

## Spring arrival of birds depends on the North Atlantic Oscillation

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The timing of arrival of 81 migratory species in response to the North Atlantic Oscillation (NAO) was studied at two Finnish bird observatories (1970–99). Timing was determined for the first migrants and for the peak of migration, as well as for the early, median and late phases of migration, defined as the dates when the seasonal cumulative sum of birds reached 5%, 50% and 95%, respectively. For most species, the timing of arrival correlated negatively with the NAO in all phases of migration: the correlation was significant for 79% of species studied. Thus, most species arrived in Finland early when the NAO was positive and indicative of mild and rainy winters in northern Europe. Although all phases of migration correlated negatively with the NAO, the correlations were more negative for the early than for the late phases of migration. Since the NAO did not show a significant trend during the study period, the correlations indicate that the timing of birds followed stochastic fluctuations in the NAO. This finding suggests that most Finnish migratory birds are able to adjust the timing of spring arrival in response to climatic change without time delay.

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A majority of birds breeding at temperate and high latitudes have adapted to cold winters by migrating seasonally between breeding and wintering regions. Although genetic traits determine approximate timing of migration (Gwinner 1986, Pulido et al. 2001), timing is also regulated by many exogenous factors. These include climatic factors, such as temperature, wind conditions, ice and snow cover (Richardson 1990, Forchhammer et al. 2002, Hüppop and Hüppop 2003). Numerous studies have shown a relationship between spring arrival and local temperature (Richardson 1990, Huin and Sparks 1998, Sparks 1999, Sokolov 2001, Tryjanowski et al. 2002). Migratory behaviour is also regulated by conditions in the wintering region and throughout the migratory route (Sæther et al. 2000, Sillett et al. 2000). These conditions can be estimated in

terms of large-scale climatic phenomena, such as the North Atlantic Oscillation (NAO; Sillett et al. 2000, Forchhammer et al. 2002, Jonzén et al. 2002, Hüppop and Hüppop 2003).

In this study, the NAO is quantified as an index of the winter NAO, which describes the annual fluctuation of the sea-level difference in pressure between the subtropical center of high surface pressure, and the subarctic center of low surface pressure over the long-term mean in December–March (Hurrell 1995). The NAO affects the climatic and ecological dynamics over large areas, including parts of North America, Europe and Africa (for recent reviews see Ottersen et al. 2001, Stenseth et al. 2002, Walther et al. 2002). In northern Europe, a positive NAO has correlated with warm and moist winters, while a negative NAO has indicated cold and dry winters (Hu-

rell 1995). Recently, Forchhammer et al. (2002) found that the first individuals of five terrestrial bird species arrived early in Norway when the NAO was positive. The mean passage of 24 terrestrial bird species showed a similar response to the NAO on the island of Helgoland in the North Sea (Hüppop and Hüppop 2003).

In this study, we studied the timing of migration of 81 bird species, in order to determine (1) whether species of boreal and arctic zone respond to the NAO, and (2) how the responses differ at different phases of each species' migration.

## Methods

The birds were observed every spring during 1979–99 (excluding 1990) and 1970–99, at the Hanko (60°N 23°E) and Jurmo (60°N 22°E) bird observatories (Fig. 1), respectively, using standardized routines. One to seven observers trapped birds for ringing, and counted birds in migratory flight and those resting at the observatories (details in Lehtikoinen and Vähätalo 2000, Lehtikoinen et al. 2003). The combination of all observation activities including the number of ringed birds resulted in a daily bird count. At Hanko,

observation activity covered 76% (mean, range 50–95%) of the days between 27 March and 12 June (i.e. during the period when most birds migrated). At Jurmo, observation activity covered 84% (mean, range 57–100%) of the days between 1 April and 8 June.

The timing of the first arrivals and that of the maximum number of birds (i.e. the migration peak) were determined as Julian days. The timing of the early, median and late phases of migration were defined as the dates when the season's cumulative bird sum reached 5%, 50% and 95%, respectively. Cumulative sums were calculated for species specific migration seasons, which were defined to include the earliest and latest migrant individuals of each species (Table 1). Arrival dates were determined for migratory species, observed on at least five days with seasonal sums exceeding twenty individuals in more than eight springs. Details of the seasonal dynamics of bird migration at Hanko and Jurmo can be found elsewhere (Lehtikoinen and Vähätalo 2000, Lehtikoinen et al. 2003). The NAO indices were obtained from <http://www.cru.uea.ac.uk/cru/data/nao.htm> and corresponded to those used by Hurrell (1995).

