



# Responses to climate change in avian migration time—microevolution versus phenotypic plasticity

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**ABSTRACT:** While the evidence for advancement of spring phenology of animals and plants in response to recent climate change is overwhelming and undisputed, formal meta-analyses of avian migratory phenologies in response to climate change have not been conducted. Likewise, attempts to evaluate the relative roles of phenotypic plasticity versus evolutionary responses of observed advances in arrival times have been few. We conducted a meta-analysis of published data on timing of avian spring migration, with particular emphasis on evaluating whether the observed patterns are consistent with evolutionary explanations. In addition, we compared the observed rates of advancement with the theoretically expected rates of 'sustainable evolution'. The meta-analysis confirmed a general advancement of avian migration time and that this advancement is correlated with climatic parameters. However, large-scale geographical patterns and relationships with age at first reproduction—a proxy of generation time—were less clear. The average rate of advancement expressed in haldanes ( $h = 0.07$ ) was within theoretically predicted limits of 'sustainable evolution'. All in all, while the results are in clear agreement with the assertion that birds are advancing their migratory schedules, they do not unambiguously support or refute the possibility that the observed responses would be genetic, rather than examples of phenotypic plasticity.

**KEY WORDS:** Climate change · Avian migration · Phenology · Meta-analysis · Evolution · Haldane · NAO

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## 1. INTRODUCTION

Over the past 3 decades or so, climate change has been advancing the phenology of important life-history events in a wide array of taxa from different trophic levels. For instance, plants are now flowering earlier (e.g. Fitter & Fitter 2002, Penuelas et al. 2002), insects appearing earlier in spring (e.g. Woiwod 1997, Roy & Sparks 2000), mammals emerging earlier from hibernation (Inouye et al. 2000) and birds are breeding earlier (e.g. Crick et al. 1997). Apart from these case studies of particular species or taxa, large meta-analyses have verified a clear and general signature of climate change driving advancement of spring phenology (Parmesan & Yohe 2003, Root et al. 2003). In line with

these results, it has also been observed that many species of migratory birds have advanced the timing of their spring migration (reviewed in Lehikoinen et al. 2004, Rubolini et al. 2007, this issue).

Two distinct but not mutually exclusive processes could be responsible for the observed changes: phenotypic plasticity and/or microevolution. Phenotypic plasticity allows individuals to quickly track environmental changes and can even be adaptive in novel environments (Price et al. 2003, Yeh & Price 2004), but it is unlikely that it will enable populations to cope with very rapid and prolonged directional changes, such as those brought on by ongoing climate change. In the long run, only adaptation to the novel conditions will ensure persistence. However, adaptation cannot be

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taken at face value, and it has been suggested that a lack of genetic variation could indeed hamper adaptation to environmental change (Bradshaw & McNeilly 1991, Hoffmann et al. 2003). Distinguishing between genetic adaptation and phenotypic plasticity is important if we want to understand and assess the possible long-term impacts and consequences of climate change (Gienapp et al. 2007).

Phenotypic plasticity refers to the ability of a genotype to produce different phenotypes in response to different environmental conditions. In different environments, the optimal phenotypes (the phenotypes with the highest fitness) differ, and genotypes that are able to adjust their phenotype accordingly will be selected for. Phenotypic plasticity is therefore often highly adaptive in variable environments (e.g. Gomulkiwicz & Kirkpatrick 1992, Scheiner 1993). The degree and extent of phenotypic plasticity in a given trait and population is expected to be adapted to current conditions and, thus, be 'useful' only when conditions remain within the current range of environmental conditions (Pigliucci 1996, DeWitt et al. 1998), which is, however, unlikely in the case of climate change.

