

Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy

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Large-scale climate fluctuations, such as the North Atlantic Oscillation (NAO), have a marked effect on the timing of spring migration of birds. It has however been suggested that long-distance migrants wintering in Africa could respond less to NAO than short-distance migrants wintering in Europe, making them more vulnerable to climatic changes. We studied whether migratory boreal and arctic bird species returning from different wintering areas show differences in responses to the NAO in the timing of their spring migration. We used data on 75 species from two bird observatories in northern Europe (60°N). By extending the examination to the whole distribution of spring migration and to a taxonomically diverse set of birds, we aimed at finding general patterns of the effects of climate fluctuation on the timing of avian migration. Most species arrived earlier after winters with high NAO index. The degree of NAO-response diminished with the phase of migration: the early part of a species' migratory population responded more strongly than the later part. Early phase waterfowl responded strongest to NAO, but in later phases their response faded to non-significant. This pattern may be related to winter severity and/or ice conditions in the Baltic. In the two other groups, gulls and waders and passerines, all phases of migration responded to NAO and fading with phase was non-significant. The difference between waterfowl and other groups may be related to differences between the phenological development of their respective macrohabitats. Wintering area affected the strength of NAO response in a complicated way. On average medium distance migrants responded most strongly, followed by short-distance migrants and partial migrants. Our results concerning the response of long-distance migrants were difficult to interpret: there is an overall weak yet statistically significant effect, but patterns with phase of migration need further study. Our results highlight the importance of examining the whole distribution of migration and warrant the use of data sets from several sampling sites when studying climatic effects on the timing of avian life-history events.

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The global climate has changed rapidly during the last few decades (Intergovernmental Panel on Climate Change (IPCC) 2001). Having been predicted that the change continues with accelerating speed, the impacts of climate change on the ecology of species, including the timing of life history events (phenology), have become a major concern of biologists (reviewed by McCarty 2001, Schneider and Root 2002, Walther et al. 2002, Parmesan

and Yohe 2003). One of the most prominent phenological events is the spring migration of birds. An analysis of 1100 time series revealed that during the last 30–40 years of the 20th century, first arrival dates of Eurasian bird species have advanced -0.37 days per year (Lehikoinen et al. 2004). Similar results have been obtained in NE North America where spring arrival of birds has advanced on average by 8 days during the 20th

century (Butler 2003). In another study in North America, the progress of spring migration between two areas 2500 kms apart was found to be one day less for every 1°C increase in spring temperature, i.e. the interval between median migration times in the two locations has been shorter in warm springs (Marra et al. 2005). Advancements in spring migration times have been generally attributed to rising spring temperatures (Lehikoinen et al. 2004).

Several approaches have been applied when studying changes in spring migration timing. The arrival dates have been correlated against local temperatures in the target area of spring migration (Sparks 1999, Tryjanowski et al. 2002), against temperatures of several locations along the migration route (Huin and Sparks 1998, Huin and Sparks 2000, Strode 2003, Ahola et al. 2004), or against large-scale climate indices such as the North Atlantic oscillation (NAO) (Forchhammer et al. 2002, Hüppop and Hüppop 2003, Vähätalo et al. 2004). The North Atlantic Oscillation is the most prominent pattern of atmospheric variability over the Northern Hemisphere that has a marked effect on the European weather especially during winter months and early spring (Hurrell et al. 2003).

The advantage of the two last approaches is that they summarize (Hallett et al. 2004) or better take into account the climatic conditions and advancement of overall phenology the birds face during their migratory journey. For example, the median arrival time of the Pied Flycatcher to Finland is strongly affected by *en route* temperatures in the last stages of spring migration (Ahola et al. 2004), which explain arrival better than NAO, but the latter captures almost as well the relationship of migration timing and weather. Also in the Helgoland bird observatory, off the German coast of North Sea, the timing of spring migration was affected by both local spring temperatures and the NAO (Hüppop and Hüppop 2003). The NAO index (see Materials and methods) is also a measure of the severity of the winter preceding the spring migration (Hurrell et al. 2003). Therefore the NAO effect may also include effects on timing of spring migration of varying wintering range (Austin and Rehfisch 2005, Root 1988) and the condition of birds (Møller and Erritzøe 2003, Bairlein and Hüppop 2004).

