the years 1960–2000. For long-distance migrants, the Ottenby dataset comprises a somewhat longer period,

including some few years from the 1950's, whereas for many short/medium-distance migrants a shorter period is analysed at Ottenby. This latter fact was taken into account when investigating the correlations between the trends at the two different sites at a species-specific level. When comparing the average slope of msp time on year at Helgoland and Ottenby we excluded species analysed as early since for these species the study period at Ottenby only includes 1971 and the last 23 years, when the trend in winter NAO index was less pronounced (see below). This leaves thirteen species for the comparison, of which ten are long-distance migrants and three are short/medium-distance migrants. However, when comparing the average slope of msp time on winter NAO index at Helgoland and Ottenby, it was not obvious whether species analysed as early should be excluded, as in the previous analysis. On one hand, the less consistent changes in winter NAO index during the analysis period early should not influence to what degree a species' msp time is affected a given year. On the other hand, the longer analysis period and the larger variations in winter NAO index in this longer period, the greater the chance to obtain a correlation. We therefore made a twofold comparison of the average slope of msp time on winter NAO index at Helgoland and Ottenby and calculated the correlation for all 20 comparable species (ten long-distance migrants and ten short/medium-distance migrants) and for the 13 species not analysed as early, respectively.

The North Atlantic Oscillation

The NAO is one of the oldest known world weather patterns, for which data are available from the beginning of the 19th century. It dictates climate variability from the east coast of the USA to Siberia and from the Arctic to the subtropical Atlantic (Hurrell et al. 2003). The NAO index is defined as the normalised sea level pressure anomaly between Ponta Delgada, the Azores, and Reykjavik, Iceland. Like Hüppop and Hüppop (2003) we used the winter NAO index, averaging the NAO indices over the December–March period. A positive winter NAO index corresponds to stronger westerly winds, causing higher temperatures and higher levels of precipitation during winter/spring in western and northern Europe (Hurrell et al. 2001, 2003). The NAO index data were obtained from the Climatic Research Unit at the University of East Anglia (http://www.cru.uea.ac.uk/cru/data/nao.htm, see Fig. 1). The winter NAO index increased significantly over the 1952–2002 period (Fig. 1; $b = 0.023$, $r^2 = 0.087$, $P = 0.036$) but did not change significantly over the last 23 years ($b = 0.002$, $r^2 < 0.001$, $P = 0.951$) that constitute the main part of the analysis period early.

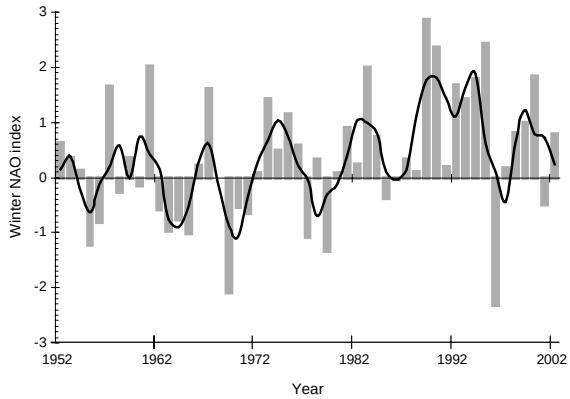

Fig. 1. The winter North Atlantic Oscillation (NAO) index over the period 1952–2002 ($b = 0.023$, $r^2 = 0.087$, $p_{(1)} = 0.036$). The smoothed curve shows running three-year averages. Data from http://www.cru.uea.ac.uk/cru/data/nao.htm.

Statistics

The effect on msp times of year and winter NAO index respectively were investigated by linear regressions. Following Chatfield (1999) residuals of the regressions were analysed for autocorrelation using the autocorrelation and partial autocorrelation functions and the crude significance limits of $\pm 2/\sqrt{N}$, where N is the length of the residual time series. Since autocorrelations were found in only 3 out of 39 species and these values were close to not being significant, we decided to keep the original regression models. The relationship between corresponding regression coefficients at Ottenby and Helgoland were examined by Pearson correlation. All statistics were calculated using SPSS 11.0 (SPSS Inc. 2001) for Windows.

