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North Atlantic Oscillation and timing of spring migration in birds

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Migrant birds have been trapped on the island of Helgoland (southeastern North Sea) since 1909, with methods and sampling effort remaining unchanged throughout the last four decades. In 12 short/medium-distance migrants and 12 long-distance migrants (23 passerines plus the European woodcock) sample sizes were sufficient to calculate mean spring passage (msp) times and to relate these to climate change. All but one species, passing Helgoland en route to their breeding areas (mainly in Scandinavia), show a trend towards earlier msp-time, which is significant in 7 short/medium-distance migrants and 10 long-distance migrants. The msp-times advanced by 0.05–0.28 days per year, short/medium-distance migrants not differing from long-distance migrants. In 23 out of the 24 species, earlier msp-times coincide with local warmer msp-temperatures (significantly in 11 and 7 species of the two groups, respectively). Even more striking is the relation to a large-scale phenomenon, the North Atlantic Oscillation (NAO), during the last four decades. Again, in 23 out of the 24 species, an earlier msp-time coincides with higher NAO indices (significantly in 9 and 12 species, respectively). The NAO index can also explain differences and similarities in spring migration strategies, as well as migration routes within Europe.

Keywords: spring migration; climate change; North Atlantic Oscillation; temperature; migration strategies; migration routes

1. INTRODUCTION

There is sufficient evidence that, in spring, the timing of various activities in birds is correlated with climate, although long-term datasets are scarce (Mason 1995; Sokolov & Payevsky 1998; Sokolov *et al.* 1998; Sparks *et al.* 1999; Bairlein & Winkel 2001; Tryjanowski *et al.* 2002). In particular, an earlier arrival date, earlier start of breeding and the changes of several other breeding parameters together with northwards range extensions, have been attributed to an increase in spring temperature in the northern hemisphere during recent decades, in a variety of migratory bird species (Crick *et al.* 1997; Winkel & Hudde 1997; Forchhammer *et al.* 1998; McCleery & Perrins 1998; Sokolov *et al.* 1998; Brown *et al.* 1999; Crick & Sparks 1999; Dunn & Winkler 1999; Thomas & Lennon 1999; Walther *et al.* 2002). However, Visser *et al.* (1998), Both & Visser (2001) and Møller (2002) demonstrated that, at least in long-distance migrants, the endogenous control of migration might hamper adaptation and limit this trend.

In fact, more short/medium-distance migrants than long-distance migrants have been found to arrive earlier in spring (Sokolov *et al.* 1998; Both & Visser 2001; Tryjanowski *et al.* 2002). Two suggestions have been made to explain this difference. First, the stronger endogenous control of migration in long-distance migrants might prohibit a flexible reaction to a changing environment. If these differences in the reaction to climate change between long-distance and short/medium-distance migrants were real, the odds would be in favour of the latter (Berthold 2001; Both & Visser 2001), since there is strong interspecific and intraspecific selection towards early arrival (Perrins 1970; Lozano *et al.* 1995; Crick *et al.* 1997; Potti 1998; Møller 2001). Second, first-arrival dates, typically used to describe time of migration, are not a reliable reflection of the mean arrival time of the whole population (Mason 1995; Sparks *et al.* 2001; Tryjanowski & Sparks 2001; Tryjanowski *et al.* 2002) and hence require caution in interpretation. Recently, Sparks *et al.* (2001) demonstrated that recording the whole distribution of migration arrivals gives more reliable information about changes in migration time in relation to climate change, although it is extremely labour intensive and is complicated by birds that decide to breed in the area of observation. Bird observatories on remote islands with negligible numbers of breeders, covering whole migration periods, with standardized trapping routines over a long period, provide ideal datasets.

The large number of migrants trapped year-round at the bird observatory on the island of Helgoland, where the methods and sampling effort have remained constant over more than 40 years, were used to calculate mean spring passage (msp) times. This enabled us to avoid the uncertainties referred to above and answer the following questions.

(i) Can the trend towards earlier spring migration be confirmed by the large Helgoland long-term dataset?