For many traits showing phenotypic plasticity, the environment in which the phenotype is determined (i.e. the 'decision' to grow to a certain size or mature) is not necessarily the same than the one where the phenotype is expressed and its fitness determined. This means that at the time when the phenotype is determined, specific environmental factors are needed that can be used to predict the environmental conditions ultimately determining fitness. These environmental factors can then be used as 'cues' to determine the optimal phenotype. For instance, many bird species initiate breeding several weeks before environmental conditions (e.g. food abundance for growing nestlings) crucial for their reproduction, and, thus, fitness are determined. By responding to the 'right' cues available in early spring, they are able to target the optimal time for reproduction later in spring. Similarly, there is also an optimal arrival time for migratory birds (Møller 1994). On the one hand, arriving too early can be costly when environmental conditions are still too harsh or too unpredictable and can deteriorate severely, e.g. during a cold spell (Brown & Brown 2000). On the other hand, individuals arriving late can face stronger competition for mates or territories (Forstmeier 2002) and may also experience reduced reproductive success due to rapid decline in seasonal resources in summer (e.g. van Noordwijk et al. 1995, Visser et al. 2006). Such constraints can be particularly harsh in arctic areas, where summers are very short.

Since the optimal arrival time varies among years, depending on the progression of spring, the optimal phenotype also varies from year-to-year. Accordingly,

avian migration time shows phenotypic plasticity similar to avian breeding time. It has been shown that birds adjust the timing of their migration to climate and arrive earlier in warmer springs and after milder winters (e.g. Forchhammer et al. 2002, Sparks et al. 2005, Stervander et al. 2005). However, long- and short-distance migrants may differ in the degree of phenotypic plasticity expressed in arrival time. Short-distance migrants are likely to show more flexible responses, since climatic conditions at their wintering areas are more closely related to the ultimately important conditions at the breeding areas (e.g. Hoetker 2002). Thus, more reliable cues may be available to them, than to long-distance migrants. For long-distance migrants (e.g. those wintering south of the Sahara), climatic conditions at the wintering areas correlate less closely with climatic conditions at the breeding areas (Stenseth et al. 2003). Long-distance migrants are therefore supposed to rely mainly on internal rhythms and photoperiod to time their departure from the wintering areas (Berthold 1996, Gwinner 1996). However, this would mean that their departure time is more or less constant among years, but by adjusting their migration speed to environmental conditions en route (e.g. Ahola et al. 2004) they may still express some degree of phenotypic plasticity. Yet, no consistent differences in the way long- and short-distance migrants respond to climatic variables, such as the NAO index, have so far been found (e.g. Vähätalo et al. 2004).

If one wants to demonstrate that the advancement in avian migration time is a microevolutionary response to climate change rather than a result of phenotypic plasticity, two things need to be shown. First, directional selection on migration or arrival time caused by altered climatic conditions needs to be demonstrated. Second, heritability of migration time needs to be demonstrated as any evolutionary change requires selection on inherited differences among individuals in the trait under selection. Demonstrating selection on arrival time requires quantifying individual arrival dates at the breeding area using reliable fitness estimates, such as the number of offspring recruited into the population. Although an earlier optimal arrival time can be expected from the general advancement in phenology at all trophic levels, this may not necessarily be the case. Although the general phenological advancement is undisputable (e.g. Butler 2003, Beaumont et al. 2006, Thorup et al. 2007), it is still possible that the environmental factor ultimately determining fitness in relation to arrival date, which is likely to be food abundance during breeding, may not have advanced. Even if formal estimation of selection on arrival time is difficult, it would still be desirable to have some proxy for selective factors (e.g. food availability) with which to compare migration time. Fur-