Results

In total, 39 passerine bird species fulfilled the selection criteria used at Helgoland. However, the house martin *Delichon urbica* and common starling *Sturnus vulgaris* were excluded because trapping figures include local breeders to a significant extent. The common chiffchaff *Phylloscopus collybita* was also left out, because during the last decades the southern subspecies *Phylloscopus c. collybita* has started to appear in large numbers in southern Sweden, and this subspecies arrives much earlier than the northern subspecies *Phylloscopus c. abietinus* (Ellegren and Pettersson 1985, Håkansson and Rhönnstad 1993). Of the remaining 36 species, 19 are long-distance migrants and 17 are short/medium-distance migrants (for detailed values for all species, see Table 1).

Table 1. Main migration direction, study period, number, mean msp time (mmsp time), and regressions of mean spring passage (msp) time on year and on winter North Atlantic Oscillation (NAO) index, respectively, for 19 long-distance and 17 short/medium-distance migrants at Ottenby. Further, corresponding values at Helgoland (data from Hüppop and Hüppop (2003)) regarding mmsp time, regression coefficient for msp time on year and regression coefficient for msp time on winter NAO index are shown for the 20 species studied at both sites (+$p_{(1)}$ <0.1, *$p_{(1)}$ <0.05, **$p_{(1)}$ <0.01, ***$p_{(1)}$ <0.001).

No.[a]	Species	Migration direction	Period of analysis[c]	Number of years analysed	Study period	Number of individuals	Mms-p-time (Julian day[d])	Msp-time on year			Msp-time on winter NAO index			Corresponding values at Helgoland		
								b	p(1)	r^2	b	p(1)	r^2	Mms-p-time (Julian day)	b for msp-time on year	b for msp-time on winter NAO index
Long-distance migrants																
1	Barn swallow *Hirundo rustica*	S–N	L	35	1955–2002	937	150	−0.133	0.153	0.061	−1.307	0.178	0.054			
2	Tree pipit *Anthus trivialis*	S–N	L	42	1955–2002	1,187	133	−0.073	0.114	0.061	−0.743	0.132	0.056			
3	White wagtail *Motacilla a. alba*	SE–NW	M	32	1971–2002	585	131	0.066	0.688	0.005	1.279	0.338	0.031			
4	Thrush nightingale *Luscinia luscinia*	SE–NW	L	42	1952–2002	1,092	139	−0.132	0.001***	0.241	−0.444	0.384	0.019			
5	Bluethroat *Luscinia svecica*	SE–NW	L	38	1959–2002	1680	137	−0.062	0.198	0.046	−0.251	0.596	0.008			
6	Common redstart *Phoenicurus phoenicurus*	SW–NE	L	45	1952–2002	10,665	138	−0.004	0.923	0.000	−1.293	0.006**	0.163	138	−0.173**	−3.01***
7	Whinchat *Saxicola rubetra*	SW–NE	L	34	1952–2002	381	135	−0.064	0.148	0.064	−0.687	0.215	0.048			
8	Marsh warbler *Acrocephalus palustris*	SE–NW	L	34	1968–2002	722	154	−0.072	0.249	0.041	0.676	0.197	0.051			
9	Eurasian reed warbler *Acrocephalus scirpaceus*	SW–NE	L	45	1952–2002	1,335	153	−0.087	0.019*	0.121	−0.311	0.503	0.010	149	−0.202***	−1.29*
10	Icterine warbler *Hippolais icterina*	S–N	L	45	1952–2002	2,078	151	−0.082	0.010**	0.145	−0.667	0.089+	0.066	151	−0.045*	−1.01*
11	Lesser whitethroat *Sylvia curruca*	SE–NW	L	45	1952–2002	9,323	141	−0.185	0.000***	0.376	−1.581	0.003**	0.187	135	−0.202**	−2.23**
12	Common whitethroat *Sylvia communis*	S–N	L	45	1952–2002	5,874	146	−0.046	0.232	0.033	−0.898	0.052+	0.085	142	−0.167**	−2.39***
13	Garden warbler *Sylvia borin*	SW–NE	L	45	1952–2002	3,468	149	−0.107	0.002**	0.196	−0.868	0.049*	0.087	146	−0.181***	−0.86*
14	Blackcap *Sylvia atricapilla*	SE–NW	L	45	1952–2002	2,638	140	−0.248	0.000***	0.387	−2.401	0.001***	0.246	134	−0.249**	−1.60*
15	Willow warbler *Phylloscopus trochilus*	S–N[b]	L	45	1952–2002	44,924	137	−0.078	0.013*	0.134	−1.155	0.002**	0.198	139	−0.231***	−2.56***
16	Spotted flycatcher *Muscicapa striata*	S–N	L	45	1952–2002	2,713	147	−0.108	0.004**	0.174	−0.990	0.035*	0.099	150	−0.260***	−1.48**
17	Red-breasted flycatcher *Ficedula parva*	SE–NW	L	39	1955–2002	458	145	−0.179	0.000***	0.368	−1.122	0.028	0.124			
18	Pied flycatcher *Ficedula hypoleuca*	SW–NE	L	45	1952–2002	2,038	136	−0.053	0.171	0.043	−1.512	0.001***	0.241	138	−0.156*	−2.16**