(ii) To what degree can changes in the msp-time of the stream of birds heading towards northern Europe be related to large-scale climatic phenomena? Probably even better than to local temperatures? Winter and spring temperatures in Europe are mainly determined by a large-scale climatic phenomenon, the North Atlantic Oscillation (NAO). The NAO index is defined as the difference between the normalized sea-level pressures at the Azores and Iceland averaged over the period December–March, describing

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the meteorological situation in winter and early spring. Positive NAO indices correspond to stronger winds from the west, which bring higher temperatures and higher levels of precipitation from the Atlantic Ocean to northwest Europe. By contrast, negative values, with weaker west winds, indicate a stronger influence of the continental winter high (with low temperatures and less precipitation) on the climate in northwest Europe (Hurrell 1995; Hurrell *et al.* 2001; Ottersen *et al.* 2001; Visbeck *et al.* 2001). The weather of the months included in the NAO index *prepares* the environment for the spring migrating birds. The weather both during and prior to the birds' arrival will affect food availability (e.g. the quantity of insects present) and habitat suitability (e.g. the trees must be in leaf for woodland species; Huin & Sparks 2000). Owing to its large-scale effects, the NAO causes a striking temporal coherence of food-web interactions (Ottersen *et al.* 2001; Straile 2002). Hence, the NAO index should better explain the shift in spring migration time than temperatures that are relatively local or restricted to the migration period. Recently, the NAO index was found to be negatively correlated with the egg-laying date in the collared flycatcher (*Ficedula albicollis*; Przybylo *et al.* 2000); it was found to be positively correlated with clutch size and quality of offspring in the barn swallow (*Hirundo rustica*; Møller 2002) and evenly correlated with predator–prey relationships (Post & Stenseth 1998; Post *et al.* 1999; Ottersen *et al.* 2001).

(iii) Is the change in msp-time in Europe generally more pronounced in short/medium-distance migrants than in long-distance migrants, or is this difference a geographical phenomenon in populations less affected by climate change? We propose that the length of migration route within Europe substantially influences the timing of migration in both long-distance and short/medium-distance migrants. We therefore expect long-distance migrants to react to climate change in the same manner as short/medium-distance migrants, along those sections of their migration routes that are influenced by climate change.

(iv) Can the suggestion of Tryjanowski *et al.* (2002) that changes in bird arrival are more marked on the continental margin than within the interior continent be related to the NAO index? Since the influence of the NAO on the environment is more pronounced in coastal west and central Europe (Visbeck *et al.* 2001), birds having flyways in these areas should be most affected.

2. MATERIAL AND METHODS

Since 1909, birds have been trapped and ringed at the 'Inselstation' of the 'Vogelwarte Helgoland' at Helgoland (54°11′ N, 07°55′ E), with interruptions in 1915–1918 and 1946–1952 caused by the two World Wars. In 1920, Weigold introduced the use of funnel traps at Helgoland, and since about 1960, trapping conditions in the trapping garden have remained relatively constant, allowing comparative analyses of the trappings over a period of more than 40 years. Species trapped and ringed are mainly migrating songbirds that breed in Scandinavia, as shown by thousands of recoveries (Zink 1973, 1975, 1981, 1985; Zink & Bairlein 1995).

In the period 1960–2000, more than 480 000 individuals of 202 species were ringed in the trapping garden of Helgoland, including more than 220 000 individuals of 158 species trapped during the spring migration. In our analysis, only species in which a minimum of five birds were trapped in at least 75% of the 41 spring migration periods were considered. Within the resulting species, all data from springs with less than five trapped birds were excluded. Common blackbirds (*Turdus merula*) were not ringed between 1961 and 1967. The greenfinch (*Carduelis chloris*) was excluded from this analysis because there has been only one spring with more than five trappings in the last decade.

The remaining 24 species include 12 long-distance migrants (names after the British List 2000 of the British Ornithologists' Union): common redstart (*Phoenicurus phoenicurus*); sedge warbler (*Acrocephalus schoenobaenus*); Eurasian reed warbler (*Acrocephalus scirpaceus*); icterine warbler (*Hippolais icterina*); lesser whitethroat (*Sylvia curruca*); common whitethroat (*Sylvia communis*); garden warbler (*Sylvia borin*); blackcap (*Sylvia atricapilla*); common chiffchaff (*Phylloscopus collybita*); willow warbler (*Phylloscopus trochilus*); spotted flycatcher (*Muscicapa striata*); and pied flycatcher (*Ficedula hypoleuca*). Following Zehnder & Karlsson (2001), the blackcap and chiffchaff are regarded as long-distance migrants, because birds trapped at Helgoland belong to northern populations. The remaining 12 species are short/medium-distance migrants: Eurasian woodcock (*Scolopax rusticola*); winter wren (*Troglodytes troglodytes*); hedge accentor (*Prunella modularis*); European robin (*Erithacus rubecula*); ring ouzel (*Turdus torquatus*); common blackbird (*Turdus merula*); fieldfare (*Turdus pilaris*); song thrush (*Turdus philomelos*); redwing (*Turdus iliacus*); great tit (*Parus major*); chaffinch (*Fringilla coelebs*); and brambling (*Fringilla montifringilla*).