The relationship between the arrival dates and the NAO was studied with Spearman rank correlation analysis. These correlations may have been biased if the observation activity was dependent on the NAO. We checked for this by calculating the dates when the cumulative number of observation days reached 5%, 50% and 95% of the total number of observations days each spring, and performed Spearman correlation analyses between the dates and the NAO. Observation activity did not depend on the NAO at Hanko (5% dates:  $r_s = -0.05$ ,  $P = 0.821$ ; 50%:  $r_s = -0.09$ ,  $P = 0.686$ ; 95%:  $r_s = -0.10$ ,  $P = 0.670$ ), but at Jurmo a significant dependence was found (5% dates:  $r_s = -0.49$ ,  $P < 0.001$ ; 50%:  $r_s = -0.67$ ,  $P < 0.001$ ; 95%:  $r_s = -0.25$ ,  $P = 0.241$ ). During some of the coldest springs, early access to the island of Jurmo was restricted by ice cover, and this explains why observation activity was dependent on the NAO. In order to correct the bias caused by the differences in observation activity, cumulative dates of observation activity were used as partial variables in the correlation analysis between the NAO, and the dates describing the early, median and late phases of migration. The partial variables were calculated as follows. We first determined the earliest 5% date and the latest 95% date for each species. Within these periods, we determined the dates when cumulative observation activity reached 5%, 50% and 95% in each year, and used these dates as partial variables in the correlations for the early, median and late phases of migration, respectively. When observation activity started to accumulate after 20 March, it was no longer dependent on the NAO (5% dates:  $r_s = -0.17$ ,  $P = 0.378$ ; 50%:  $r_s = -0.20$ ,  $P = 0.280$ ; 95%:  $r_s = -0.12$ ,

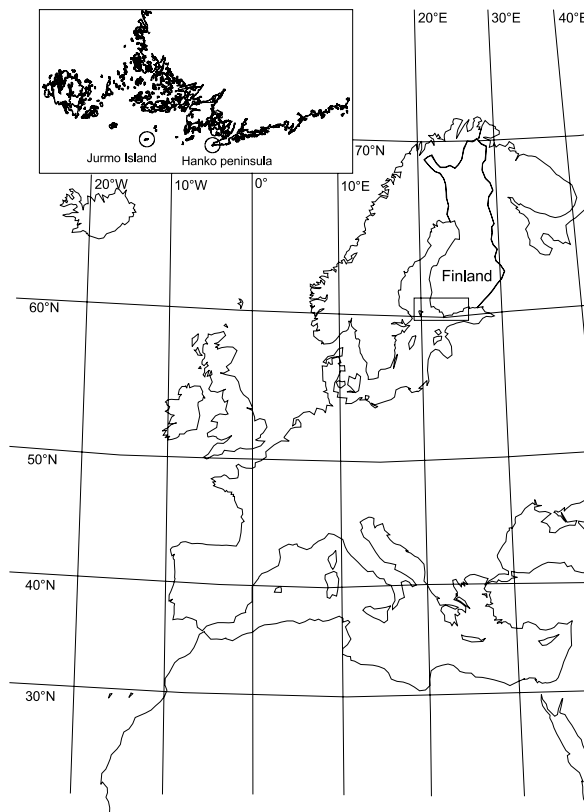


Fig. 1. Location of Hanko and Jurmo bird observatories.

$P = 0.542$ ). This date is used to distinguish between biased and unbiased species in the following examinations. It is also used to exclude those species that occasionally winter at either of the stations.

If autocorrelation is present in the time series, the significance levels of correlation analyses may not be accurate. The NAO index was not significantly autocorrelated (lag 1,  $r = 0.14$ ,  $P > 0.05$ ). Autocorrelation at lag 1 was present in 9% of the analysed arrival dates of birds and at similar frequency as in a previous study (Hüppop and Hüppop 2003). Correlation coefficients from series with significant autocorrelations are shown in *italics* in Table 1.

The arrival dates of birds may change with time independently of the NAO. We examined the effect of possible time trends on the correlation between the NAO and the arrival dates by introducing year as a partial variable. The correlations between arrival dates and the NAO were similar with and without year as an additional partial variable. Therefore we chose to present partial correlations where only the observation activity (see above) was accounted for.

Statistical analyses were carried out with the SAS statistical package (ver. 8.02). Before calculating the 95% confidence limits, the correlations were z-transformed. The figures show back-transformed values of means and confidence limits.

## Results

The timing of spring migration correlated negatively with the NAO for most of the 81 species studied (Table 1, Figs. 2 and 3). For 79% of species studied, the timing of at least one migratory phase showed a statistically significant negative correlation with the NAO (Table 1). A negative correlation indicates early arrival in those years when the NAO was positive. The NAO did not show a significant trend during the study period (regression analysis,  $F_{1,28} = 2.01$ ,  $P = 0.170$ ). Thus the relationship observed between the timing of migration and the NAO (Table 1) indicates that the timing followed the stochastic variation of the NAO.