Table 1 (*Continued*)

No.[a]	Species	Migration direction	Period of analysis[c]	Number of years analysed	Study period	Number of individuals	Mms-p-time (Julian day[d])	Msp-time on year			Msp-time on winter NAO index			Corresponding values at Helgoland		
								b	p(1)	r^2	b	p(1)	r^2	Mms-p-time (Julian day)	b for msp-time on year	b for msp-time on winter NAO index
Short/medium-distance migrants																
19	Red-backed shrike *Lanius collurio*	SE–NW	L	45	1952–2002	2,016	147	−0.032	0.421	0.015	0.274	0.569	0.008			
20	Winter wren *Troglodytes troglodytes*	SW–NE	E	24	1971–2002	2,353	108	−0.235	0.094+	0.122	−0.797	0.400	0.032	110	−0.215*	−2.03*
21	Hedge accentor *Prunella modularis*	SW–NE	E	24	1971–2002	1,772	101	0.024	0.872	0.001	−1.207	0.218	0.068	91	−0.126+	−2.78**
22	European robin *Erithacus rubecula*	SW–NE	M	35	1961–2002	57,742	114	−0.164	0.025*	0.143	−0.698	0.293	0.033	108	−0.168*	−0.99
23	Black redstart *Phoenicurus ochrurus*	SW–NE	M	33	1961–2002	449	123	−0.111	0.433	0.020	−1.346	0.288	0.036			
24	Common blackbird *Turdus merula*	SW–NE	E	24	1971–2002	3,857	95	−0.126	0.358	0.039	−2.248	0.007**	0.283	86	−0.282**	−2.95**
25	Fieldfare *Turdus pilaris*	SW–NE	M	30	1961–2002	323	125	0.421	0.016*	0.190	−1.234	0.461	0.020	122	−0.032	−1.53*
26	Song thrush *Turdus philomelus*	SW–NE	E	24	1971–2002	2,524	112	0.119	0.364	0.038	−0.316	0.718	0.006	111	−0.160**	−1.12*
27	Redwing *Turdus iliacus*	SW–NE	E	24	1971–2002	980	105	−0.059	0.681	0.008	−2.027	0.025*	0.209	98	−0.166*	−2.76**
28	Goldcrest *Regulus regulus*	SW–NE	E	24	1971–2002	5,119	101	0.006	0.973	0.000	−1.206	0.267	0.056			
29	Blue tit *Parus caerulaeus*	SW–NE	E	22	1981–2002	478	93	0.092	0.657	0.010	−1.585	0.152	0.100			
30	Great tit *Parus major*	SW–NE	E	24	1971–2002	1,355	92	−0.295	0.046*	0.169	−1.671	0.091+	0.124	76	−0.094	−3.86**
31	Chaffinch *Fringilla coelebs*	SW–NE	E	24	1971–2002	3,577	113	0.213	0.073+	0.139	0.322	0.692	0.007	95	−0.252**	−1.72*
32	Brambling *Fringilla montifringilla*	SW–NE	M	33	1961–2002	539	117	0.001	0.983	0.000	−0.943	0.134	0.071	108	0.068	0.12
33	European greenfinch *Carduelis chloris*	SW–NE	E	24	1971–2002	979	115	0.452	0.008**	0.278	1.138	0.347	0.040			
34	Common linnet *Carduelis cannabina*	SW–NE	M	32	1961–2002	1,392	133	0.088	0.433	0.021	−1.088	0.309	0.034			
35	Yellowhammer *Emberiza citrinella*	SW–NE	E	24	1971–2002	463	102	0.066	0.710	0.006	−0.764	0.515	0.019			
36	Reed bunting *Emberiza schoeniclus*	SW–NE	E	22	1971–2002	293	116	−0.027	0.865	0.001	1.624	0.102	0.128			