For each species, msp-times were calculated as arithmetic means of the daily trapping totals for each spring from 1960 to 2000. We decided to use the arithmetic mean instead of the often-used median, because normal probability plots (Legendre & Legendre 1998) showed that in all species the data followed a sufficiently normal distribution, and because the arithmetic mean provides the best measure of the whole distribution of spring passage through Helgoland. Local msp-temperatures were calculated for each species and each spring by averaging the mean daily surface air temperatures for a $2.5° \times 2.5°$ area, including Helgoland, over the mean 90% (mean ± 1.64 s.d.) of the overall species-specific migration period. The National Centers for Environmental Prediction reanalysis temperature data used were provided by the NOAA–CIRES Climate Diagnostics Center, Boulder, CO, USA (http://www.cdc.noaa.gov/data). The NAO index data were derived from the Climatic Research Unit at the University of East Anglia, Norwich, UK (http://www.cru.uea.ac.uk/cru/data/nao.htm).

Student's *t*-statistics were used to test for the significance of regression slopes. Residuals of the regressions were tested for autocorrelation using the Ljung–Box Q-statistics (Ljung & Box 1978). Autocorrelations were found in only two out of the 24 species: redwing ($Q = 4.24$, $p = 0.040$) and winter wren ($Q = 6.28$, $p = 0.012$). Following Tryjanowski *et al.* (2002), we examined which species responded over time, in a similar manner, by non-metric multidimensional scaling (nMDS). The annual msp-times of each species were z-transformed. Euclidean

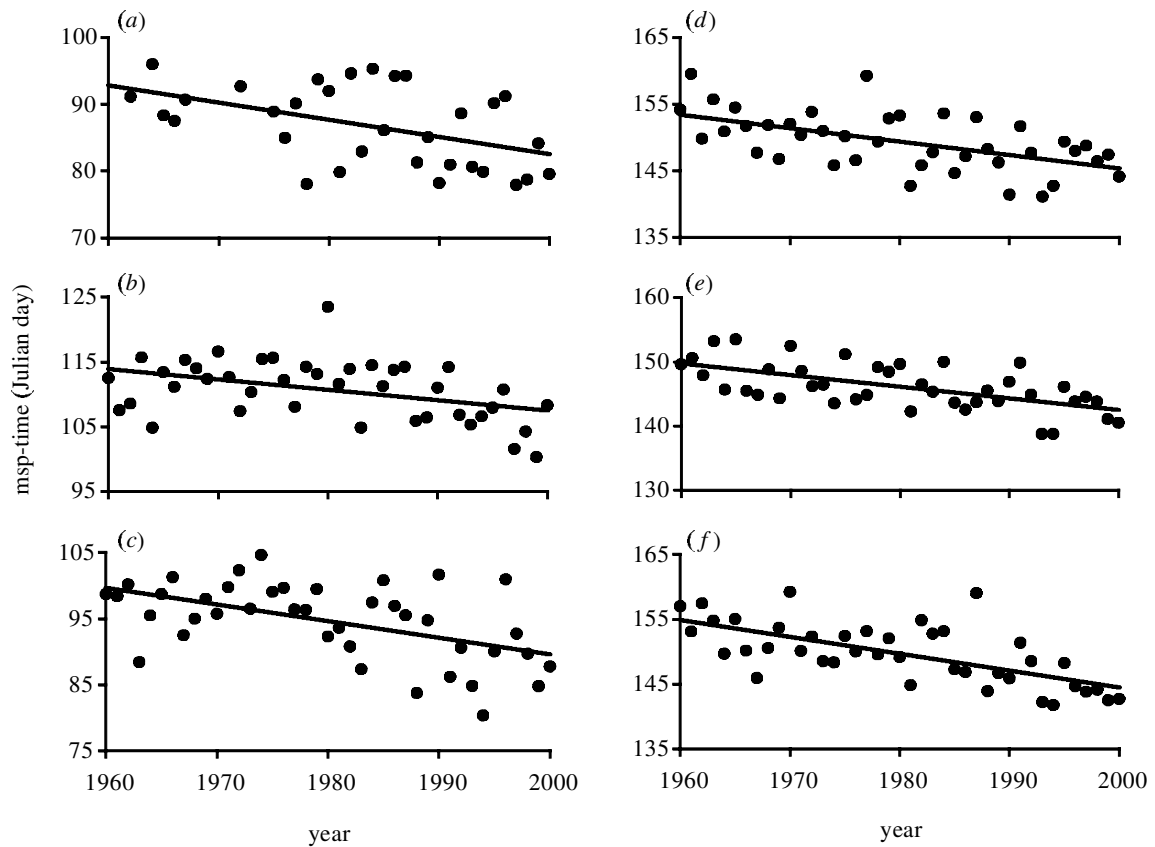Figure 1. Trends of msp-time over four decades in three short/medium-distance migrants ((a) Eurasian woodcock ($y = -0.258x + 597.6$); (b) song thrush ($y = -0.160x + 426.6$); (c) chaffinch ($y = -0.252x + 592.9$)) and three long-distance migrants ((d) Eurasian reed warbler ($y = -0.202x + 548.7$); (e) garden warbler ($y = -0.181x + 503.8$); (f) spotted flycatcher ($y = -0.260x + 663.9$)); examples out of 24 species. Julian day = number of days since 1 January. For R^2-values and p-values see table 1.
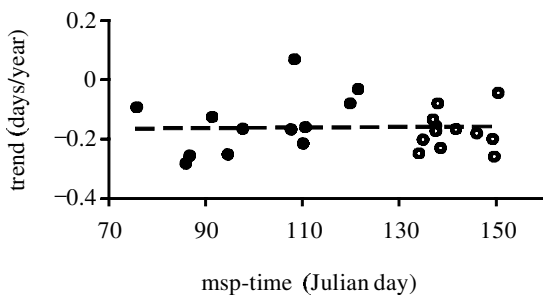