Birds responded to the NAO differently at different phases of migration (Fig. 2). When all 81 species were examined, the timing of arrival correlated most negatively with the NAO at an early migration phase, while in the late phase of migration correlations were least negative (Fig. 2A).

The correlations between the first arrivals and the NAO are shown only for those species which were not observed during the winter, or were observed at Jurmo after 20 March (Table 1, Fig. 2B). For these species, the correlation between timing and the NAO was more negative for birds arriving first than for those arriving at the peak and late phases of migration at Jurmo (Fig.

2B). At Hanko, the correlations for the first migrants were similar to other phases of migration (Fig. 2B).

Breeding species and passing migrants responded similarly to the NAO, except that at Hanko the late phase of migration correlated more negatively for passing migrants than for breeding species (Fig. 3; t-test,  $t_{77} = 3.23$ ,  $P = 0.002$ ).

## Discussion

The results of this study show that most of the 81 migratory bird species arrived early after positive NAO winters, indicating a warm and rainy weather in northern Europe (Hurrell 1995). Similar to this study, the timing of spring arrival of many terrestrial birds has correlated negatively with the NAO in northern Europe (Forchhammer et al. 2002, Hüppop and Hüppop 2003). In agreement with earlier studies concerning terrestrial species, this study shows that a majority of migratory birds, including shorebirds and waterfowl, are able to adjust their spring arrival in relation to a large-scale climatic oscillation.

The relationship observed between the NAO and the timing of migration can be explained in several ways: (1) in positive NAO years, the stronger than average SW-W winds over northern Europe (Hurrell 1995) provide tail-winds for migratory flight, (2) wintering birds achieve good condition during positive NAO winters and are able to arrive early (Møller 1994, Sæther et al. 2000), (3) in positive NAO winters the wintering regions are located close to breeding regions, and (4) after positive NAO winters the development of spring is early (Post et al. 2001). The explanations are not mutually exclusive, but explanations 1–3 fit only some species. Winds from SW–W speed up the migratory flight of species arriving from those directions. Explanations 2–3 fit birds wintering in western and northern Europe, since in these areas the mild temperatures during positive NAO winters favor wintering birds and may shift wintering regions northwards. The early development of spring after positive NAO winters in northern Europe (Forchhammer et al. 1998, Post et al. 2001) can be expected to affect all the species studied.

This study shows that the timing of all phases of migration typically correlates negatively with the NAO. These results suggest that the results of earlier studies concerning the arrival of the first individuals (e.g. Huin and Sparks 1998, Sparks 1999, Forchhammer et al. 2002, Tryjanowski et al. 2002) can be roughly extended to the behavior of populations more generally. In this study, the correlation between the NAO and arrival dates often became progressively less negative, from 5% cumulative sums through the median to 95% cumulative sums. These results may be partly explained by a

Table 1. Spearman correlation coefficients ( $r_s$ ) between the NAO and the timing of migration at different phases of migration, and the characteristics of species studied.  $r_s$  significantly ( $P < 0.05$ ) different from zero are shown in **bold**. *Italics* show significant ( $r > 2 \times$  standard deviation) autocorrelation in the time series of arrival dates at lag 1. Season: start and end of the migratory season used for calculation of cumulative sums of migrants. "First" shows  $r_s$  for species without observations in winter or before 20 March at Jurmo. "Springs" and "birds" show number of springs studied and mean number of birds observed in those springs, respectively. Species breeding at observatories marked with b (bre).