[a] No. refers to the numbers shown in Fig. 2 and 3.
[b] See the text for further explanation.
[c] E = Early coverage years, M = Medium coverage years, L = Late coverage years.
[d] Julian day = number of days since the turn of the year.

Long-distance migrants

As many as 18 of the 19 long-distance migrant species tended to pass Ottenby earlier over the study period (32–45 years per species in 1952–2002), the trends being statistically significant in nine species. Only one species, the white wagtail, showed an insignificant tendency to pass later in recent years. The average trend was −0.088, which is to say that the 19 species tended to pass 0.088 days earlier on average per year (range: −0.248 to 0.066).

The annual variation in msp time correlated negatively to the winter NAO index in 16 of the 19 species, so that milder, wetter winter/spring weather resulted in earlier passage at Ottenby in the spring. The correlations were statistically significant in eight species. Among these eight species, three arrive from wintering areas to the south-east, two from wintering areas to the south and three from wintering areas to the southwest of Sweden (Table 1).

Short/medium-distance migrants

In short/medium-distance migrants, eight of the 17 species tended to pass earlier over the study period (22–35 years per species in 1961–2002), and only two of them, the European robin *Erithacus rubecula* and the great tit *Parus major*, significantly so. In contrast, the passage of the fieldfare *Turdus pilaris* and the European greenfinch *Carduelis chloris* was significantly later over the study period. The average trend for all species was 0.013, which is to say that the 17 species tended to pass Ottenby on average 0.013 days later per year (range: −0.295 to 0.452).

In 14 of the 17 species the msp time correlated negatively with the winter NAO index, but only in two of them, the common blackbird *Turdus merula* and the redwing *Turdus iliacus*, were these patterns significant (Table 1). The picture regarding NAO dependence is thus similar to the long-distance migrants, but less pronounced.

Comparison between Ottenby and Helgoland

For 20 of the species, of which ten are long-distance migrants and ten are short/medium-distance migrants, comparable data are available from Helgoland (Hüppop and Hüppop 2003). For these species the correlation between mmsp times at Ottenby and Helgoland was very high ($r_{18} = 0.980$, $P < 0.001$), although absolute dates varied to some extent. Short/medium-distance migrants passed Helgoland on average 8 days earlier than at Ottenby (range: 18 days earlier to 2 days later) and long-distance migrants were on average 2 days earlier at Helgoland (range: 6 days earlier to 3 days later).

Overall, the patterns at the two sites are similar: most species at both sites passed progressively earlier over the study period, and most species show a negative correlation with NAO (Table 1). The average slope of msp time on year for the 13 species was significantly steeper at Helgoland than at Ottenby (−0.15 vs. −0.06 days per year; paired t-test, $t_{12} = 2.65$, $P = 0.021$). Hence, the trend of progressively earlier spring passage is stronger at Helgoland than at Ottenby. There was a significant correlation between the regression coefficients of msp time on year at the two sites (Fig. 2; $r_{11} = 0.566$, $P = 0.044$), which is to say that for a given species, the direction and relative strength of the trend were similar at the two sites.