Figure 2. Change of msp-time in short/medium-distance migrants (black circles) and in long-distance migrants (white circles). $R^2 = 0.0008$, $p_{(2)} = 0.9$, $y = 0.0001x - 0.1729$.

distances were used for the (dis)similarity matrix. All statistics were calculated using SPSS for Windows 8.0.0.

3. RESULTS

There is evidence of a trend towards earlier msp-time at Helgoland for 23 out of the 24 species, over the 41 year period (examples in figure 1); for 17 species this trend is significant (table 1). The msp-times advanced by between 0.05 days per year for the icterine warbler and 0.28 days per year for the common blackbird. In seven species, no significant changes were found, but only the brambling has a positive, though not significant, trend (table 1). The slopes of the trend towards earlier msp-time are the same

for long-distance and short/medium-distance migrants (figure 2). Generally, the long-distance migrants have higher coefficients of determination (R^2) in the regressions of msp-time on year than do the short/medium-distance migrants (table 1; mean ± s.d. = 0.202 ± 0.130 versus 0.110 ± 0.090; t-test: $p_{(2)} = 0.058$).

In all species, except the brambling, local warmer msp-temperatures coincide with earlier msp-times. The regression of the msp-time on the species-specific (local) msp-temperature is significant in seven out of the 12 long-distance migrants, and in 11 out of the 12 short/medium-distance migrants (examples in figure 3). Generally, msp-temperature explains less of the observed variance in msp-time in the long-distance migrants than it does in the short/medium-distance migrants (table 1; mean $R^2 = 0.124 ± 0.095$ versus $0.245 ± 0.156$; t-test: $p_{(2)} = 0.034$).

Again, in all species except the brambling, the NAO index is negatively related to msp-time. The regressions of msp-time on the NAO index are significant in all species except the brambling, European robin and ring ouzel (examples in figure 3). In contrast to local msp-temperatures, the NAO index generally explains more of the observed variance in msp-time in the long-distance migrants than in the short/medium-distance migrants (table 1; mean $R^2 = 0.220 ± 0.118$ versus $0.145 ± 0.097$; t-test: $p_{(2)} = 0.103$).