It is known that the NAO is a good predictor of timing of spring events in Europe (Mysterud et al. 2003), but details of the relationship are relatively unexplored. Particularly, interspecific differences in the strength of NAO-responses have not been studied in detail. It has been suggested that trans-Saharan migrants would not be able to detect changes in climate of their breeding areas, and would thus not be able to arrive earlier in warm springs. If short-distance migrants are better able to follow variation of conditions (evident in stronger NAO-correlations) they could benefit over long-distance

migrants in the long run (Berthold 1990). In addition, the weak ability of long-distance migrants to follow climate changes (evident in weak or non-existent NAO-correlations) may lead to asynchrony with optimal breeding conditions (Berthold 1990, Both and Visser 2001). However, in contrast with this hypothesis, some recent analyses have shown that many long-distance migrants do respond to climate fluctuations (Forchhammer et al. 2002, Cotton 2003, Hüppop and Hüppop 2003, Vähätalo et al. 2004, Stervander et al. 2005, but see Hubalek 2003). This suggests that at least some species or populations within species of tropical migrants respond to warming trends in the European climate.

Most studies have used single point estimates of migration (first arrival date, FAD or median migration time, MMT (see Lehikoinen et al. 2004). This probably gives an inadequate picture of the patterns of migration. The few studies that have examined the impacts of climate change on the total arrival distribution of birds (Ahola et al. 2004, Vähätalo et al. 2004, Sparks et al. 2005, Tøttrup et al. 2006) reported intraspecific variation in responses among the phases of migration. Taking the whole distribution of migration into account gives information about possible climate change effects on the length of the migration period. In our earlier study (Vähätalo et al. 2004) we showed that 79% of 81 species studied responded significantly to NAO, arriving earlier in its positive phase. We also observed that the average response weakened within species from earliest to latest arriving individuals. However the variability of NAO-responses between species is not yet well understood.

Our aim is to examine the importance of three potential sources of variation in the correlations between bird arrival and the NAO-index. First, we tested for the intraspecific variability in the strength of correlation between the NAO and the timing of early, medium and late phases of migration. Second, we studied the dependence of interspecific variability of NAO-correlations on wintering areas. Third, we examined whether birds belonging to different "eco-taxonomic" groups differ in their NAO-responses.

Material and methods

Bird migration data

We used data from two Finnish bird observatories. Jurmo (60°N, 22°E) is an island situated at the southern edge of the SW archipelago in the Finnish Baltic Sea, whereas Hanko bird observatory (60°N, 23°E) is located at the southernmost tip of a mainland peninsula. The birds were counted every spring during 1979–99 (excluding 1990 at Hanko) using standardized routines. One to seven observers trapped birds for ringing, and

counted birds in migratory flight and resting at the observatories. The combination of all observation activities, including the number of ringed birds, resulted in a daily bird count. In 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). In Jurmo, observation activity covered 84% (mean, range 57–100%) of the days between 1 April and 8 June.

To control for additional error variance introduced by small samples, we included only species and years in which the species was observed on ≥ 5 days per spring and the sum of observed individuals/spring was ≥ 20 at each observatory. Both conditions had to be fulfilled in at least nine years. After this selection process, 80 species were left, but five species were later dropped due to classification criteria (see below). Thus we had 150 series (75 species and two locations) of bird migration data to analyse, and of these 44 were less than 20 years in length (median 20 years, range 10–21 years). Dates of 5th, 50th and 95th percentiles of migration dates (the phases of migration) were identified for each species, year, and observatory. These dates will be hereafter referred to as early, median, and late phase dates of migration, respectively. We acknowledge that different phase dates need not reflect the bird populations of exactly the same geographical area, but there is currently not enough information to separate phase of migration within a population from timing differences between populations.

We classified the bird species to long-distance, medium-distance, short-distance and partial migrants according to the distance they cover before reaching southern Finland (Table 1). Long-distance migrants are species wintering in sub-Saharan Africa. Medium and short-distance migrants are intra-European migrants, which migrate approximately 2000 and 1000 kilometres on average, respectively. Finally, partial migrants are species that migrate maximally to distances of up to 1000 km (i.e. to just south of the Baltic Sea), and part of them, if at all, only migrate within Finland. The long-distance migrants could be expected to react to fluctuations in the NAO the least, since they presumably cannot detect the strength of the NAO in Europe during the preceding winter before they have left their wintering quarters and crossed the Sahara desert. Medium distance migrants include species which winter over wide areas from west to east Mediterranean. Short distance migrants and partial migrants winter on the areas the NAO is most affecting, West and Northwest Europe (Hurrell et al. 2003). Thus one could expect weaker responses to the NAO in medium distance migrants than in short distance migrants and partial migrants. However, Stervander et al. (2005) found that the migratory direction within Europe did not

significantly affect the effect of NAO on the timing of mean spring passage.