Also the average slope of msp time on winter NAO index for these 13 species was significantly steeper at Helgoland than at Ottenby (−1.61 vs. −1.12; paired t-test, $t_{12} = 2.18$, $P = 0.05$). Thus, the influence of NAO on the timing of spring migration was stronger for the birds passing Helgoland. There was no significant correlation between the regression coefficients of msp time on NAO at the two sites (Fig. 3; $r_{11} = 0.357$, $P = 0.231$). When following a bit less conservative line and analysing all 20 comparable species, the average slope of msp time on winter NAO index was also significantly steeper at Helgoland than at Ottenby (−1.78 vs. −1.07; paired t-test, $t_{19} = 3.25$, $P = 0.004$). In

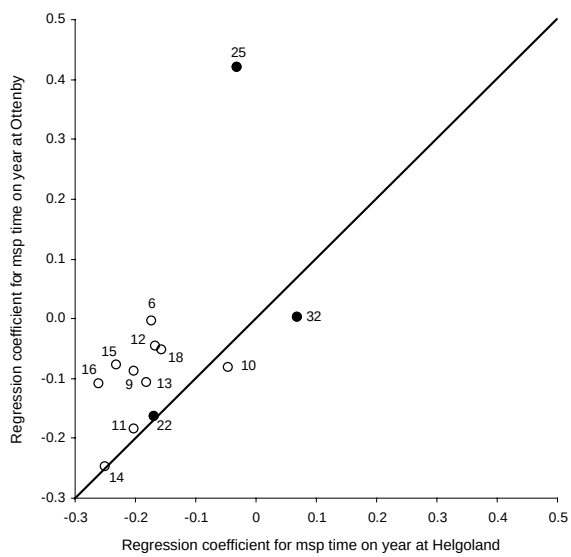

Fig. 2. Correlation between the regression coefficients for mean spring passage (msp) times on year at Helgoland (data from Hüppop and Hüppop (2003)) and Ottenby, respectively, for comparable species (n = 13 after excluding species analysed as early coverage years (early)): $r_{11} = 0.566$, $p = 0.044$. The diagonal line represents 1:1 ratio. Open circles signify long-distance migrants and filled circles correspond to short/medium-distance migrants. Numbers indicate species and refer to the No. column in Table 1.

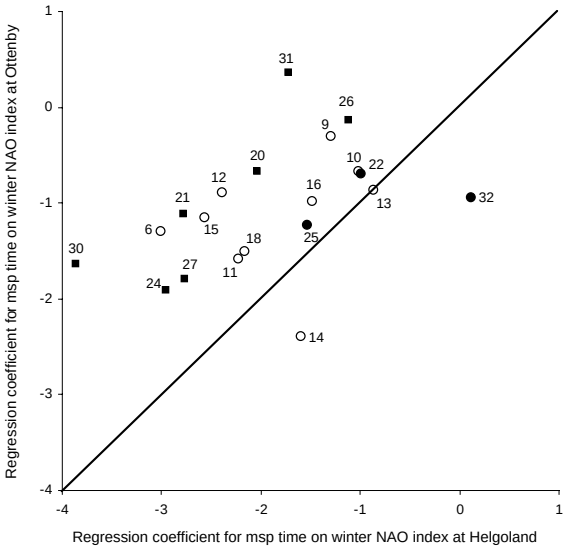

Fig. 3. Correlation between the regression coefficients for mean spring passage (msp) times on winter North Atlantic Oscillation (NAO) index at Helgoland (data from Hüppop and Hüppop (2003)) and Ottenby, respectively. Two correlations are relevant; for all comparable species (n = 20): $r_{18} = 0.450$, $p = 0.047$, and for species with a minimum study period of 42 years (n = 13): $r_{11} = 0.357$, $p = 0.231$. The diagonal line represents 1:1 ratio. Circles represent species with a minimum study period of 42 years (medium or late), while squares represent species analysed as early coverage years (early). Open symbols signify long-distance migrants and filled symbols correspond to short/medium-distance migrants. Numbers indicate species and refer to the No. column in Table 1.

this case, there was a significant correlation between the regression coefficients of msp time on NAO at the two sites (Fig. 3; $r_{18} = 0.450$, $P = 0.047$), which is to say that for a given species, the sensitivity to NAO is similar at the two sites.