thermore, even if this proxy has advanced it is possible that the expected selection is counteracted by survival costs of early arrival (see Jonzén et al. 2007 for a theoretical treatment). For instance, ambient temperatures have not warmed up uniformly in all seasons and regions (Easterling et al. 1997, Luterbacher et al. 2004). This could have led to the situation that optimal breeding time has advanced, but conditions during the time of migration and/or arrival have remained stable, thus possibly imposing a fitness cost on earlier migration. So far, no study has directly demonstrated selection on migration time caused by climate change, most likely due to logistic difficulties. Measuring individual arrival dates by field observations is a very tedious task. Reliable fitness estimates require reasonable recruitment rates and, depending on the species, at least 2 yr of study, preferably many more. The same technical difficulties hamper also the study of quantitative genetics of migratory behaviour in the wild, and most evidence for the heritability of migratory behaviour is derived from laboratory experiments, which have demonstrated a genetic component in the timing of autumn migration (see Pulido 2007, this issue, for an overview). Until now, only 3 studies have attempted to estimate the heritability of timing of spring migration using field observations (Rees 1989, Potti 1998, Møller 2001), and only one of them found a significant heritability of arrival dates (Møller 2001). There is additional evidence that other traits related to avian migration, such as migratory activity, migratory direction and size of the fat deposits, are heritable (Pulido & Berthold 2003), and it has been shown that the tendency to migrate at all can respond quickly to selection (e.g. Berthold et al. 1992, Bearhop et al. 2005). It is however not entirely clear how the observed heritability of single migratory behaviours would combine with the heritability of migratory timing, which is likely to be a composite trait influenced by many individual traits.

As mentioned above, the distinction between phenotypic plasticity and microevolution is important for our understanding of the impact of climate change, but solid evidence for either of them in a climate change context is currently scarce (Gienapp et al. 2007). In the present study we took an indirect approach to disentangle the outcomes of these processes. First, we converted the observed advances in timing of migration to rates of change expressed as phenotypic standard deviations per generation (i.e. haldanes). By doing this, we were able to address the question whether the observed rate of advancement in the timing of spring migration is within reasonable limits to be considered an evolutionary response (see Lynch & Lande 1993, Bürger & Lynch 1995). Second, we use a formal meta-analysis to explore how general patterns in the advancement of spring migration are related to age at

first reproduction and to explicitly test whether the observed advancements are related to this characteristic—a proxy for generation time—as would be expected if they are microevolutionary changes. The logic here is that, if the observed responses are evolutionary, they should be more readily observed in species with short, rather than long generation times, because the rate of evolutionary responses scales negatively with generation time. Furthermore, formal meta-analysis has several advantages over narrative reviews and vote counting. It assesses the magnitude rather than the statistical significance of the effect, weighs it by within-study variance and allows testing of the importance of different traits/characteristics contributing to the magnitude of the effects of interest (Gurevitch & Hedges 2001).

## 2. METHODS

### 2.1. Data acquisition

To search for relevant studies we conducted key word searches in the Web of Science (ISI) database using the following search string '(climate change and phenology and migration) and (bird or avian)'. In addition, we scanned the cited literature in every publication found for new un-encountered references. The final dataset consisted of 27 studies on 307 species published between 1995 and 2006 (see Appendix 1 available in CR Supplementary Material at [www.int-res.com/articles/suppl/c035p025\\_app.pdf](http://www.int-res.com/articles/suppl/c035p025_app.pdf)). We included studies reporting associations between temperature, year, or the NAO index and the arrival dates of the birds. We included only local temperature measures from breeding areas or from bird observatories at which passage dates were recorded. The different measures of arrival were classified as first arrival date (FAD), mean spring passage date (MSP), or first spring passage date (FSP). 'Arrival' refers to arrival in the breeding ground, while 'passage' refers to capture at bird observatories. Since there was no difference in the association of migration time and year depending on the measure of arrival date used ( $Q_b = 4.48$ ,  $df = 2$ ,  $p = 0.10$ ), the data using different arrival date measures were pooled per species. Although the association between MSP and temperature ( $r = -0.39$ ) was significantly stronger than that between FAD and temperature ( $r = -0.28$ ,  $Q_b = 7.31$ ,  $df = 1$ ,  $p = 0.006$ ), these data were also pooled, since subsequent comparisons would have been impossible due to small sample sizes.

We used the Pearson product-moment correlation coefficient  $r$  as a measure of effect size in our analysis, since most studies reported the association between timing of migration and temperature, year, or NAO as

correlation coefficients. When data were provided only in graphical format, we used the TechDig 2.0 software to obtain means from figures for calculating the correlation coefficients. If results from a regression analysis were presented, we transformed coefficient of determination ( $r^2$ ) by taking the square root and multiplying with the sign of the regression coefficient. Some of the studies reported several correlation coefficients for 1 species obtained from different ringing stations and/or populations. We avoided non-independent correlations by averaging the calculated effect sizes by species, by type of association (year, temperature, NAO), by continent (Europe, North America, Australia), and by arrival date measure (FAD, FSP, MSP) when appropriate.