Species	Season		Jurmo 1970–1999							Hanko 1979–1989+1991–1999									
	start	end	$r_s$					springs	birds	bre	$r_s$					springs	birds	bre	
			First	5%	50%	Peak	95%				First	5%	50%	Peak	95%				
<i>Gavia stellata</i>	1 Mar	15 Jun	<b>-0.80</b>	-0.52	-0.34	0.14	0.04	13	43		-0.33	-0.44	-0.04	-0.19	17	109			
<i>G. arctica</i>	1 Mar	15 Jun	<b>-0.48</b>	0.08	<i>0.16</i>	<i>0.20</i>	29	423		-0.40	-0.34	-0.35	-0.36	20	542				
<i>Podiceps cristatus</i>	15 Mar	15 Jun	<b>-0.51</b>	<b>-0.43</b>	-0.35	0.19	25	81		-0.42	-0.23	-0.21	0.33	15	138				
<i>Anser anser</i>	15 Feb	15 May		-0.17	<b>0.37</b>	-0.10	<b>0.46</b>	30	404	b	-0.41	<b>-0.58</b>	-0.35	-0.08	-0.26	20	320	b	
<i>Branta bernicla</i>	15 Feb	15 Jun	<b>-0.78</b>	<b>-0.54</b>	-0.40	-0.36	-0.01	15	2451		-0.35	-0.27	-0.25	<b>-0.56</b>	<b>-0.65</b>	17	7425		
<i>Tadorna tadorna</i>	15 Feb	31 May		<b>-0.69</b>	0.05	-0.19	0.12	30	304	b	<b>-0.68</b>	<b>-0.77</b>	-0.39	-0.05	-0.29	20	145	b	
<i>Anas penelope</i>	15 Feb	31 May		<b>-0.53</b>	<b>-0.58</b>	<b>-0.51</b>	<b>0.45</b>	30	280			<b>-0.54</b>	-0.23	-0.04	-0.21	20	434	b	
<i>A. crecca</i>	15 Feb	31 May		<b>-0.57</b>	<b>-0.52</b>	-0.32	-0.04	30	558			<b>-0.57</b>	-0.34	-0.26	-0.03	20	322		
<i>A. platyrhynchos</i>	1 Mar	15 May		-0.29	0.12	-0.26	-0.27	30	961	b		<b>-0.64</b>	<b>-0.74</b>	<b>-0.63</b>	0.14	20	1155	b	
<i>A. acuta</i>	15 Feb	15 May		<b>-0.50</b>	-0.37	0.00	-0.26	30	106	b	<b>-0.66</b>	<b>-0.49</b>	-0.28	-0.36	-0.17	18	79		
<i>A. clypeata</i>	15 Feb	31 May	<b>-0.64</b>	<b>-0.52</b>	-0.05	0.04	-0.16	30	273	b	-0.43	-0.20	0.22	-0.08	0.05	20	123	b	
<i>Aythya fuligula</i>	15 Feb	31 May		-0.17	-0.03	0.09	0.02	30	590	b		-0.26	0.06	0.31	0.31	20	1738	b	
<i>Somateria mollissima</i>	15 Feb	15 May		-0.27	0.11	-0.10	0.22	30	32123	b		<b>-0.61</b>	<b>-0.64</b>	-0.44	-0.14	20	87656	b	
<i>Clangula hyemalis</i>	15 Feb	15 Jun		-0.26	-0.27	-0.19	-0.31	30	6052			<b>-0.81</b>	<b>-0.54</b>	-0.11	<b>-0.46</b>	20	31713		
<i>Melanitta nigra</i>	15 Feb	31 May		-0.33	<b>-0.48</b>	<b>-0.41</b>	<b>-0.48</b>	28	426			-0.41	-0.35	0.05	<b>-0.56</b>	19	350		
<i>M. fusca</i>	15 Feb	31 May		<b>-0.58</b>	<b>-0.56</b>	<b>-0.57</b>	0.08	30	2091	b		<b>-0.46</b>	-0.11	-0.17	0.37	20	918	b	
<i>Bucephala clangula</i>	1 Mar	15 May		-0.15	-0.04	-0.26	0.25	30	1590			<b>-0.58</b>	<b>-0.60</b>	<b>-0.62</b>	0.14	20	3259	b	
<i>Mergus serrator</i>	1 Mar	31 May		-0.24	-0.31	-0.26	-0.06	30	1141	b		<b>-0.76</b>	-0.09	0.25	0.21	20	1090	b	
<i>Accipiter nisus</i>	1 Mar	15 Jun		-0.26	-0.17	-0.25	0.03	22	47			-0.40	-0.27	-0.35	-0.13	18	92		
<i>Buteo lagopus</i>	15 Feb	15 Jun	-0.27	-0.02	-0.03	-0.15	0.26	9	43		<b>-0.57</b>	-0.32	-0.40	-0.36	-0.45	18	62		
<i>Haematopus ostralegus</i>	15 Feb	15 May		<b>-0.65</b>	0.06	0.05	-0.28	30	1094	b	<b>-0.60</b>	<b>-0.68</b>	0.07	-0.22	-0.22	20	1759	b	