As found by Mason (1995), the msp-time is significantly more variable in those species that arrive earlier

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Table 1. Number of years, number of individuals, mean msp-time (mmsp-time) and regressions of msp-time on year, on msp-temperature and on NAO index for 12 long-distance migrants and 12 short/medium-distance migrants. (mmsp-time is the mean of the yearly msp-times from 1960 to 2000; Julian day = number of days since 1 January; msp-temperature refers to the mean yearly air temperature in the area of Helgoland during species-specific msp-time as defined in §2; no. refers to numbers shown in figure 5.)

| species	no.	number of years	number of individuals	mmsp-time (Julian day)	msp-time on year			msp-time on msp-temperature			msp-time on NAO index		
					b	$p_{(1)}$	R^2	b	$p_{(1)}$	R^2	b	$p_{(1)}$	R^2
long-distance migrants													
common redstart	1	41	10 747	138	−0.173	0.009	0.135	−2.04	0.006	0.154	−3.01	0.000	0.415
sedge warbler	2	38	691	138	−0.081	0.164	0.027	−0.36	0.338	0.005	−2.24	0.002	0.219
Eurasian reed warbler	3	41	1605	149	−0.202	0.000	0.312	−0.75	0.079	0.051	−1.29	0.010	0.130
icterine warbler	4	39	1150	151	−0.045	0.029	0.094	−0.38	0.196	0.020	−1.01	0.016	0.118
lesser whitethroat	5	38	750	135	−0.202	0.006	0.167	−2.43	0.002	0.213	−2.23	0.003	0.196
common whitethroat	6	41	5777	142	−0.167	0.003	0.182	−0.98	0.053	0.066	−2.39	0.000	0.381
garden warbler	7	41	17 577	146	−0.181	0.000	0.360	−0.36	0.202	0.018	−0.86	0.034	0.083
blackcap	8	41	3615	134	−0.249	0.001	0.223	−3.87	0.000	0.317	−1.60	0.026	0.094
common chiffchaff	9	41	3257	137	−0.134	0.107	0.039	−5.19	0.002	0.197	−3.08	0.001	0.213
willow warbler	10	41	10 830	139	−0.231	0.000	0.311	−1.67	0.006	0.153	−2.56	0.000	0.392
spotted flycatcher	11	41	3860	150	−0.260	0.000	0.438	−1.53	0.011	0.128	−1.48	0.007	0.144
pied flycatcher	12	41	2363	138	−0.156	0.011	0.130	−1.85	0.005	0.161	−2.16	0.001	0.252
short/medium-distance migrants													
Eurasian woodcock	13	32	646	87	−0.257	0.003	0.227	−2.70	0.000	0.388	−2.12	0.008	0.179
winter wren	14	39	949	110	−0.215	0.016	0.118	−3.22	0.002	0.205	−2.03	0.017	0.116
hedge accentor	15	41	10 279	91	−0.126	0.071	0.054	−3.71	0.000	0.434	−2.78	0.001	0.268
European robin	16	41	13 118	108	−0.168	0.017	0.110	−2.19	0.013	0.120	−0.99	0.109	0.039
ring ouzel	17	41	1766	120	−0.082	0.081	0.050	−1.66	0.004	0.173	−0.86	0.068	0.056
common blackbird	18	34	47 932	86	−0.282	0.004	0.202	−4.17	0.000	0.591	−2.95	0.001	0.299
fieldfare	19	37	666	122	−0.032	0.365	0.003	−2.69	0.017	0.123	−1.53	0.030	0.097
song thrush	20	41	36 181	111	−0.160	0.004	0.172	−2.04	0.004	0.174	−1.12	0.031	0.088
redwing	21	41	3841	98	−0.166	0.029	0.089	−3.14	0.001	0.268	−2.76	0.001	0.252
great tit	22	32	606	76	−0.094	0.282	0.011	−4.11	0.001	0.288	−3.86	0.004	0.214
chaffinch	23	41	9495	95	−0.252	0.001	0.267	−1.92	0.009	0.137	−1.72	0.011	0.127
brambling	24	39	3604	108	0.068	0.232	0.015	1.39	0.107	0.042	0.12	0.450	0.000
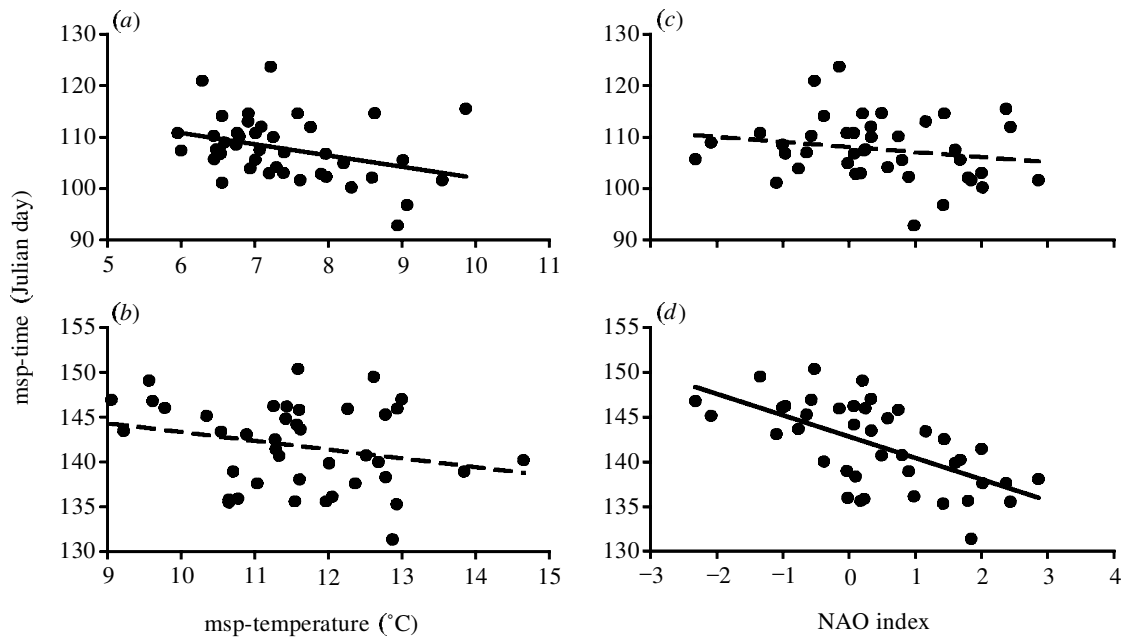
Figure 3. Relation of msp-time to msp-temperature and to the NAO index in two representative species: (*a,c*) a short/medium-distance migrant (European robin) and (*b,d*) a long-distance migrant (common whitethroat). For R^2-values and *p*-values see table 1. (*a*) $y = -2.185x + 123.9$; (*b*) $y = -0.984x + 153.2$; (*c*) $y = -0.988x + 108.1$; (*d*) $y = -2.387x + 142.8$.
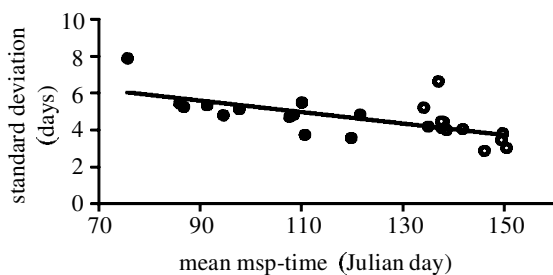

