



SYMPOSIUM

Local Temperature Fine-Tunes the Timing of Spring Migration in Birds

Anders P. Tøttrup,^{1,*} Kalle Rainio,[†] Timothy Coppack,^{‡,§} Esa Lehikoinen,[†] Carsten Rahbek* and Kasper Thorup[¶]

*Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark; [†]Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland; [‡]Institute of Avian Research, Vogelwarte Helgoland, An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany; [§]Institute of Applied Ecology Ltd, Alte Dorfstrasse 11, D-18184 Broderstorf, Germany; [¶]Center for Macroecology, Evolution and Climate, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

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¹E-mail: aptottrup@bio.ku.dk

Synopsis Evidence for climate-driven phenological changes is rapidly increasing at all trophic levels. Our current poor knowledge of the detailed control of bird migration from the level of genes and hormonal control to direct physiological and behavioral responses hampers our ability to understand and predict consequences of climatic change for migratory birds. In order to better understand migration phenology and adaptation in environmental changes, we here assess the scale at which weather affects timing of spring migration in passerine birds. We use three commonly used proxies of spring-time climatic conditions: (1) vegetation “greenness” (NDVI) in Europe, (2) local spring temperatures in northern Europe, and (3) the North Atlantic Oscillation Index (NAO) as predictors of the phenology of avian migration as well as the strength of their effect on different subsets of populations and the dependence of correlations on species-specific migratory strategy. We analyze phenological patterns of the entire spring migration period in 12 Palaearctic passerine species, drawing on long-term data collected at three locations along a longitudinal gradient situated close to their northern European breeding area. Local temperature was the best single predictor of phenology with the highest explanatory power achieved in combination with NAO. Furthermore, early individuals are more affected by climatic variation compared to individuals on later passage, indicating that climatic change affects subsets of migratory populations differentially. Species wintering closer to the breeding areas were affected more than were those travelling longer distances and this pattern was strongest for the earliest subsets of the population. Overall, our results suggest that at least early subsets of the population are affected by local conditions and early birds use local conditions to fine-tune the date of their spring arrival while individuals arriving later are driven by other factors than local conditions e.g. endogenous control. Understanding what cues migratory organisms use to arrive at an optimum time is important for increasing our knowledge of fundamental issues like decision making in organisms during migration and is crucial for future protection of migratory organisms.

Introduction

Evidence showing that global climatic change is driving changes in the timing of seasonal activities in various organisms at all trophic levels, including migratory birds, is compelling (Walther et al. 2002; Root et al. 2003; Parmesan 2006, 2007). However, our overall poor understanding of the mechanisms controlling bird migration at the genetic, hormonal,

and organismic level calls for a more integrative approach and currently hampers our ability to predict consequences of climatic change on bird migration. Organisms on migration need to constantly adjust to local conditions, e.g. new food resources, highly variable environmental conditions, and different levels of predation. To successfully complete their annual cycle, which for many species includes travelling

thousands of kilometers, they need to adjust their physiology, immunology, and even morphology (Alerstam 1990; Berthold 1996). Because the environmental impact of climatic change is expected to vary spatially and temporally between regions (Stöckli and Vidale 2003; IPCC 2007), predicting responses of migratory species to such changes requires detailed knowledge of the factors and of the mechanisms of response that fine-tune and limit the migratory process.

Although a vast number of studies have dealt with the impact of climatic change on phenology (the timing of seasonal events) (Lehikoinen et al. 2004; Gordo 2007), knowledge of which—and on what scale—climatic conditions affect migrants at different stages of their life cycle and how phenological responses translate into viability of the population and individual fitness is still limited (but see Sillett et al. 2000). Likewise, we still have a poor understanding of how endogenous annual cycles and external cues are orchestrated to ensure appropriate timing of migration and arrival at the breeding grounds.

In migratory birds, phenological changes in both spring and autumn migration have already been reported from Australia (Beaumont et al. 2006), North America (Marra et al. 2005; Mills 2005), Europe and Asia (Jenni and Kéry 2003; Tøttrup et al. 2006a, 2006b; Gordo et al. 2007). Timing of migration can be adjusted prior to departure where ecological conditions can affect individuals' physiology, e.g. body condition (Norris et al. 2004), as well as during the migration period (Ahola et al. 2004), where improved ecological conditions at stopover sites can reduce the time required for replenishing fuel stores (Schaub and Jenni 2001). At the same time, timing of migration is controlled by endogenous circadian and circannual rhythms synchronized with changes in day length, which stay fixed as the Earth's climate changes (Coppack and Pulido 2004; Bradshaw and Holzapfel 2008).

Several former studies have highlighted the importance of considering variation at the spatial scale in phenological studies (Both et al. 2004). Most of these studies, however, have focused on the onset of breeding and not on evaluating climatic effects on the migratory prebreeding period (but see Both and te Marvelde 2007; Macmynowski et al. 2007). Furthermore, most former studies have explained climate-induced changes in timing of seasonal events by single-proxy measures of environmental conditions. Hence, there are still unanswered questions such as the spatial scale at which phenological adjustments take place and the factors controlling timing of migration. To achieve a better

understanding of these important aspects of the life-history strategies of migrants, we need to assess the significance of multiple factors potentially affecting the phenology of migration, e.g. including a range of different environmental variables into long-term phenological analyses. Here, we directly compare the performance of three different environmental measures as indicators of avian phenology and focus on the importance of each variable affecting the decisions made by birds during migration.