<i>Charadrius hiaticula</i>	15 Feb	15 Jun		<b>-0.63</b>	<b>-0.59</b>	<b>-0.45</b>	-0.20	30	995	b	<b>-0.66</b>	<b>-0.55</b>	-0.33	-0.26	-0.41	20	243	b	
<i>Pluvialis squatarola</i>	15 Feb	15 Jun	-0.21	-0.17	0.17	0.20	0.03	26	1134			-0.09	0.12	-0.35	-0.43	-0.45	17	1195	
<i>Vanellus vanellus</i>	15 Feb	15 May		-0.22	0.00	-0.01	<b>0.37</b>	30	570	b	<b>-0.31</b>	<b>-0.64</b>	-0.38	-0.18	-0.34	20	657		
<i>Calidris alpina</i>	15 Feb	15 Jun	<b>-0.48</b>	-0.35	0.00	-0.08	-0.21	30	1948	b	0.04	-0.31	-0.40	-0.44	<b>-0.70</b>	15	1718		
<i>Gallinago gallinago</i>	15 Feb	15 May		<b>-0.45</b>	-0.20	-0.15	-0.05	30	171	b	-0.39	-0.35	<b>-0.77</b>	-0.14	<b>-0.56</b>	17	75		
<i>Scolopax rusticola</i>	15 Feb	15 May		<b>-0.60</b>	-0.40	-0.23	0.10	25	42	b		<b>-0.73</b>	-0.54	-0.43	-0.43	12	55	b	
<i>Limosa lapponica</i>	15 Feb	15 Jun	-0.28	<b>-0.43</b>	<b>-0.46</b>	<b>-0.41</b>	-0.19	26	964		0.06	-0.39	-0.48	-0.27	-0.44	17	983		
<i>Numenius phaeopus</i>	15 Feb	15 Jun	-0.32	<b>-0.60</b>	<b>-0.41</b>	-0.26	-0.09	27	154		0.08	0.28	-0.28	0.07	0.04	15	156		
<i>N. arquata</i>	15 Feb	31 May	-0.35	-0.22	-0.11	-0.19	0.23	30	533	b	<b>-0.52</b>	0.22	0.21	-0.03	-0.31	20	739		
<i>Actitis hypoleucos</i>	15 Feb	15 Jun	-0.33	-0.07	-0.19	0.11	0.41	18	30		-0.09	-0.31	-0.18	-0.21	-0.40	19	71	b	
<i>Stercorarius parasiticus</i>	15 Feb	15 Jun	<b>-0.54</b>	<b>-0.47</b>	<b>-0.51</b>	-0.23	0.03	27	92	b	-0.38	-0.05	-0.27	0.14	-0.45	18	85	b	
<i>Larus ridibundus</i>	1 Mar	15 Jun		<b>-0.41</b>	<i>0.04</i>	0.03	0.23	30	1601			<b>-0.61</b>	-0.16	-0.10	-0.26	20	2595		
<i>L. canus</i>	1 Mar	15 Jun		<b>-0.56</b>	<b>-0.41</b>	-0.18	0.15	30	3425	b		<b>-0.69</b>	-0.42	<b>-0.46</b>	-0.37	20	3009	b	
<i>L. fuscus</i>	15 Feb	15 Jun	-0.20	<b>-0.65</b>	<b>-0.40</b>	-0.32	0.01	30	167	b	<b>-0.73</b>	-0.38	-0.21	0.12	<b>-0.48</b>	20	315	b	
<i>L. argentatus</i>	1 Mar	15 Jun		-0.35	-0.29	-0.34	-0.27	30	2386	b		-0.10	-0.23	-0.20	-0.07	20	4097	b	
<i>Sterna paradisaea</i>	15 Feb	15 Jun	-0.33	<b>-0.41</b>	<b>-0.40</b>	-0.08	-0.01	30	1898	b	-0.10	0.06	-0.26	-0.10	-0.19	19	490	b	
<i>Columba oenas</i>	15 Feb	15 Jun		-0.40	0.37	0.26	-0.06	18	46		-0.11	0.02	0.00	-0.35	0.20	19	103		
<i>C. palumbus</i>	15 Feb	15 Jun		-0.22	<b>-0.40</b>	-0.17	<b>-0.57</b>	30	1183			-0.22	-0.08	0.01	-0.15	20	1685		
<i>Apus apus</i>	15 Feb	31 Jun	-0.09	-0.29	-0.02	0.26	-0.33	29	302		0.14	-0.28	-0.17	0.07	0.10	19	959	b	
<i>Alauda arvensis</i>	15 Feb	15 May		-0.14	-0.36	-0.05	-0.13	30	2676	b	-0.28	<b>-0.54</b>	<b>-0.67</b>	<b>-0.62</b>	<b>-0.58</b>	20	746	b	
<i>Riparia riparia</i>	15 Feb	15 Jun	-0.46	<b>-0.59</b>	-0.52	-0.30	0.07	14	51		0.12	-0.24	0.20	0.01	-0.34	12	52		
<i>Hirundo rustica</i>	15 Feb	15 Jun	-0.26	-0.28	-0.33	-0.08	0.17	30	313	b	-0.04	-0.05	-0.20	-0.05	-0.26	19	500	b	
<i>Anthus trivialis</i>	15 Feb	15 Jun	-0.07	<b>-0.46</b>	-0.20	-0.04	0.24	30	376		-0.11	-0.43	-0.14	-0.15	0.09	19	337	b	