The main source of the wintering area classification was Väisänen et al. (1998), which we checked against ring recoveries of Finnish birds provided by the Ringing Centre of the Finnish Museum of Natural History. We changed the northern shoveler *Anas clypeata* from the medium distance to the long distance migrant group. The brent goose *Branta bernicla*, which was not categorised in Väisänen et al. (1998), was classified as a short-distance migrant because the distance from the wintering areas at the North Sea coasts are approximately 1000 km from the southern coast of Finland (Rowcliffe and Vickery 2002).

The bird species were also classified to three ecologically relevant taxonomic groups: waterfowl (Gaviiformes, Podicipediformes and Anseriformes), gulls and waders (Charadriiformes) and passerines (Passeriformes). This classification dropped 5 species because they would have added categories with too few species. We finally had 75 migratory species wintering in Europe and Africa to analyse.

North Atlantic Oscillation

The North Atlantic Oscillation is described as the annual fluctuation of the difference in sea-level pressure between the subtropical centre of high surface pressure and the sub-arctic centre of low surface pressure over the long-term mean (Hurrell et al. 2003). Since the influence of the NAO on the North European weather is most pronounced in winter (Jones et al. 2003), and the recent temperature anomalies are strongly related to the persistent and exceptionally strong positive phase of the NAO index (Hurrell et al. 2003), we used the winter NAO index (December to March) as a large-scale measure of climate. The winter NAO has been shown to affect the climatic and ecological dynamics over large areas in Europe and North America, including spring and early summer events (Ottersen et al. 2001, Stenseth et al. 2002, Myrseth et al. 2003). The values of NAO indices were obtained from the website of Climatic Research Unit at the University of East Anglia (<http://www.cru.uea.ac.uk/cru/data/nao.htm>). Within our study period from 1979 to 1999, the NAO was consistently positive from 1989 to 1995, but there was no statistically significant trend through the whole period.

Statistical analyses

The relationship of arrival dates and the NAO can be studied e.g. by correlation or regression analysis. We used correlation analysis, which gives the strength and direction of the relationship between two variables. The

Table 1. The division of study species according to their wintering areas.