In the present study, we use a long-term multi-species dataset covering a longitudinal gradient in northwestern Europe. The environmental variables are commonly used proxies for the conditions birds experience during migration but reflect conditions at different spatial scales: spring vegetation "greenness" (NDVI) in Europe, local spring temperature in northern Europe and the regional climatic index: (NAO). Further, we aim to investigate how different population subsets and species with different migration strategies are affected by these climatic factors at different scales.

Methods

Phenological data

We used spring data on migratory passerines from three constant-effort ringing stations located on isolated islands: Heligoland in the North Sea (54°10'N, 7°53'E; Germany; Hüppop and Hüppop 2003) as well as Christiansø (55°19'N, 15°11'E; Tøttrup et al. 2006b) and Jurmo (59°50'N, 21°37'E; Finland; Vähätalo et al. 2004) in the Baltic Sea (Fig. 1). For Jurmo, we also included standardized observational data. The ringing stations monitor migrants prior to their arrival at the breeding areas in Scandinavia and Finland and cover the entire migration period each year.

Only species of which a minimum of 20 individuals were trapped or observed per season at each ringing station for a minimum of 12 years were included in the analyses (Appendix 1). By visual inspection of ring-recoveries (Bønløkke et al. 2006; Zink 1973), we excluded species showing migratory divides between the ringing stations. Following these criteria, 12 species covering a period of 16 years from 1982 to 1997 were included in the study. Six of these are short-distance migrants wintering in Europe: Blackbird *Turdus merula*, Wren *Troglodytes troglodytes*, Dunnock *Prunella modularis*, Robin *Erithacus rubecula*, Redwing *Turdus iliacus* and Song Thrush *Turdus philomelos*; while the other six species are long-distance migrants wintering in sub-Saharan Africa: Redstart *Phoenicurus*



Fig. 1 Map of Europe presenting the three ringing stations (black circles, Hel: Heligoland; Chr: Christiansø; and Jur: Jurmo) and locations of the eight weather stations from where temperature data was taking (circles). Gray area roughly indicates the area included in the NDVI measurement (see text for details) and the broad breeding range of the species included in the study are also indicated (striped area; Rabøl and Rahbek 2002; Bønløkke et al. 2006).

phoenicurus, Pied Flycatcher *Ficedula hypoleuca*, Whitethroat *Sylvia communis*, Garden Warbler *Sylvia borin*, Willow Warbler *Phylloscopus trochilus* and Spotted Flycatcher *Muscicapa striata*.

For each species, three measures of timing of migration were analyzed; the day (in Julian days where day one = 1 January) of trapping by which the first 5, 50, and 95% of the spring total had been caught. Subsequently these are referred to as “migration phases” (Tøttrup et al. 2006b). To avoid potential biases caused by birds arriving later at northern localities than at more southerly ones, and to meet the assumption of the statistical tests (see below), all data on species-specific time of arrival were standardized to mean zero and unit standard deviation.

Environmental data

Three proxy measures of the environmental conditions in Europe were included. First, the monthly

normalized difference vegetation index (NDVI, www.clarklabs.org) maximum value composite was included as a proxy measure for the actual environmental conditions in Europe for the months March, April, and May. NDVI offers a fully comparable measure of ecological conditions between regions and years (Pettoelli et al. 2005) (Fig. 1). Second, we used a mean monthly temperature from eight weather stations located in Holland (De Bilt), northern Germany (Hamburg and Berlin), southern Sweden (Växjö), eastern Russia (Kaliningrad), Estonia (Vilsandi and Võru), and southwestern Finland (Turku) (Fig. 1). For each of the months of March, April, and May, we used a mean over all stations, thereby achieving an overall regional average for the months (Appendix 2). The temperature data were obtained from the European Climate Assessment & Dataset (ECA&D) project and the Finnish Meteorological Institute. Monthly mean

values were chosen because the temporal resolution in the species-specific arrival patterns defer between ringing stations and because of our limited knowledge of the spatial positions of the birds prior to their arrival at the ringing stations. Third, we included the winter index (December–March) of the North Atlantic Oscillation (NAO), calculated as the mean monthly value of the normalized differences in pressure between the Azores and Iceland. NAO was chosen because it correlates with temperature, precipitation, and wind during winter and is frequently used as a predictor of spring conditions in Europe (Hurrell et al. 2003). As these climatic variables show some degree of multicollinearity (Appendix 3), we apply the appropriate analyses described below.

Statistical analyses

Based on ring-recovery analyses (Zink 1973; Bønløkke et al. 2006), we divided the species into five migration groups according to the distance of migration from northwestern Europe (Appendix 2) where the effect of NAO is most pronounced (Visbeck et al. 2001). For spring NDVI and spring temperature, each species-specific migration phase was modeled with environmental measures corresponding to the time window when the different phases of migration through Europe occur (Appendix 2).

First, by running a model (Proc GLM in SAS 2003) including all three climatic variables (spring NDVI, spring temperature, winter NAO), we estimated the overall variation in migration phenology explained by climate for each species and migration phase. The explanatory power (r^2) of each model (36 in total) was then modeled with Migration Group, Migration Phase, and their interaction term (Proc Mixed in SAS 2003) to investigate how climate affects the different phases of migration and the migrating groups. Migration Phase was included in the models as a repeated factor. The interaction term Migration Phase \times Migration Group indicates whether migration groups are affected differently in the three migration phases of migration. Since we aim to assess how much each individual climatic variable affects phenology in contrast to general analysis of how climatic variables generally affect avian phenology, we chose r^2 as dependent variable here and below. Furthermore, in this multi-species approach species-specific migration and phenological patterns influences the results, e.g. slopes from general linear modeling approaches are difficult to compare because changes over time will affect the modeling outputs differently. Overall, r^2 is the most unbiased and directly comparable measure

across models independent of statistical significance (because our models have the same number of variables an Akaike's information criterion (AIC) approach would not add additional power [Burnham and Anderson 2002]).