Passage time in relation to migratory routes

Since all of the short/medium-distance migrants migrate along a SW–NE axis, the test of whether the degree of influence from NAO is correlated to migratory direction was carried out on long-distance migrants only. In long-distance migrants, five are SW migrants, six are S migrants and eight are SE migrants (Table 1). There was no significant effect of migratory direction on the regression coefficient of msp time on NAO (one-way ANOVA, $F_{2,17} = 0.75$, $P = 0.49$), with average regression coefficients being −0.85, −0.97, and −0.44 respectively for the three groups. Nor was there any effect of migratory direction on the average regression coefficient of msp time on year (one-way ANOVA, $F_{2,17} = 0.37$, $P = 0.70$). Hence, neither the influence of NAO nor the tendency to pass earlier over time was correlated to migratory direction.

Discussion

Overall trends and relationships to NAO

The results from Ottenby, with birds in general passing progressively earlier over the last 30–50 years and a negative correlation between passage date and winter NAO index for most species, are consistent with the situation at Helgoland (Hüppop and Hüppop 2003) and at other sites in north-western and central Europe (Mason 1995, Forchhammer et al. 1998, Sparks et al. 2001, Tryjanowski et al. 2002).

The fact that the short/medium-distance migrants fieldfare and European greenfinch passed Ottenby significantly later over the study period could possibly be explained by changes in the migratory habits (T. Fransson pers. comm.). Analyses of ringing recoveries of Swedish birds found in December–January give some indications. Fieldfare wintered 0.89° further south after 1960 than before ($n = 236$, $P < 0.05$), and a more detailed analysis indicates that it spent the winter 2.64° further south in the period of 1991–2002 than in 1981–1990 ($n = 46$, $P < 0.05$). The later passage in recent years at Ottenby may possibly be caused by the birds wintering further away than before. The results of corresponding analyses for European greenfinch are less clear. They show that the winter grounds were 1.05° further south after 1970 compared to before ($n = 374$, $P < 0.05$), but on the other hand that the species wintered 2.57° further north in 1991–2002 than in 1981–1990 ($n = 119$, $P < 0.001$; T. Fransson pers. comm.).

It may come as no surprise that short-distance migrants, which winter close to the breeding grounds and therefore can respond directly to changes in weather relevant to conditions at the breeding grounds, are profoundly affected by the winter NAO index. For example, looking at first arrival dates, Sokolov et al. (1998) found that a greater proportion of short/medium-distance migrants than long-distance migrants on the Courish Spit of the Baltic Sea showed significant long-term trends during the 1961–1990 period. This was also the case in western Poland in 1913–1996 (Tryjanowski et al. 2002). However, for two reasons it is remarkable that we also found the pattern in long-distance migrants to correlate strongly with the winter NAO index.

First, given that the onset of spring migration in long-distance migrants is endogenously controlled, as found in studies of caged birds (Berthold 1984, Gwinner 1996), the potential for these species to be affected by exogenous factors would be lower than for short/medium-distance migrants if the continuation of the migration also would be under endogenous control. Very little is known, however, of the variation in departure dates, and its potential causes, of free-living long-distance migrants from their tropical wintering grounds (but see Kok et al. 1991).

Second, although the long-distance migrants in spring pass through Europe weeks to months later than the winter NAO index was measured, these birds still seem to be affected. Hüppop and Hüppop (2003) suggested that this was because winter conditions affected the environment at stopover sites in Europe with carry-over effects into the time period when the long-distance migrants pass this area. Thus, after winters with a high NAO index, food for migrants would be available earlier. This reasoning may well be true as long as the migrants have arrived from the wintering grounds early enough to make use of the food availability in the early years. Accordingly, in years with a low winter NAO index they would have to wait for stopover conditions to improve before moving further north. It has been shown for geese and swans that the period of maximum foraging and fuelling possibilities at stopover sites can be short (Prop and Deerenberg 1991, Nolet and Drent 1998). It is therefore very important to be in place during this period since rapid fuelling is crucial for fast migration (Alerstam and Lindström 1990).