Figure 4. Decline of the standard deviation in msp-time throughout the spring migration (black circles: short/medium-distance migrants; white circles: long-distance migrants). For the species-specific *n* refer to 'number of years' in table 1. $R^2 = 0.424$, $p_{(2)} < 0.001$, $y = -0.031x + 8.410$.
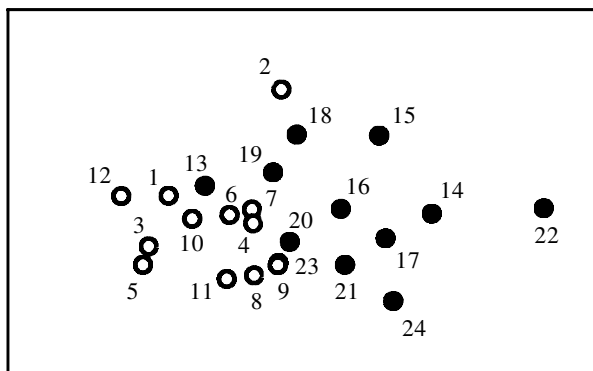

Figure 5. Two-dimensional non-metric multidimensional scaling of msp-time of all 24 bird species (black circles: short/medium-distance migrants; white circles: long-distance migrants; numbers refer to the 'no.' column of table 1).