Second, we analyzed the explanatory power (r^2) of each climatic variable on arrival day in each migration phase by running a model (Proc GLM in SAS 2000) for each species, Migration Phase and Climate Variable. The explanatory power (r^2), of each model (108 in total) was then included in a statistical model as a dependent variable with Migration Phase, Migration Group, Climate Variable and interactions as the independent variables and Migration Phase as a repeated factor (Proc Mixed in SAS 2003). The interaction term Migration Group \times Climate Variable indicates whether migrants with different migration strategies are affected differently by the climatic variables. The interaction term Migration Group \times Migration Phase indicates differences in how the different phases of migration are reacting in migrants with different migration strategies.

Third, we performed standard partial correlation analyses on the first migration phase (5%), correlating day of arrival with each of the three climatic variables while holding the other two variables constant (following Sokal and Rohlf 1998). This approach was applied as the three climatic variables show some degree of multicollinearity (Appendix 3). The partial correlation approach estimates the amount of variation explained by a single variable that is not explained by the other variables, thereby taking the collinearity between climatic variables into account. Hence, we use the explanatory power (r_p^2) as indicators of the unique degree of variation explained by each of the climatic variables using nonparametric tests (i.e. Friedman's test and Wilcoxon's test).

Finally, we evaluated the strength of each climatic variable as a predictor of migration phenology in the first phases of migration using an information-theoretic model-selection approach based AIC (Burnham and Anderson 2002). Observatory and Species were included as fixed variables in all seven combinations of models with the three climate variables. This analysis was performed in SAS (2003).

Results

In a GLM, with all variables included, we found no overall differences in explanatory power between the different measures of climate ($F=0.63$, $P=0.532$, $df=2$; Table 1). However, comparing partial correlation coefficients of the first phases of

Table 1 Effect of Migration Phase, Migration Group, and Climate Variable (spring NDVI, spring temperature, and winter NAO) on climate explained variation in passage day

	df	F	P	Estimate	SE	Parameter
Intercept	96		0.479	0.0302	0.0426	
Migration Phase	2	22.78	<0.0001	0.2607	0.0386	5% phase
				0.1273	0.0386	50% phase
				0		95% phase
Migration Group	1	25.76	<0.0001	0.0043	0.0105	
Climate Variable	2	0.63	0.532	-0.0327	0.0386	NAO
				0.0086	0.0386	NDVI
				0		Temp
Migration Group × Migration Phase	2	11.61	<0.0001	-0.0550	0.0115	5% phase
				-0.0222	0.0115	50% phase
				0		95% phase
Migration Phase × Climate Variable	4	1.09	0.341	0.0046	0.0115	NAO
				-0.0118	0.0115	NDVI
				0		Temp

The migration distance is affecting the phases of migration differently (Fig. 3). We used mixed models (SAS 2003) with migration phase as repeated factor.

migration, we found an overall difference between the three climatic variables ($\chi^2=8.17$, $n=8$, $P<0.02$, Friedman's test; Fig. 2A) with temperature being a better predictor than NAO (Rank_{min}=1, $P<0.005$, $n=8$, Wilcoxon's test; Fig. 2A). The explanatory power of NDVI was not found to be different from the other two variables. While no differences were found between the predictor variables within the group of short-distance migrants ($\chi^2=5.33$, $P=0.1$, $n=4$, Friedman's test; Fig. 2B), we found spring temperature to be a better predictor of spring arrival than winter NAO in the group of long-distance migrants (Rank_{min}=0, $P<0.05$, $n=4$, Wilcoxon's test; Fig. 2C). Model selection based on AIC confirmed this pattern, as temperature was included in all the best models (Table 2). Models with NDVI and NAO as single predictors were not strong compared to temperature but models including temperature combined with either NDVI or NAO came out as the most powerful. Repeating the analyses using other temporal envelopes for spring temperature and spring NDVI (Appendix 2) did not change the results.

We found the earliest migration phases (first 5 and 50%) to be more affected by environmental conditions en route compared to later phases of migration. For the majority of species (67%, $n=8$), the highest explained variation did occur for the first 5% subsets of the population, whereas this was not the case for three (25%) and one (8%) for the first 50 and 95% subsets of the population, respectively.

This result was supported by the GLM approach ($F=5.59$, $P=0.009$, $df=2$; Table 3 and Fig. 3). Migration distance affected these patterns. Species wintering in areas furthest away from northwestern Europe showed a smaller degree of explained phenological change (mean $r^2=0.31$) compared to species wintering further to the north (mean $r^2=0.22$; $F=4.36$, $P=0.045$, $df=1$; Table 3). When analyzing each climatic variable separately, we found that distance of migration had an effect for the first phases of migration whereas this had less impact on later individuals. This effect was stronger in short- than in long-distance migrants with the highest explained variation in short-distance migrants occurring for 13 (72%), 4 (22%), and 1 (6%) for the first 5, 50, and 95%, respectively, whereas for long-distance migrants the corresponding numbers were 6 (33%), 9 (50%), and 3 (17%), respectively. This pattern was supported by the statistical model (Migration Group × Migration Phase; $F=11.61$, $P<0.001$, $df=2$; Table 1 and Fig. 4). Figure 5 presents mean difference in degree of response to each of the three climatic variables by short-distance and long-distance migrants, respectively.