Information on migration distance, classified as long or short distance, was either given by the authors or extracted from 'Handbook of the birds of Europe, the Middle East and North Africa' (Cramp 1985) for the European species and from 'The birds of North America Online' (Poole 2007) for the American species. Generation time, defined as the weighted mean age of reproducing females in the population (Charlesworth 1994), which ultimately determines how fast a species or population can respond to selection, was unknown or unavailable for the majority of species. Therefore, we used data on age at first reproduction as a proxy of generation time, since the two were highly correlated for a subset of species for which both measures were available ( $r_s = 0.80$ ,  $n = 83$ ,  $p < 0.0001$ ). Data on age at first reproduction for each species were obtained from the sources listed. All primary data used in the analyses are given in Appendix 1.

## 2.2. Meta-analyses

The final dataset for the meta-analysis consisted of data from 18 studies on 249 species published between 1995 and 2006 (see Appendix 1). The meta-analysis was carried out using the Meta Win 2.0 statistical program (Rosenberg et al. 2000). Effect sizes were calculated by  $z$ -transforming correlation coefficients and weighting them by the sample size. These effect sizes were combined across studies using the mixed effects model, which assumes that differences among studies within a class are due to both sampling error and random variation. In ecological data synthesis, the assumptions of mixed models are more likely to be met than those of fixed effects models, and the former are thus preferred (Gurevitch & Hedges 2001). We used bias-corrected 95% bootstrap confidence intervals (Adams et al. 1997) of the mean effect sizes to define the significance of the effect. The bias-corrected 95% bootstrap confidence intervals were generated from 4999 iterations. A relationship was considered signifi-

cant if the confidence interval did not include zero. A negative effect size indicates earlier arrival in warmer years or years with greater NAO value, or advancing arrival over time, i.e. negative correlation with year. To test the importance of different sources of variation in determining the sign and magnitude of the correlation between migration rates and year, temperature, or NAO, we subdivided studies in terms of various study characteristics and examined among-group heterogeneity using a chi-square test statistic,  $Q_b$ . The following sources of variation were examined: continent (America, Europe and Australia), migration distance (short, long), age at first reproduction, and measure of arrival date. We also conducted a continuous mixed-model meta-analysis to examine if the strength of the effect is associated with the time when the data were collected. Since we were dealing with time-series data, we used the mid-point of the years included in each study as time point in this analysis.

The funnel plot technique (Light & Pillemer 1984, Palmer 1999) did not reveal any significant evidence for publication bias. Moreover, effect size was not correlated with sample size ( $r = 0.006$ ,  $p = 0.88$ ), further supporting the lack of publication bias.

In a formal meta-analysis, the appropriate metric of effect size for the correlative data is Fisher's  $z$ -transformation, which is calculated from correlation coefficients and their sample sizes (Rosenberg et al. 2000). The calculated effect sizes are thus only directly indicative of the strength of the correlation between variables and about the slope of the corresponding linear regression. We aimed at comparing rates of advancement in migration time, for which the effect sizes are not meaningful. However, in the studies from our dataset that reported correlation coefficient and regression slope, both were significantly correlated ( $r = 0.81$ ,  $t = 27.2$ ,  $df = 395$ ,  $p < 0.0001$ ). This means that a stronger effect size also implies a steeper slope of the relationship.