Table 1. (Continued)

Species	Season		Jurmo 1970–1999							Hanko 1979–1989+1991–1999								
	start	end	$r_s$					springs	birds	bre	$r_s$					springs	birds	bre
			First	5%	50%	Peak	95%				First	5%	50%	Peak	95%			
<i>A. pratensis</i>	15 Feb	15 May		<b>-0.40</b>	-0.34	<b>-0.39</b>	-0.09	30	1263	b		<b>-0.72</b>	-0.42	-0.30	<b>-0.64</b>	20	281	b
<i>Motacilla flava</i>	15 Feb	15 Jun	<b>-0.48</b>	-0.17	0.18	-0.14	0.35	30	321		0.26	0.07	0.15	-0.10	<i>-0.12</i>	15	83	
<i>M. alba</i>	15 Feb	15 May	-0.32	-0.37	-0.01	-0.15	<b>-0.42</b>	30	570	b	-0.12	0.11	-0.22	<i>-0.06</i>	-0.38	20	579	b
<i>Prunella modularis</i>	15 Feb	15 Jun		-0.18	-0.22	-0.04	-0.22	30	357			<b>-0.74</b>	<b>-0.55</b>	-0.43	<b>-0.49</b>	20	162	
<i>Erithacus rubecula</i>	15 Feb	15 Jun		-0.18	<b>-0.45</b>	<b>-0.53</b>	<b>-0.50</b>	30	3397			-0.13	-0.21	-0.35	-0.27	20	473	b
<i>P. phoenicurus</i>	15 Feb	15 Jun	-0.34	<b>-0.43</b>	<b>-0.40</b>	-0.32	-0.27	30	824		0.12	0.02	-0.04	-0.31	-0.08	16	61	
<i>Saxicola rubetra</i>	15 Feb	15 Jun	-0.19	-0.27	<b>-0.47</b>	-0.16	-0.26	30	507		0.32	0.30	-0.12	-0.02	-0.22	14	54	
<i>Turdus merula</i>	1 Mar	15 Jun		<i>-0.20</i>	-0.02	-0.17	0.02	30	636	b		<b>-0.56</b>	-0.31	<b>-0.51</b>	0.04	20	380	b
<i>T. pilaris</i>	1 Mar	15 Jun		0.08	-0.16	0.02	-0.21	30	1204			-0.34	-0.26	-0.33	-0.06	20	2065	b
<i>T. philomelos</i>	1 Mar	15 Jun		-0.29	<b>-0.45</b>	-0.20	<b>-0.49</b>	30	2008			-0.19	-0.18	-0.24	-0.25	20	323	
<i>T. iliacus</i>	1 Mar	15 Jun		-0.10	<b>-0.45</b>	-0.08	<b>-0.40</b>	30	1256			<b>-0.69</b>	-0.25	-0.09	-0.10	20	3742	b
<i>T. viscivorus</i>	1 Mar	15 Jun		-0.08	<i>-0.30</i>	-0.22	-0.26	30	111			-0.47	<b>-0.57</b>	-0.32	<b>-0.62</b>	19	90	
<i>Sylvia curruca</i>	15 Feb	15 Jun	-0.25	-0.32	-0.20	-0.35	<b>-0.41</b>	30	368	b	-0.15	-0.08	-0.01	-0.09	-0.24	19	168	b
<i>S. communis</i>	15 Feb	15 Jun	-0.08	-0.32	-0.13	-0.02	-0.05	30	244	b	0.23	0.06	-0.22	-0.23	-0.13	19	136	b
<i>S. borin</i>	15 Feb	15 Jun	-0.17	<b>-0.40</b>	-0.15	-0.09	-0.24	30	394	b	-0.08	-0.13	<b>-0.58</b>	-0.33	0.07	16	66	b
<i>S. atricapilla</i>	15 Feb	15 Jun	<b>-0.50</b>	<b>-0.47</b>	-0.35	-0.19	<b>-0.43</b>	30	218	b	0.47	0.40	-0.03	0.52	<b>-0.67</b>	10	29	b
<i>Phylloscopus collybita</i>	15 Feb	15 Jun	<b>-0.57</b>	<b>-0.51</b>	-0.16	-0.28	0.00	30	77		-0.22	-0.16	-0.12	-0.37	0.06	12	48	
<i>P. trochilus</i>	15 Feb	15 Jun	-0.21	0.09	-0.29	-0.22	-0.28	30	1075	b	0.26	-0.15	-0.12	<i>-0.11</i>	-0.46	19	474	b