Discussion

We are currently far from understanding the causes of perceived phenological changes at the individual level or, vice versa, from resolving how individual reaction norms may translate into population

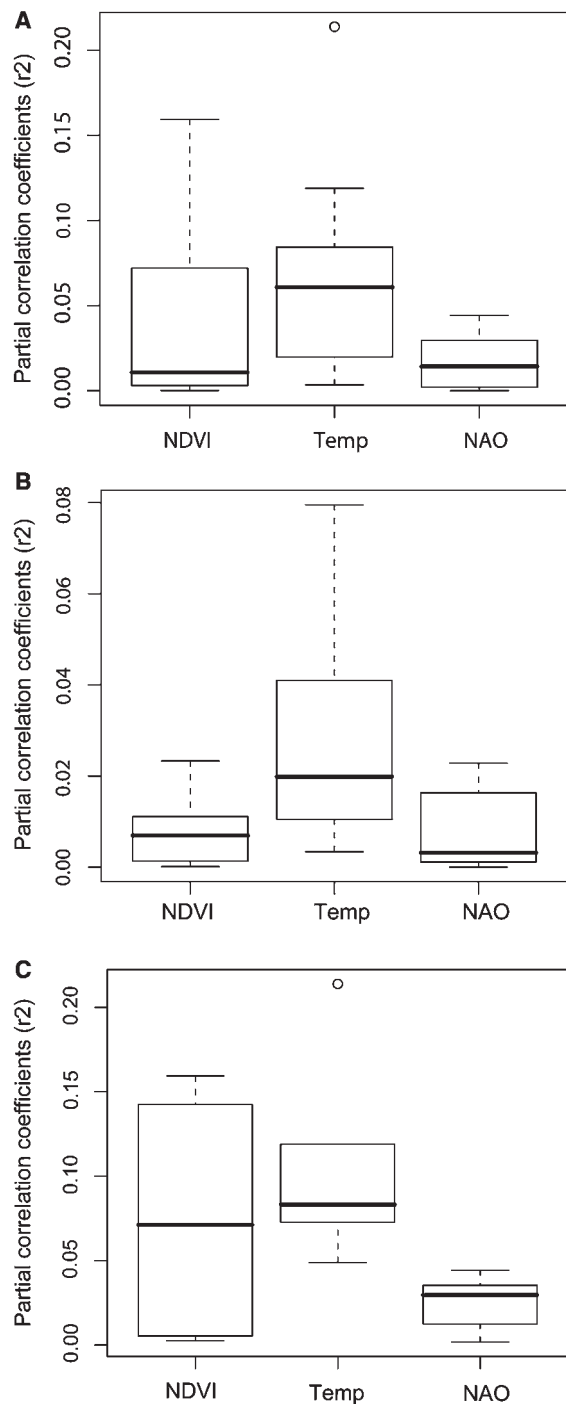


Fig. 2 Comparing the unique variation explained by spring NDVI, spring temperature, and winter NAO (see text for details) for all species (A), short-distance migrants (B), and long-distance migrants (C), respectively. Figures are box plots of the squared standard partial correlation coefficients (r_p^2). Note the different scales to facilitate comparisons within groups.

responses in the future (Coppack 2007). Such understanding requires an integrative approach including ecological and evolutionary responses to climatic variation at the physiological and behavioral level. Our

Table 2 Information-theoretic model-selection approach based on Akaike's information criterion (Burnham and Anderson 2002) with observatory and species included as variables in the full model, which was directly compared with the six other model combinations including the three climate variables: spring NDVI, spring temperature (Temp), and winter NAO

Model	All species included ΔAIC	Short-distance migrants ΔAIC	Long-distance migrants ΔAIC
NDVI + Temp + NAO	1.93	1.34	2.19
NDVI + Temp	3.80	0.00	1.26
Temp + NAO	0.00	1.43	1.51
NDVI + NAO	31.17	12.05	21.56
NDVI	44.28	17.55	28.04
Temp	1.81	0.62	0.00
NAO	33.38	29.88	19.40

The difference in AIC value between each model and the best model are given. Models with a ΔAIC less than 2 are in bold.

focus here is the relative importance of those climatic variables that have been commonly used as predictors of avian phenology in a large number of publications throughout the past decade (Gordo 2007). Winter NAO is widely used in phenological studies as a proxy measure of overall spring conditions (Forchhammer et al. 2002; Hüppop and Hüppop 2003; Rainio et al. 2007), and with high explanatory power (Hallett et al. 2004). In our study, however, local spring temperatures en route are better predictors of avian phenology in direct comparison with NAO. This result holds for species that migrate different distances and have different times of migration. Furthermore, our results indicate that the fine-tuning of arrival time at the breeding area is directly influenced by local environmental factors experienced during migration. Hence, at least individuals are influenced by local conditions in their decision making during the later part of their spring migration.