Long-distance migrants: species wintering south of Sahara desert (N = 20 species)			
Northern shoveller	<i>Anas clypeata</i>	Yellow wagtail	<i>Motacilla flava</i>
Grey plover	<i>Pluvialis squatarola</i>	Common redstart	<i>Phoenicurus phoenicurus</i>
Whimbrel	<i>Numenius phaeopus</i>	Whinchat	<i>Saxicola rubetra</i>
Common sandpiper	<i>Actitis hypoleucos</i>	Lesser whitethroat	<i>Sylvia curruca</i>
Arctic skua	<i>Stercorarius parasiticus</i>	Whitethroat	<i>S. communis</i>
Lesser black-backed gull	<i>Larus fuscus</i>	Garden warbler	<i>S. borin</i>
Arctic tern	<i>Sterna paradisaea</i>	Willow warbler	<i>P. trochilus</i>
Sand martin	<i>Riparia riparia</i>	Spotted flycatcher	<i>Muscicapa striata</i>
Swallow	<i>Hirundo rustica</i>	Pied flycatcher	<i>Ficedula hypoleuca</i>
Tree pipit	<i>Anthus trivialis</i>	Red-backed shrike	<i>Lanius collurio</i>
Medium-distance migrants: species wintering in SW Europe and in the Mediterranean region (N = 15 species)			
Black-throated diver	<i>Gavia arctica</i>	European robin	<i>Erithacus rubecula</i>
Ringed plover	<i>Charadrius hiaticula</i>	Song thrush	<i>Turdus philomelos</i>
Dunlin	<i>Calidris alpina</i>	Redwing	<i>T. iliacus</i>
Common snipe	<i>Gallinago gallinago</i>	Mistle thrush	<i>T. viscivorus</i>
Bar-tailed godwit	<i>Limosa lapponica</i>	Blackcap	<i>Sylvia atricapilla</i>
Meadow pipit	<i>Anthus pratensis</i>	Chiffchaff	<i>Phylloscopus collybita</i>
White wagtail	<i>Motacilla alba alba</i>	Reed bunting	<i>Emberiza schoeniclus</i>
Duncock	<i>Prunella modularis</i>		
Short-distance migrants: species wintering in western Europe (N = 32 species)			
Red-throated diver	<i>Gavia stellata</i>	Paleartic oystercatcher	<i>Haematopus ostralegus</i>
Great crested grebe	<i>Podiceps cristatus</i>	Northern lapwing	<i>Vanellus vanellus</i>
Greylag goose	<i>Anser anser</i>	Eurasian woodcock	<i>Scolopax rusticola</i>
Brent goose	<i>Branta bernicla</i>	Western curlew	<i>Numenius arquata</i>
Common shelduck	<i>Tadorna tadorna</i>	Black-headed gull	<i>Larus ridibundus</i>
European wigeon	<i>Anas penelope</i>	Mew gull	<i>L. canus</i>
Green-winged teal	<i>A. crecca</i>	Herring gull	<i>L. argentatus</i>
Mallard	<i>A. platyrhynchos</i>	Eurasian skylark	<i>Alauda arvensis</i>
Northern pintail	<i>A. acuta</i>	Blackbird	<i>Turdus merula</i>
Tufted duck	<i>Aythya fuligula</i>	Fieldfare	<i>T. pilaris</i>
Common eider	<i>Somateria mollissima</i>	Rook	<i>Corvus frugilegus</i>
Long-tailed duck	<i>Clangula hyemalis</i>	Common starling	<i>Sturnus vulgaris</i>
Black scoter	<i>Melanitta nigra</i>	Chaffinch	<i>Fringilla coelebs</i>
Velvet scoter	<i>M. fusca</i>	Brambling	<i>F. montifringilla</i>
Common goldeneye	<i>Bucephala clangula</i>	Linnet	<i>Carduelis cannabina</i>
Red-breasted merganser	<i>Mergus serrator</i>	Snow bunting	<i>Plectrophenax nivalis</i>
Partial migrants: species wintering in central and N Europe (N = 8 species)			
Goldcrest	<i>Regulus regulus</i>	Hooded crow	<i>C. corone cornix</i>
Blue tit	<i>Parus caeruleus</i>	Western greenfinch	<i>Carduelis chloris</i>
Great tit	<i>P. major</i>	Spruce siskin	<i>C. spinus</i>
Jackdaw	<i>Corvus monedula</i>	Yellowhammer	<i>Emberiza citrinella</i>

dates describing each species' first, median and late phases of migration were first correlated (Spearman rank correlations) with the winter NAO index using observation activity in the bird observatories as a partial variable (SAS, PROC CORR). Observation activity was partialled out because it also correlates with NAO (see Vähätalo et al. 2004). Therefore our NAO-correlations are conservative. We preferred to remove the effect of observation activity by partial correlations because adding observation activity in the linear model would have made it too complicated. We z-transformed the values of correlation coefficients to achieve normality of residuals in linear models (Sokal and Rohlf 1981, p. 583).

We modelled the effects on the phase date correlation coefficients of observatory, wintering area, and taxonomy (SAS, PROC MIXED). Because we had independent datasets from two bird observatories, we used observatory as a fixed factor to account for the combined effect of locality and differing observatory practices at different observatories. Although it makes

the model a bit more complicated, using two datasets increases strength of the analysis and the effects of factors of interest are conservative. Since the phases of migration are not independent of each other, we adopted a repeated-measures design where the phase of migration was entered as the within-subject repeated factor. Species was considered a random clustering factor nested within the observatory because each species has a migration time that is more or less the same in the two observatories and thus the observations from the two observatories are not independent of each other.

When analysing repeated measures data, modelling an appropriate covariance structure is essential so that inferences about the fixed effects are valid. To find out which covariance structure fitted the data best according to likelihood ratio tests, we first performed full-model analyses with the following alternative structures: 'unstructured', 'Toeplitz', 'compound symmetry' and first-order autoregressive (Littell et al. 1996). Once the best variance-covariance structure was determined, we

performed the analyses with backward elimination of non-significant terms from full models, starting from the highest-level interactions.