Among long-distance migrants, the past 40 years have seen an earlier msp time of four days on average, with as much as ten days in species like the blackcap *Sylvia atricapilla* and the spotted flycatcher *Muscicapa striata* (Hüppop and Hüppop 2003, this study). Although these trends are statistically significant in many cases, the biological significance of earlier passage of a few days over many decades is not clear. Should all other important ecological factors, for example food availability and vegetation cover for nests, change in tandem, the influence on the birds both at an individual and a population level may be negligible. However, if the timing of important factors such as spring arrival and peak food availability for breeding falls out of phase, the effects are potentially dramatic. Such a scenario has been proposed for pied flycatchers (Both and Visser 2001) and great tits (Visser et al. 1998) in the Netherlands.

Comparison between Ottenby and Helgoland

Ottenby and Helgoland are 600 km apart along an ENE–WSW axis, which is almost parallel to the general migration direction for many species wintering in, or migrating through, western Europe. Thus, a proportion of many species are likely to pass both sites during their spring migration. As expected, there are many similarities. The order of spring passage among species is close to identical, although the short/medium-distance migrants are about eight days earlier at Helgoland. The difference among long-distance migrants is only two days. We do not put any weight at the values as such, but the smaller difference for long-distance migrants is expected given the generally higher migration speed of long-distance migrants (Alerstam and Lindström 1990; see also Huin and Sparks 2000).

At the species-specific level, the trends for msp time on year are similar (Fig. 2). For example, the lesser whitethroat *Sylvia curruca*, blackcap and spotted flycatcher belong to the species with the most prominent progression towards earlier passage, whereas the brambling *Fringilla montifringilla* and the fieldfare both seem relatively unaffected by recent climate change. This suggests that either the same populations are being studied at the two sites, or, if the migrants at the two sites belong to different populations, they have reacted similarly to environmental changes. The trends for earlier passage over time are on average stronger at Helgoland. There is congruence to the extent that a given species is affected by NAO, when comparing all 20 species (Fig. 3), although in general the msp time of a given species is more profoundly affected by NAO at Helgoland. When restricting the analysis to the 13 species with a minimum study period of 42 years, the picture is less clear and there is no congruence to the extent that a given species is affected by NAO. All species but the chaffinch *Fringilla coelebs* and the brambling show a negative slope of msp time on winter NAO index at both sites. The most divergent species is the blackcap, clearly being more strongly affected by NAO at Ottenby than at Helgoland. This is also the only of the 20 species where completely separated populations probably are studied, given that Blackcaps at Ottenby migrate towards south-east whereas they should be south-west migrants at Helgoland (Zink 1973). The lesser whitethroat is considered a south-east migrant both at Helgoland and Ottenby, and the sites should then be passed by somewhat different populations.

Passage time in relation to migratory routes

An important difference between the dataset at Helgoland and the one at Ottenby is that the latter contains many species migrating towards the south and south-east. It has been suggested by Tryjanowski et al. (2002) that birds migrating over the interior of the European continent show less marked changes in arrival time than those following the western margin. Hüppop and Hüppop (2003) explain the more pronounced changes found in msp time and arrival in migrants passing e.g. Helgoland (Hüppop and Hüppop 2003) and Britain (Sparks et al. 1999) than in those migrants passing sites further east in Europe, such as the Slovak Republic (Sparks et al. 1999), Poland (Tryjanowski et al. 2002), and Russia (Sokolov et al. 1998), by the different effect of the winter NAO index along an east–west gradient. Their conclusion is based on the notion that the effect of the NAO is more distinct in coastal west and central Europe than further east (Visbeck et al. 2001). In

contrast, our data indicate no general difference in the extent to which birds with different migration routes react to the winter NAO index. Three species with a clearly easterly migration route – the red-breasted flycatcher *Ficedula parva,* the lesser whitethroat, and the blackcap – show a significant negative correlation between msp time and NAO. Note that in the lesser whitethroat at Helgoland, the only SE migrant analysed at that site (blackcaps ringed at Helgoland should mainly include populations migrating towards SW (Zink 1973)), the variation in the msp time is significantly negatively correlated to the winter NAO index (Hüppop and Hüppop 2003). Hence, the winter climate in (mainly) westernmost Europe explains – for one reason or another – the variation in spring passage time in May in the southern Baltic region of birds that have migrated through eastern Europe.