Concern for a climate-driven mismatch between timing of breeding and the time of the peak in food has been raised (Both et al. 2006; but also see Jonzén et al. 2007). In the present study, we show that the population subsets arriving first are responding more to climatic conditions during migration than are later subsets (Vähätalo et al. 2004; Rainio et al. 2006; Tøttrup et al. 2008). This indicates that the population subsets arriving first use climatic cues for optimal timing of arrival, while individuals arriving later are driven by, or to a larger degree rely on, other factors than local conditions, e.g. endogenous control. As first arrivals are usually adult males, closely followed by adult females (Tøttrup and

Table 3 Effect of migration phase (first 5, 50, and 95% of the total number of trapped individuals) and Migration Group (according to the distance from north-western Europe to the wintering area, see text and Appendix 1) on the degree of climate explained variation in passage day

	df	F	P	Estimate	SE	Parameter
Intercept	30		0.123	0.1016	0.0640	
Migration Phase	2	5.59	0.009	0.2998	0.0905	5% phase
				0.1853	0.0905	50% phase
				0		95% phase
Migration Group	1	4.36	0.045	0.0003	0.0236	
Migration Group × Migration Phase	2	1.49	0.241	−0.0577	0.0334	5% phase
				−0.0286	0.0334	50% phase
				0		95% phase

The first migration phases and species with longer migration distances are more affected by climate (Fig. 2). We used mixed models (SAS 2003) with migration phase as repeated factor.

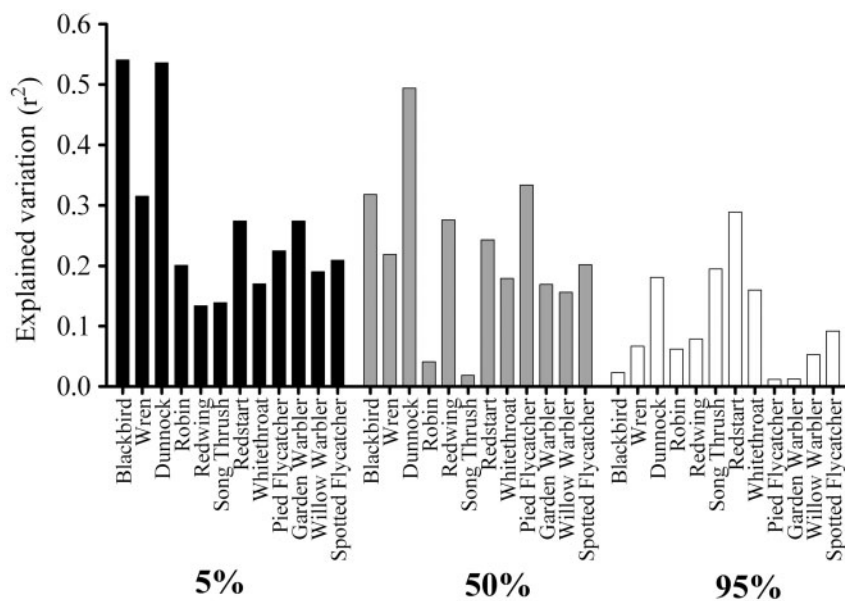


Fig. 3 Degree of explained variation (r^2) in passage day for 12 migratory songbirds when including spring NDVI, spring temperature, and winter NAO in general linear regression models for three phases of migration (first 5, 50, and 95% of the total number of trapped individuals).

Thorup 2008; Coppack and Pulido 2009), the patterns found may be driven by experienced birds while young and inexperienced individuals merely rely on endogenous cues. Overall, if only a smaller fraction of the populations are able to follow changes in environmental conditions, rapid climatic change may have a high impact on migratory bird populations.

As endogenous control of onset of migration is unlikely to differ between early and late birds (Gwinner 1996), the temperature ranges that different species and population subsets experience (Stöckli and Vidale 2003; IPCC 2007) may explain

the different patterns of arrival. Hence, temperature increase in early spring may have a stronger effect, because temperature is generally low at this time, whereas later in the year, mean temperatures are generally high and an increase in temperature may not have the same effect. On the other hand, species migrating shorter distances, are more affected by climate or track the actual environmental conditions to a higher extent compared to species that migrate longer distances. As sub-Saharan migrants are entering Europe later in the season, compared to migrants wintering around the Mediterranean, they will have a shorter time window for adjusting their timing of