<i>Regulus regulus</i>	15 Feb	15 Jun		-0.11	-0.08	-0.02	-0.08	30	672			<b>-0.56</b>	<b>-0.53</b>	-0.39	-0.31	20	221	
<i>Muscicapa striata</i>	15 Feb	15 Jun	-0.21	0.03	<b>-0.46</b>	-0.29	<b>-0.60</b>	30	681		0.09	0.28	-0.18	-0.46	0.04	18	96	b
<i>Ficedula hypoleuca</i>	15 Feb	15 Jun	<b>-0.51</b>	<b>-0.43</b>	<b>-0.47</b>	-0.07	<i>-0.36</i>	30	437		-0.09	-0.09	0.23	0.04	0.27	18	54	b
<i>Parus caeruleus</i>	15 Feb	15 Jun		-0.05	-0.26	-0.53	-0.16	13	82	b		0.11	-0.14	-0.44	-0.19	19	270	b
<i>P. major</i>	15 Feb	15 Jun		0.07	-0.18	<b>-0.43</b>	-0.05	30	278	b		-0.18	0.22	0.06	0.19	20	389	b
<i>Lanius collurio</i>	15 Feb	15 Jun	<i>0.02</i>	0.25	<i>0.07</i>	-0.15	0.09	30	420	b	0.15	0.22	<i>-0.26</i>	-0.30	-0.04	13	42	b
<i>Corvus monedula</i>	15 Feb	15 Jun		<b>-0.40</b>	0.05	<i>-0.09</i>	-0.21	29	238			-0.20	0.05	-0.26	-0.24	20	807	
<i>C. frugilegus</i>	15 Feb	15 Jun		-0.23	<b>0.57</b>	0.02	0.03	25	253		-0.24	<b>-0.63</b>	-0.12	-0.01	0.06	19	163	
<i>C. cornix</i>	15 Feb	31 Apr		<b>-0.49</b>	-0.24	-0.02	-0.19	30	1379	b		<b>-0.58</b>	-0.11	<i>-0.32</i>	0.22	20	683	b
<i>Sturnus vulgaris</i>	15 Feb	31 May		-0.08	0.02	-0.27	0.09	30	2878	b	-0.42	<b>-0.75</b>	<b>-0.49</b>	-0.29	<b>-0.60</b>	20	2188	
<i>Fringilla coelebs</i>	15 Feb	15 May		-0.10	-0.28	-0.14	-0.11	30	3959	b		-0.35	-0.28	-0.30	-0.13	20	13867	b
<i>F. montifringilla</i>	15 Feb	15 Jun		<b>-0.42</b>	-0.28	<b>-0.41</b>	-0.35	30	1219			-0.19	<b>-0.48</b>	-0.32	<b>-0.57</b>	20	302	
<i>Carduelis chloris</i>	15 Feb	15 Jun		-0.36	0.05	-0.32	<b>-0.51</b>	30	303	b		-0.30	0.10	-0.30	-0.01	20	631	b
<i>C. spinus</i>	15 Feb	15 Jun		0.07	-0.15	-0.07	-0.03	30	535			-0.04	-0.26	-0.15	-0.22	20	1201	
<i>C. cannabina</i>	15 Feb	15 Jun		-0.12	-0.09	-0.19	0.25	29	86	b	-0.28	-0.34	-0.03	-0.44	<i>-0.05</i>	20	207	b
<i>Carpodacus erythrinus</i>	15 Feb	15 Jun	-0.06	<i>0.11</i>	<i>0.14</i>	0.19	0.18	29	130	b	0.34	0.03	-0.33	-0.41	0.05	18	149	b
<i>Plectrophenax nivalis</i>	15 Feb	15 Jun		<b>-0.62</b>	-0.35	<b>-0.59</b>	-0.36	27	235			-0.26	-0.25	-0.33	<b>-0.62</b>	13	184	
<i>Emberiza citrinella</i>	15 Feb	15 Jun		-0.11	0.02	0.07	-0.29	30	224			<b>-0.62</b>	<b>-0.47</b>	-0.08	<b>-0.50</b>	20	647	
<i>E. schoeniclus</i>	15 Feb	15 Jun		-0.22	-0.23	-0.28	<b>-0.46</b>	30	178		-0.33	<b>-0.69</b>	<b>-0.53</b>	-0.38	-0.12	20	167	b