Results

Overall, the timing of spring migration was significantly dependent on the winter NAO index and the response to the NAO diminished with the phase of migration (mean and 95% confidence intervals) of all species: early phase -0.34 (-0.39 , -0.29), median phase -0.26 (-0.30 , -0.22) and late phase -0.16 (-0.20 , -0.11). That is, birds arrived earlier after winters with high NAO index and the early part of the migrating bird populations was more responsive to the NAO fluctuations. According to the likelihood ratio test, a model with first-order autoregressive variance-covariance structure was found to fit the data best. After the elimination of non-significant four- and three-way interactions, taxonomy \times phase, wintering area \times phase, observatory \times phase and wintering area \times observatory interactions remained significant (Table 2 A).

The timing of the early phase of migration was affected significantly more strongly by the NAO in both waterfowl and gulls and waders groups than in passerines. The timing of the late phase of migration was not affected by the NAO in waterfowl but it was

significantly affected in both gulls and waders and passerines (Fig. 1). In the median phase of migration all taxonomic groups responded similarly and significantly to NAO.

Because both wintering area and phase had significant interactions with observatory, we examined the wintering area \times phase interaction separately for the two bird observatories. In both observatories the interaction was statistically significant, indicating among- wintering area differences in the responses to the NAO among phases of migration (Table 2 B, C, and Fig. 2.).

In Jurmo (Fig. 2 A), the pattern of responses is rather clear with stronger responses in early phases with a gradual decrease of response towards later phases. In short-distance migrants the decrease of response strength with phase is steep, which causes the interaction between wintering area and phase. In Hanko (Fig. 2 B) the pattern is more complicated. There is an overall trend of decreasing responses with phase of migration, but the patterns differ between wintering area groups more than in the Jurmo dataset. In summary: 1) the responses of long-distance migrants were weaker than those of short- and medium-distance migrants in the early and median phases, but did not differ from other groups in the late phase, 2) the responses of the medium-distance migrants were similar in all phases, 3) the responses of the short-distance migrants were similar than those in Jurmo, decreasing steeply with

Table 2. Results of mixed model repeated-measures ANOVAs, in which the response variable was the correlation coefficient between the NAO and timing of migration, and the phase of migration (phase) was entered as the within-subject repeated factor. Species was considered a random clustering factor nested within the observatory. Since two interactions with observatory were significant (a), we did further analyses separately for the two bird observatories (b, c).

	df	F	P
(a) Models with pooled data from both observatories			
<i>Fixed effects-final model</i>			
wintering area	3, 140	6.00	0.0007
phase	2, 286	13.97	<0.0001
observatory	1, 140	0.01	0.9311
taxonomy	2, 140	0.62	0.5417
wintering area \times phase	6, 286	2.91	0.0090
wintering area \times observatory	3, 140	6.32	0.0005
observatory \times phase	2, 286	4.78	0.0091
phase \times taxonomy	4, 286	3.31	0.0113
<i>Removed fixed effects</i>			
wintering area \times observatory \times phase \times taxonomy	8, 260	0.43	0.9048
wintering area \times phase \times taxonomy	8, 268	1.12	0.3467
wintering area \times observatory \times taxonomy	4, 130	1.20	0.3160
observatory \times phase \times taxonomy	4, 276	1.46	0.2135
wintering area \times observatory \times phase	6, 280	1.59	0.1502
wintering area \times taxonomy	4, 134	0.37	0.8325
observatory \times taxonomy	2, 138	0.33	0.7162
(b) Jurmo			
<i>Fixed effects-final model</i>			
wintering area	3, 71	1.78	0.1581
phase	2, 142	12.39	<0.0001
wintering area \times phase	6, 142	2.57	0.0217
(c) Hanko			
<i>Fixed effects-final model</i>			
wintering area	3, 71	8.97	<0.0001
phase	2, 142	0.71	0.4934
wintering area \times phase	6, 142	5.88	<0.0001