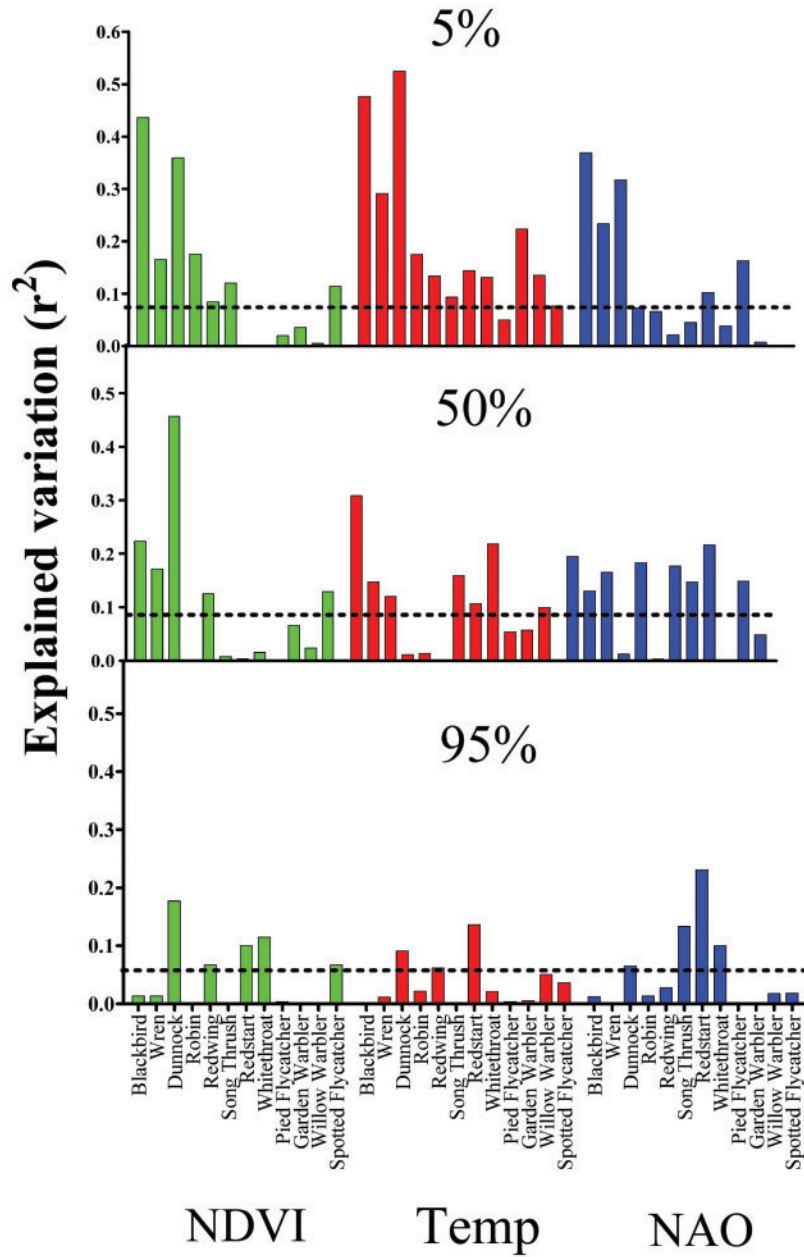


Fig. 4 Degree of variation explained (r^2) in passage day for 12 migratory songbirds when doing specific general linear regression models for spring NDVI (green bars), spring temperature (red bars), and winter NAO (blue bars) for three phases of migration (first 5, 50, and 95% of the total number of trapped individuals). The dotted line indicates level of significance.

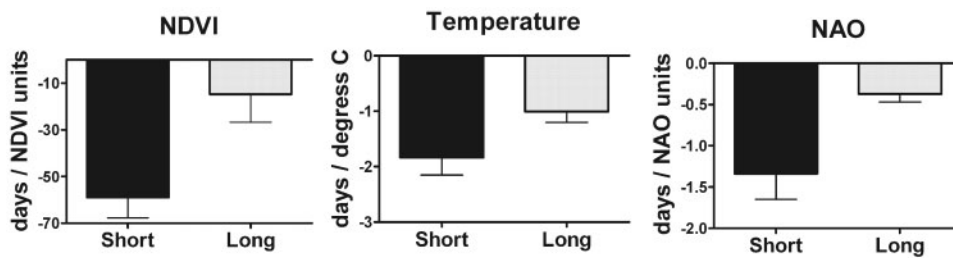


Fig. 5 Mean effect of spring NDVI, spring temperature and winter NAO on the arrival day in short- and long-distance migrants (dark and light bars, respectively) for the 5% migration phase (see text for details). Error bars indicate standard error.

migration to the European conditions en route. Indeed, sub-Saharan migrants seem to adjust timing of migration to environmental conditions during migration (Tøttrup et al. 2008), and long-term advancement of spring migration has been shown in sub-Saharan migrants, even at far lower latitudes (Jonzén et al. 2006). However, the degree of apparent adjustment to conditions en route as reflected by phenological responses is still not as pronounced as in short-distance migrants. This finding is contrary to the study at a single site by Hüppop and Hüppop (2003) and corroborates Berthold's early assumptions on how songbird species with different migration strategies may respond differentially to global climatic change (Berthold 1991).

Causes of phenological changes

Environmental conditions during the nonbreeding period may directly affect both the departure time in spring and the timing of migration en route (Norris et al. 2004). Although the majority of studies have found advanced timing of spring migration in northern Europe (Lehikoinen et al. 2004), patterns of delayed passage over the Sahara Desert have likewise been reported (Gordo and Sanz 2005; Askeyev et al. 2007; Tøttrup et al. 2008). Combining the large number of studies reporting different phenological patterns with studies showing that timing of migration is adjusted en route as a response to environmental conditions (Marra et al. 2005; Tøttrup et al. 2008) indicates that at least some degree of phenotypic plasticity affects timing of arrival at the breeding area.

Other phenological studies attempt to decipher whether observed phenological changes represent climate-driven evolutionary change as opposed to phenotypic responses to environmental cues (Jonzén et al. 2006). Currently, there is neither support for, nor reason to reject, evolutionary and plastic phenotypic responses in avian migration phenology (Gienapp et al. 2007). It seems that the "nature versus nurture" debate concerning the relative importance of innate and acquired behavioral traits has so far not led to a better understanding of phenotypic responses of birds to climatic change. Evolutionary changes in the timing of migration are likely to involve evolutionary (genetic) changes in reaction norms, i.e. the framework in which populations or individuals may respond plastically to environmental cues (Coppack and Pulido 2004; Pulido 2007).

Detailed analyses of the factors determining the onset and progression of spring migration (e.g.

from tropical wintering areas) and arrival at the site of reproduction, as well as studies on the fitness consequences of variation in spring arrival are urgently needed. Overall, this will add valuable information to our still rather limited understanding of the factors that gauge annual life cycle in birds. To further develop an integrative approach to research on the biology of bird migration we need to extend our view from single-site and single-factor analyses. Here the rapid development of techniques for following a large number of individuals throughout their annual cycle in their natural settings (Wikelski et al. 2007; Robinson et al. in press) will allow addressing questions and performing experiments that were previously only approachable in laboratory settings (Thorup et al. this issue).