What could then possibly explain these correlations? Even though the effect of NAO is most pronounced in coastal Europe, NAO has climatic effects all across Europe to the Middle East (Visbeck et al. 2001, Stenseth et al. 2003). Cullen and deMenocal (2000) found a rather strong correlation between high winter NAO index and cold, dry winters in Turkey, an area that many of the south-east migrants would pass each spring. This means, however, that the same pattern of correlation with NAO is shown for spring birds passing an area where winter was mild and humid, south-western Europe, as for birds passing an area where winter was cold and dry, south-eastern Europe. It seems unlikely that two drastically different winter weather types would create the same type of good (or bad) conditions for passing migrants. But if we look further north in Europe than the Mediterranean, winter temperatures seem to be correlated to NAO in a comparable way for birds using both westerly and easterly routes (Visbeck et al. 2001). Accordingly, as far as temperature is concerned, it is realistic to assume that NAO has effects also on the North European breeding populations following a more easterly migration route.

Also, south of the Sahara winter temperatures correlate to NAO (Visbeck et al. 2001). However, sub-Saharan rainfall, another potentially important climatic variable for our migrants, does not show any consistent correlation with NAO (Wang 2003), which speaks against finding a mechanistic link south of the Sahara between NAO and spring migration phenology. Cotton (2003) reports, based on the records of first arrivals of 20 species in Oxfordshire in the UK, no correlation between advanced spring arrival and winter NAO index over the 1971–2000 period. Yet, these results may be influenced by the use of first arrival dates, which may not necessarily reflect the mean spring passage (Sparks et al. 2001). Cotton (2003) found a negative correlation between the mean winter temperature anomalies for Africa south of 20° N and spring arrival in Oxfordshire but, unlike Visbeck et al. (2001), he found no correlation between sub-Saharan winter temperatures and winter NAO index. There seems to be no simple way to explain the correlation between spring migration phenology and NAO in long-distance migrants.

Temporal scale and trends in passage time

The past four–five decades have seen an overall trend towards milder and wetter winters, but was preceded by a negative trend in the winter NAO index from the beginning of the 20th century. In the 19th century (1825–1899) winter NAO index showed no clear trend at all. In addition, the winter NAO index has been fairly stable or even decreased the last 15 years (Hurrell et al. 2003; see also Fig. 1). These long-term patterns should be born in mind when interpreting phenological data from a restricted period of time. It may, for example, explain why Hüppop and Hüppop (2003), based on 32–41 years' data, can conclude that short/medium-distance migrants are passing progressively earlier, whereas we at Ottenby, based on 22–35 years' data, found no such pattern for the same species (maybe even the same populations). These different conclusions are drawn despite the fact that the past 20 years, which should be the most important when interpreting ongoing processes, are included in both analyses.

Evolution or phenotypic response?

It is likely that most of the changes in spring migration phenology observed over the past few decades are expressed at the phenotypic level, and not through evolution at the gene level (Sokolov et al. 1998, Hüppop and Hüppop 2003, Vähätalo et al. 2004). Microevolution may change the migration phenology over just a few generations (Berthold et al. 1992, Pulido et al. 2001), but the selection direction must then be consistent. Although the winter NAO index shows an overall positive trend over the last 50 years, the variation between years is large and therefore subsequent generations of the generally short-lived migrants must be facing selection pressures of varying directions. Clearly, migrating birds of northern Europe are able to adjust their arrival time to large and rapid changes in climate, at least if these are within the same magnitude as in the last hundred years. Whether the plasticity of migrants can cope with even larger magnitudes of climate changes is not known, but will hopefully never be put to the test.

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