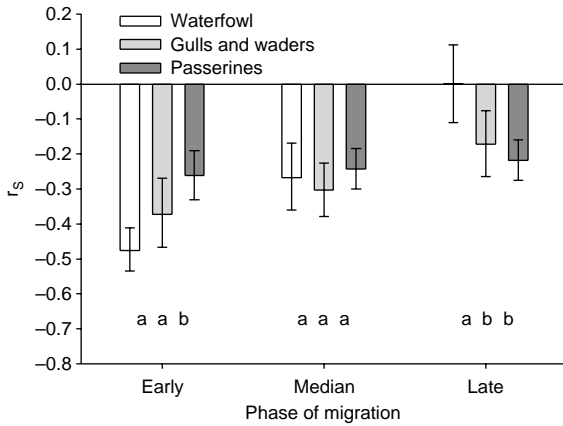


Fig. 1. Means ($\pm 95\%$ confidence intervals) of back-transformed Spearman correlation coefficients between spring migration dates (early = 5th percentile, median = 50th percentile and late = 95th percentile) and the winter NAO index in taxonomic groups. Small case letters below bars indicate whether groups differ according to post-hoc contrasts. Groups sharing same letter do not differ statistically significantly ($P > 0.05$) from each other.

phases and 4) the responses of partial migrants were hardly significant in all phases (Fig. 2 B).

Discussion

NAO-responses in relation to taxonomy

In the early phase of migration, passerines responded significantly less to the NAO than waterfowl and gulls and waders. In the median phase there were no differences between the taxonomic groups, and in the late phase the responses of waterfowl were weaker than in other groups. As the differences were not uniform among the phases, we cannot really make definitive conclusions on the differences between taxonomic groups. However, the stronger relationship in the early phase (Fig. 1) with the NAO in waterfowl and gulls and waders, that are in closer contact with water than passerines, might be explained in part by the dependence of ice conditions on the winter-NAO (Blenckner et al. 2004) and ice conditions in early spring in the study area.

NAO responses in relation to wintering area

NAO responses were on average negative as observed earlier (Vähätalo et al. 2004) and this held also within wintering area groups at large. Response strength varied, however, between wintering area groups, between phases of migration and between the two observatories. The results from the Hanko bird observatory indicated weaker NAO-responses for trans-Saharan migrants than for the other groups. In the Jurmo data the only

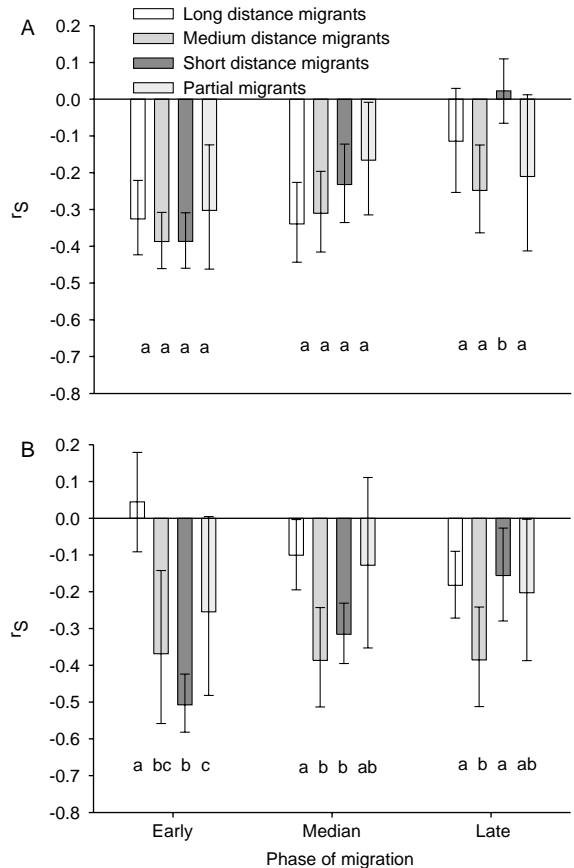


Fig. 2. Means ($\pm 95\%$ confidence intervals) of back-transformed Spearman correlation coefficients between spring migration dates (early = 5th percentile, median = 50th percentile and late = 95th percentile) and the winter NAO index in different wintering area groups. A) Jurmo bird observatory. B) Hanko bird observatory. Small case letters below bars indicate whether groups differ according to post-hoc contrasts. Groups sharing same letter do not differ statistically significantly ($P > 0.05$) from each other.

wintering area group differences were found in the late phase of migration, where short-distance migrants did not respond to NAO at all. The inconsistent results from the two observatories are at first surprising. Since the observatories are situated rather close to one another (73 km apart), it is unlikely that the migrating populations substantially differ between the two locations. However, different positions of the two observatories in relation to mainland could generate some species-specific variation in the numbers of migrants counted, which we were unable to account for in the present analysis. For example the numbers of insectivorous passerines are low in Hanko compared to Jurmo (see Vähätalo et al. 2004). This is probably because in peninsular Hanko birds can disperse inland shortly after their arrival, whereas on Jurmo Island most individuals stay for a longer time, until nightfall.