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References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob Change Biol* 10:1610–7.
- Alerstam T. 1990. *Bird migration*. Cambridge, UK: Cambridge University Press.
- Askeyev OV, Sparks TH, Askeyev IV, Tryjanowski P. 2007. Is earlier spring migration of Tatarstan warblers expected under climate warming. *Int J Biometeorol* 51:459–63.

- Beaumont LJ, McAllan IAW, Hughes L. 2006. A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Glob Change Biol* 12:1339–54.
- Berthold P. 1991. Patterns of Avian migration in light of current global greenhouse effects: a central European perspective. *Acta XX Congressus Internationalis Ornithologici* 2:780–6.
- Berthold P. 1996. Control of bird migration. London: Chapman & Hall.
- Bønlokke J, Madsen J, Thorup K, Bjerrum M, Rahbek C. 2006. Dansk Trækfugleatlas. Humlebæk, Denmark: Rhodos.
- Both C, et al. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc R Soc Lond B* 271:1657–62.
- Both C, Bouwhuis S, Lessells CM, Visser ME. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–3.
- Both C, te Marvelde L. 2007. Climate change and timing of avian breeding and migration throughout Europe. *Clim Res* 35:93–105.
- Bradshaw WE, Holzapfel CM. 2008. Genetic responses to rapid climate change: it's seasonal timing that matters. *Mol Ecol* 17:157–66.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York, USA: Springer.
- Coppack T. 2007. Experimental determination of the photoperiodic basis for geographic variation in avian seasonality. *J Orn* 148(Suppl 2):459–67.
- Coppack T, Pulido F. 2004. Photoperiodic response and the adaptability of avian life cycles to environmental change. *Adv Ecol Res* 35:131–50.
- Coppack T, Pulido F. 2009. Proximate control and adaptive potential of protandrous migration in birds. *Integr Comp Biol* 49:493–506.
- Forchhammer MC, Post E, Stenseth NC. 2002. North Atlantic Oscillation timing of long- and short-distance migration. *J Anim Ecol* 71:1002–14.
- Gienapp P, Leimu R, Meril J. 2007. Responses to climate change in avian migration time — microevolution versus phenotypic plasticity. *Clim Res* 35:25–35.
- Gordo O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58.
- Gordo O, Sanz JJ. 2005. Phenology and climate change: a long study in a Mediterranean locality. *Oecologia* 146:484–95.
- Gordo O, Sanz JJ, Lobo JM. 2007. Spatial patterns of white stork (*Ciconia ciconia*) migratory phenology in the Iberian Peninsula. *J Orn* 148:293–308.
- Gwinner E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* 138:47–63.
- Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* 430:71–5.
- Hüppop O, Hüppop K. 2003. North Atlantic Oscillation and timing of the spring migration in birds. *Proc R Soc Lond B* 270:233–40.
- Hurrell JW, Kushnir Y, Ottersen G, Visbeck M. 2003. An overview of the North Atlantic Oscillation. *Geophysical Monograph* 134:1–35.
- IPCC 2007. Impacts, adaptation and vulnerability. In: Contribution of Working Group II of the 4th assessment report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge: Cambridge University Press.
- Jenni L, Kéry M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc R Soc Lond B* 270:1467–71.
- Jonzén N, Hedenström A, Lundberg P. 2007. Climate change and the optimal arrival of migratory birds. *Proc R Soc Lond B* 274:269–74.
- Jonzén N, et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–61.
- Lehikoinen E, Sparks TH, Zalakevicius M. 2004. Arrival and departure dates. *Adv Ecol Res* 35:1–31.
- Macmynowski DP, Root TL, Ballard G, Geupel GR. 2007. Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate. *Glob Change Biol* 13:2239–51.
- Marra PP, Francis CM, Mulvihill RS, Moore FR. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–15.
- Mills AM. 2005. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* 147:259–69.
- Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc R Soc Lond B* 271:59–64.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–69.
- Parmesan C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob Change Biol* 13:1860–72.
- Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–10.
- Pulido F. 2007. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Clim Res* 35:5–23.
- Rabøl J, Rahbek C. 2002. Population trends in the Baltic passerine migrants, elucidated by a combination of ringing data and point- and summer-count indices. *Dansk Ornitologisk Forenings Tidsskrift* 96:15–38.
- Rainio K, Laaksonen T, Ahola M, Vahatalo AV, Lehikoinen E. 2006. Climatic responses in spring migration of boreal and