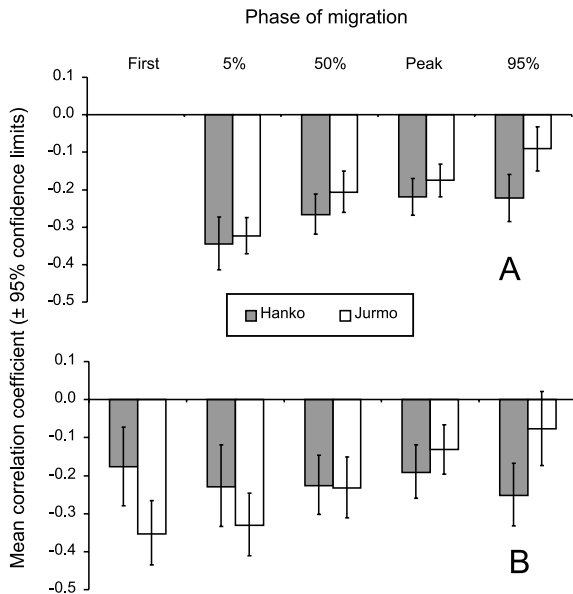


Fig. 2. Mean ( $\pm$  95% confidence limits) Spearman correlation coefficients between the NAO and the timing of migration at different phases of migration. A: All ( $n = 81$ ) species. B: Species without observations in winter or before 20 March at Jurmo ( $n = 31$  at Jurmo,  $n = 43$  at Hanko). Correlation coefficients are shown for the timing of first migrants "First", maximum number of birds "Peak", and cumulative sums reaching 5%, 50% and 95% of the seasonal sum of birds.

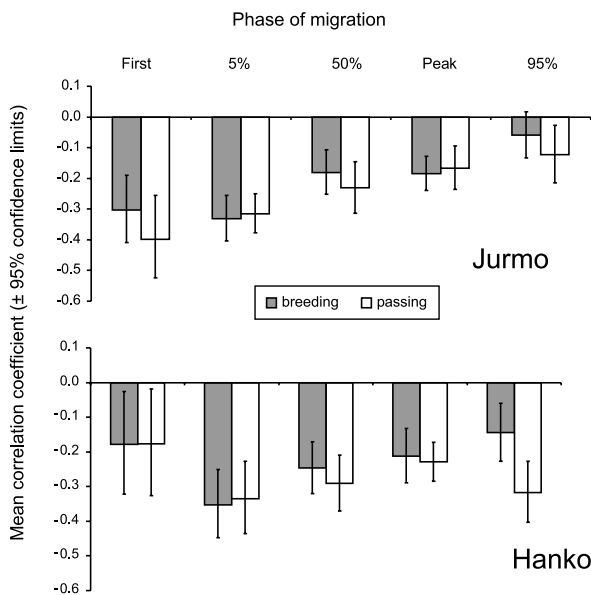


Fig. 3. Mean ( $\pm$  95% confidence limits) Spearman correlation coefficients between the NAO and the timing of migration for passing migrants and species breeding at observatories. At Jurmo,  $n = 40$  and  $41$  for breeding species and passing migrants (except for "First"  $n$  was  $15$  and  $16$ ), respectively. At Hanko,  $n = 45$  and  $36$  for breeding species and passing migrants, except for "First" ( $n = 25$  and  $18$  respectively). Phases of migration, see legend of Fig. 2.

decreasing impact of the winter-NAO on spring climate along the progression of spring. In addition, these results may indicate that migrants respond to the NAO more sensitively in the early phases of migration. Birds in the early migration phase are mostly reproducing adults, while immature birds represent the late phase of migration in many of the species studied. The reproductive advantages of early arrival (Lozano et al. 1996, Kokko 1999) may explain why birds in the early phase of migration responded most strongly to the NAO. Non-reproducing birds are not subject to similar selection as reproducing adults, which may explain the smallest negative correlation between the NAO and timing of arrival in the late phase of migration.

In this study we described the responses of birds to fluctuating NAO over a 30 year period. Since the NAO is a primary phenomenon impacting climate and climate changes in North America, Europe and Africa (e.g. Shindell et al. 1999), our results can be used to predict the arrival times of birds in response to changing climate. Birds can respond to environmental change via phenotypic plasticity and microevolutionary change. Both phenotypic plasticity and microevolution are involved in the determination of the timing of migration (Przybylo et al. 2000, Pulido et al. 2001). Phenotypic plasticity allows birds to adjust their behaviour according to real-time environmental cues, which they experience at wintering grounds, or during the progression of migration. These environmental cues are likely related to the explanations 1–4 given earlier in the discussion. Microevolution may change the timing of migration over a few generations (Berthold et al. 1992, Pulido et al. 2001), but it requires that the selection acts consistently in one direction. During the period of this study, the NAO did not show a significant trend, and thus, did not provide a consistent selection mechanism for microevolutionary change. Instead, the observed relationship between arrival dates and the NAO suggests that birds responded to the stochastic fluctuation of NAO without time delay through phenotypic plasticity. A similar non-lagged relationship between the NAO and arrival date found in the earlier studies (Forchhammer et al. 2002, Hüppop and Hüppop 2003) supports phenotypic plasticity as a major determinant of the observed relationship between the NAO and timing of spring arrival. In conclusion, this and earlier studies (Przybylo et al. 2000, Forchhammer et al. 2002, Hüppop and Hüppop 2003) suggest that most bird species are able to adjust their spring arrival according to climatic change mediated by the NAO without time delay.

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