(figure 4). Also, the nMDS of the msp-times of our 24 species clearly separates the short/medium-distance migrants from the long-distance migrants, with the latter

being more clumped (figure 5). A stress of 0.23 indicates a sufficient fit of the ordination (Backhaus *et al.* 1990).

4. DISCUSSION

The broad spectrum of species studied at Helgoland and the long-term nature of the dataset provide unique confirmation that the trend towards earlier spring passage in migrating birds is an even more general phenomenon in western and northern European migrants than previously thought. This is valid, in contrast to some recent investigations (Sokolov *et al.* 1998; Both & Visser 2001; Tryjanowski *et al.* 2002), for both short/medium-distance and long-distance migrants. The correlation with climate change during the last four decades, particularly with the change in spring temperature and, to a greater extent, the change in the NAO index, is striking. Namely, in view of the fact that daily trapping totals are variable owing to, for example, mass migration or arrested migration (as illustrated by the comparatively low R^2s), the high number of significant correlations is remarkable. The only exception is the brambling, a species with pronounced invasion migration and winter nomadism (Alerstam 1990).

The increase in the number of winters with a positive NAO index over the past four decades corresponds to an increase in the northern hemisphere's surface temperature over this period (Hurrell *et al.* 2001). Nevertheless, the NAO index is not necessarily associated with temperatures during the migration periods, especially from April to June, and along the migration routes from Spain to Helgoland. Rather, it contributes to temperature, precipitation and wind strength and direction across Europe in winter (Hurrell 1995) and thus prepares the environment for spring migrating birds. Higher NAO indices coincide with the earlier development of vegetation, making food available earlier. It remains unclear to what degree the wind component of the NAO plays a part: for example, in the

UK, warmer temperatures in March are associated with southwesterly or westerly winds from the Atlantic. Sparks *et al.* (2001) noted that these 'are also tailwinds for birds migrating from Africa'. However, the majority of trans-Sahara migrants do not reach southwestern Europe before April–May (Finlayson 1992). But, we have some evidence that tailwinds during the species-specific msp-times influence passage times at Helgoland (O. Hüppop and K. Hüppop, unpublished data). Nevertheless, our finding that the msp-times of migrating birds trapped at Helgoland, especially the long-distance migrants, are correlated with the NAO index to a greater extent than with the local species-specific msp-temperatures underlines the necessity to investigate large-scale climatic phenomena rather than local climatic factors in order to interpret changes in the timing of bird migration.

The slopes of the trend towards earlier msp-time at Helgoland are the same for long-distance and short/medium-distance migrants (in contrast to other studies, see Sokolov *et al.* 1998; Both & Visser 2001; Tryjanowski *et al.* 2002). Although long-distance migrants seem to be mainly under endogenous control for the onset of spring migration in Africa (Gwinner 1996), progress within Europe is assumed to be affected mainly by weather conditions (Alerstam 1990; Mason 1995; Huin & Sparks 1998; Sokolov *et al.* 1998; Berthold 2001). This ought to be expected considering that arrival in the breeding areas as early as possible is strongly selected in all migrating birds (Perrins 1970; Lozano *et al.* 1995; Crick *et al.* 1997; Potti 1998; Møller 2001), that is, long-distance migrants should also progress north as fast as possible. In springs following winters with high NAO indices environmental conditions will be advantageous, especially in terms of food supply, and the progress of migration to the north should be faster than in springs following winters with low, or even negative, NAO indices. The migrating birds trapped at Helgoland are breeding birds from Scandinavia and are, therefore, the birds that have to cover the longest distances within Europe. On their routes from the Iberian peninsula to their breeding grounds they pass through the regions most strongly influenced by the NAO in western Europe (fig. 1 in Visbeck *et al.* 2001) and are confronted, over a long distance, with a climate and food supply 'prepared' by the NAO. The long-distance and short/medium-distance migrants passing Helgoland share the same routes within Europe. Hence, their similar opportunities to react to the local conditions throughout this long NAO-influenced route can explain why long-distance migrants at Helgoland display the same trend in timing of migration as short/medium-distance migrants.