- arctic birds in relation to wintering area and taxonomy. *J Avian Biol* 37:507–15.
- Rainio K, Tøttrup AP, Lehikoinen E, Coppack T. 2007. Effects of climate change on the degree of protandry in migratory songbirds. *Clim Res* 35:107–14.
- Robinson WD, Bowlin MS, Bisson I, Shamoun-Baranes J, Thorup K, Diehl RH, Kunz TH, Mabey S, Winkler DW. 2009. Integrating concepts and technologies to advance the study of bird migration. *Front Ecol Environ* published online (doi:10.1890/080179).
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 241:57–60.
- SAS 2003. SAS version 9.1 Cary, NC, USA: SAS Institute Inc.
- Schaub M, Jenni L. 2001. Stopover durations of three warbler species along their autumn migration route. *Oecologia* 128:217–27.
- Sillett TS, Holmes RT, Sherry TW. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2.
- Sokal RR, Rohlf FJ. 1998. *Biometry*. New York, USA: W.H. Freeman and Company.
- Stöckli R, Vidale PL. 2003. European plant phenology and climate as seen in a 20-year AVHRR land-surface parameter dataset. *Int J Remote Sens* 25:3303–30.
- Thorup K, Holland RH, Tøttrup AP, Wikelski M. (this issue). Understanding the migratory orientation program in birds: extending laboratory studies to studying free-flying migrants in a natural setting. *Integr Comp Biol*.
- Tøttrup AP, Thorup K. 2008. Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *J Orn* 149:161–7.
- Tøttrup AP, Thorup K, Rahbek C. 2006a. Changes in timing of autumn migration in North European songbird populations. *Ardea* 94:527–36.
- Tøttrup AP, Thorup K, Rahbek C. 2006b. Patterns of change in timing of spring migration in North European songbird populations. *J Avian Biol* 37:84–92.
- Tøttrup AP, Thorup K, Rainio K, Yosef R, Lehikoinen E, Rahbek C. 2008. Avian migrants adjust migration in response to environmental conditions en route. *Biol Lett* 4:685–8.
- Vähätalo AV, Rainio K, Lehikoinen A, Lehikoinen E. 2004. Spring arrival of birds depends on the North Atlantic Oscillation. *J Avian Biol* 35:210–6.
- Visbeck M, Hurrell JW, Polvani L, Cullen HM. 2001. The North Atlantic Oscillation: past, present, and future. *PNAS* 98:12876–7.
- Walther GR, et al. 2002. Ecological responses to recent climate change. *Nature* 416:389–95.
- Wikelski M, Kays RW, Kasdin NJ, Thorup K, Smith JA, Swenson JGW. 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. *J Exp Biol* 210:181–6.
- Zink G. 1973. *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel*, 1. Möggingen, Germany: Vogelzug-Verlag.

Appendix

Appendix 1 Minimum, mean, and maximum number of individual birds of species trapped between 1982 and 1997 at different sites, as well as the number of years with more than 20 individuals (years > 20 individuals)

Species	Helgoland				Christiansø				Jurmo			
	Min	Mean	Max	Years/>20 individuals	Min	Mean	Max	Years/>20 individuals	Min	Mean	Max	Years/>20 individuals
Short-distance migrants												
Blackbird <i>Turdus merula</i>	507	1169	2255	16	112	244	500	16	299	632	1380	16
Wren <i>Troglodytes troglodytes</i>	10	29	62	12	44	142	381	16	16	33	52	14
Dunnock <i>Prunella modularis</i>	85	231	363	16	116	325	651	16	136	375	697	16
Robin <i>Erithacus rubecula</i>	114	274	571	16	760	2459	3862	16	1598	3586	6753	16
Redwing <i>Turdus iliacus</i>	31	85	228	16	45	103	175	16	608	1273	2095	16
Song Thrush <i>Turdus philomelos</i>	440	973	1624	16	221	409	790	16	819	1997	4268	16
Long-distance migrants												
Redstart <i>Phoenicurus phoenicurus</i>	66	154	269	16	186	358	577	16	463	709	1090	16
Pied Flycatcher <i>Ficedula hypoleuca</i>	21	46	72	16	75	235	439	16	274	479	753	16
Whitethroat <i>Sylvia communis</i>	23	99	165	16	65	143	254	16	129	272	422	16
Garden Warbler <i>Sylvia borin</i>	91	360	591	16	290	605	1085	16	116	411	798	16
Willow Warbler <i>Phylloscopus trochilus</i>	76	256	463	16	628	2181	3014	16	440	1219	2840	16
Spotted Flycatcher <i>Muscicapa striata</i>	15	86	218	15	56	142	353	16	271	749	1561	16

Appendix 2 Species included in the study as well as the applied migration group according to distance from wintering area to northwestern Europe and the temporal selection of climate variables (NDVI and temperature) according the general phenology and migration strategy of each species

Species	Migration group	NDVI/Temperature		
		5%	50%	95%
Short-distance migrants				
Blackbird <i>Turdus merula</i>	0	March	March	April
Wren <i>Troglodytes troglodytes</i>	0	March	April	April
Dunnoek <i>Prunella modularis</i>	1	March	April	April
Robin <i>Erithacus rubecula</i>	2	March	April	April
Redwing <i>Turdus iliacus</i>	2	March	April	April
Song Thrush <i>Turdus philomelos</i>	2	March	April	April
Long-distance migrants				
Redstart <i>Phoenicurus phoenicurus</i>	3	April	May	May
Pied Flycatcher <i>Ficedula hypoleuca</i>	3	April	May	May
Whitethroat <i>Sylvia communis</i>	3	May	May	May
Garden Warbler <i>Sylvia borin</i>	4	May	May	May
Willow Warbler <i>Phylloscopus trochilus</i>	4	April	May	May
Spotted Flycatcher <i>Muscicapa striata</i>	4	May	May	May

Appendix 3 Inter-correlation between the three climate variables included in this study [Spearman rank (r^2) and P -values]. Significant results are in bold.

		NAO		NDVI	
		r^2	P	r^2	P
Temperature	March	0.435	0.006	0.667	>0.001
	April	0.444	0.005	0.400	0.009
	May	0.117	0.196	0.005	0.803
NDVI	March	0.439	0.005		
	April	0.250	0.048		
	May	0.219	0.068		