Overall, the models for the two observatories (Fig. 2) suggest the following conclusions: 1) on average the responses to NAO are significantly negative, i.e. birds arrive earlier when NAO is in its positive phase; 2) there is a decreasing trend of response to NAO with phase of migration; 3) on average, medium distance migrants respond most strongly to NAO, followed by short-distance migrants; and 4) responses are weaker and more variable with phase for long-distance and partial migrants.

The result that long-distance migrants are able to adjust their migration timing according to the NAO can be explained so that the birds accelerate migration when they face the advanced overall phenology *en route* when crossing Europe, as suggested by Hüppop and Hüppop (2003). Similar results have recently been published from Northern and North-western Europe (Forchhammer et al. 2002, Cotton 2003, Hüppop and Hüppop 2003, Vähätalo et al. 2004, Stervander et al. 2005). In contrast, Hubalek (2003) found that in the Czech Republic, the arrival times of species having sub-Saharan wintering ranges did not correlate with the NAO whereas species having European wintering ranges did. One possible explanation for this difference between the studies could be that the effect of speeding up migration does not show in lower latitudes closer to the Sahara desert and the Mediterranean.

Phase date differences in the NAO-responses

To date most studies on the timing of avian migration have concentrated on first arrival dates, or mean or median migration times (reviewed by Lehikoinen et al. 2004). We divided the passage of migration into three phases and found heterogeneity among the responses of several species groups. In most groups the degree of response weakened with the phase of migration, the early phase date of migration responding more strongly than the late phase date to the NAO. It might be argued that the fading of the correlations with the phase date of migration is caused by the increasing time interval between the measuring time (December-March) of the NAO index and that of bird migration. Thus, we checked whether the NAO correlations of successively later periods might change the correlations. The later NAO periods gave similar (February-April) or weaker (March-May) correlation coefficients than the period December-March (unpubl.).

There are various possible reasons why the early part of the migrating population responds more strongly to the NAO than median or late parts. It may be that 1) the result arises from increasing protandry, i.e. males arrive increasingly earlier than females since they are under a stronger selective pressure for early arrival (Møller 2004), 2) only individuals in good condition are able to

speed up their migration, 3) non-breeding individuals are not in a hurry and arrive independently of the NAO, 4) wintering ranges extend during mild winters so that the birds' northern range limit lays more to the north (Root 1988; Valiela and Bowen 2003; Austin and Rehlfisch 2005) and 5) birds, whose goal area is at higher latitudes where the advancement of spring is postponed, migrate later through the study area. At present, there is not enough detailed information about arrival in breeding areas to distinguish between these alternatives.

The phase date differences in responses to the NAO suggest that the distribution of migration timing will expand if the global temperatures will continue rising, as previously observed in pied flycatchers (Ahola et al. 2004). This could have fitness consequences if, for example, males arrive earlier but later migrating females do not. Thus, instead of using only single point estimates of timing, all phases of migration should be taken into account. The exploration of the mechanisms behind the fading of the responses with the phase of migration may provide interesting insights into the evolution of avian migration patterns and their responses to global climate change. Moreover, as the present study shows, the results may vary between the sampling sites (see also Sparks et al. 2005). In future studies data from several different locations should be jointly analyzed to reveal true biological variation in climatic responses attributable to different life history characteristics or taxonomic position of birds.

Complications with bird observatory data

While observatory data is usually well standardized, different methods of measuring migration intensity may measure different aspects of migration. For example, counting birds in active migratory flight avoids some problems in counting resting birds, since without ringing, the lengths of resting periods are not known. Active migratory flight is more directly related to current weather, but counting resting birds is related to previously encountered weather conditions. When we are interested of climate change effects in rather general level, as measured with NAO, differences between species and observatories in observation practice make rather little difference. However they may explain part of the variability among observatories in this study. A possible problem in studies of climate change impacts on migration is that the observatory data in most species are mixtures of different populations (Hüppop and Hüppop 2004). Thus it follows that results of analyses of climate effects cannot be associated to any specific population. This problem is smaller the more north the bird observatory is situated.

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