The more pronounced changes in msp-time and arrival times in migrant birds passing Helgoland and breeding in Britain, respectively, than in those migrating much further east can be explained by the NAO index, and especially by the west–east gradient of its intensity within Europe. According to Visbeck *et al.* (2001) the effect of the NAO is more pronounced in coastal west and central Europe. Sparks *et al.* (1999) reported a progressively earlier arrival of the barn swallow throughout the last three decades at seven UK observatories but, in contrast, a progressively later arrival of the swallow throughout the last decades in the Slovak Republic. Compared to our Helgoland data, Sokolov *et al.* (1998) found a lower proportion of significant trends towards earlier arrival of mating birds at the Courish Spit of the Baltic Sea, and especially a smaller proportion of correlations of arrival date with temperature within the last four decades in late-migrating species than in earlier-migrating ones. We suggest that these differences are caused by the fact that the individuals of the species observed in the Slovak Republic (Sparks *et al.* 1999), in Poland (Tryjanowski *et al.* 2002) and particularly in Russia (Sokolov *et al.* 1998) are from populations that follow eastern migration routes, whereas individuals at Helgoland or in Britain are from populations migrating through western Europe. Recoveries of ringed birds reveal that the long-distance migrants from eastern Europe migrate substantially further east than migrants touching Helgoland or Britain (Zink 1973, 1975, 1981, 1985; Zink & Bairlein 1995; Bolshakov *et al.* 2001). Hence, environmental conditions and environmental changes along their migration routes are considerably less influenced by the NAO than those of birds trapped at Helgoland. It can be concluded that changes in bird arrival related to the NAO index are significantly greater on the continental margin (e.g. UK) than within the interior continent, as suggested by Tryjanowski *et al.* (2002).

In birds passing Helgoland on their route towards the north, the msp-time in those species that arrive earlier is more variable than in later-arriving rather long-distance migrants. It has been suggested that this phenomenon is caused both by more variable local temperatures in early spring (Mason 1995) and by more variable temperatures along the migration routes in early spring (Huin & Sparks 1998). Furthermore, the comparatively low Euclidian distances in the nMDS reveal congruent shifts in the msp-time, especially in the long-distance migrants at Helgoland (except the sedge warbler). This supports our theory that, in contrast to that of short/medium-distance migrants, which tend to respond to (local) temperatures, the msp-time of the long-distance migrants is more under the indirect large-scale influence of the NAO. This means that they are, during spring migration within Europe, under similar exogenous rather than endogenous control. Both & Visser (2001) concluded from the non-advanced arrival dates in the pied flycatcher in the Netherlands that its migration strategy is under strong endogenous control and therefore not affected by climate change. This contrasts with our findings and those of Leys *et al.* in Bijlsma *et al.* (2001) and with advanced egg-laying dates in the pied flycatcher shown by Both & Visser (2001) and Winkel & Hudde (1997). However, it supports our theory that the length of the migration route through NAO-influenced regions determines the degree of the reaction to climate change. Migrating birds terminating their journey to breed in central Europe are not under such a strong NAO influence for as long as those breeding in Scandinavia. In the pied flycatcher in particular, birds breeding in central Europe approach their breeding areas mainly from the south (Zink 1985) and hence do not follow the extremely NAO-influenced coastal routes.

A rapid selection towards change in endogenous control of migration times as, for example, induced by Pulido *et al.* (2001) in laboratory experiments for the onset of autumn migration, appears to be disadvantageous in spring migration because of the unpredictability of the climate in the following years. The term 'North Atlantic Oscillation'

suggests climatic variability, with changing lengths of oscillation phases within the last century (Hurrell *et al.* 2001). The observed high flexibility in the reaction to actual climatic conditions each spring, in all but one species studied at Helgoland, appears much more adaptive and is obviously a result of phenotypic plasticity rather than microevolution. Przybylo *et al.* (2000) reached the same conclusion after studying breeding time in another long-distance migrant, the collared flycatcher (*F. albicollis*). The fact that large clutch sizes were not maintained during the years following a peak in NAO indices also suggests that phenotypic plasticity was more important than evolutionary change (Møller 2002). According to Potti (1998), heritability and repeatability in arrival times in pied flycatchers were not detectable, perhaps owing to environmental variation. Despite the general trend towards a warmer climate in the northern hemisphere, the high variability of climate from year to year and the unpredictable occurrence of cold winters and springs seem to hamper an inflexible genetic fixation of change in spring migration time in birds.

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