## 2.3. Phenotypic rates of change

From the studies reporting statistically significant time trends in passage dates, we extracted these trends and transformed them to haldanes (see below for details). We restricted the analysis to studies roughly covering a period from the 1970s or 1980s onwards, as the signal of climate change has only been clearly visible since then (Folland & Karl 2001). Until the 1970s, temperatures were actually decreasing in parts of Europe (see McCleery & Perrins 1998). The average annual standard deviation (SD) in passage date was calculated from given data or kindly provided by the authors of the original articles. Years with <10 observations were

excluded. Obviously, this excluded all studies in which only first arrival (or passage) date was observed, since the standard deviation of them is not defined. This dataset (29 data points from 19 species from 3 studies) is hence much more restricted than the dataset on which the meta-analysis is based. The data were not pooled by species, since every population could potentially respond differently and, thus, constitutes an independent observation in the analyses.

The haldane ( $h$ ) is defined as the rate of (phenotypic) change per generation on a given trait expressed in phenotypic standard deviation units as:

$$h = \frac{\frac{x_2}{s_p} - \frac{x_1}{s_p}}{g} \quad (1)$$

where  $h$  is the observed change in haldanes,  $x_1$  and  $x_2$  are the trait mean values at 2 points in time,  $s_p$  is the pooled standard deviation from the 2 points in time and  $g$  is the number of generations (Hendry & Kinnison 1999). We calculated the phenotypic change, i.e. the difference between  $x_2$  and  $x_1$  (i.e. advancement in migration time) from the regression coefficient and the length of the study period. The resulting change in days was divided by the average annual standard deviation and generation time in years.

### 3. RESULTS

#### 3.1. Meta-analyses

In general, arrival date was found to be significantly associated with year, temperature and NAO, as indicated by the significant negative effect sizes (Fig. 1). These results indicate that birds arrive in general earlier than they used to and that they arrive earlier in warmer years and years with a greater NAO index value. However, the strength of these effects varied such that the effect size was significantly stronger for temperature than for year ( $Q_b = 36.15$ ,  $df = 2$ ,  $p = 0.0002$ ).

The strength of the negative association between year and arrival date did not differ among the 3 continents ( $Q_b = 3.44$ ,  $df = 2$ ,  $p = 0.19$ ; Table 1). However, the association between temperature and arrival date was significantly stronger for European species or populations as compared to the North American species or populations ( $Q_b = 4.14$ ,  $df = 1$ ,  $p = 0.04$ ), although both were found to arrive significantly earlier in warmer years (Table 1). Australian

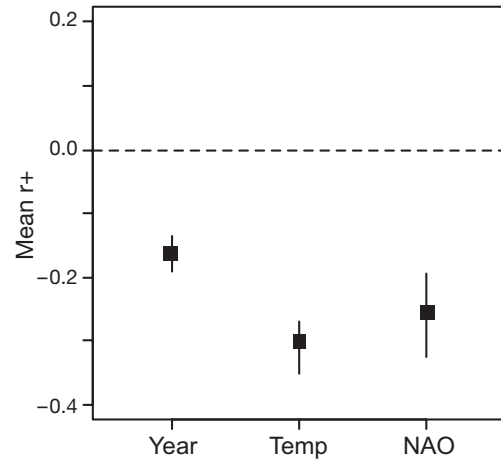


Fig. 1. Mean correlations ( $r+$ ) between arrival date and year, temperature (only North American and European species), or NAO (only European species). Whiskers indicate bias-corrected 95% confidence intervals

species had to be excluded, since no data on the relationship between arrival date and temperature were available.

For European species, the association between arrival date and year did not differ with respect to migration distance (short or long  $Q_b = 0.78$ ,  $df = 1$ ,  $p = 0.37$ ; Fig. 2). In contrast, for North American species, a significantly stronger negative association between year and arrival date was found for short-distance migrants compared to long-distance migrants ( $Q_b = 6.86$ ,  $df = 1$ ,  $p = 0.01$ ; Fig. 2), which means that arrival dates of short-distance migrants advanced more strongly. It was, however, not possible to formally test the interaction between continent and migration distance with the meta-analysis methodology used. The

Table 1. Effects of continent (on which the species or populations breed), migration distance and age at first reproduction (AFR) on the strength of the mean correlation ( $r+$ ) between the arrival and year, temperature (only North American and European species), or NAO (European species only). N: no. of species

Type of association	Category	N	$r+$	Bias-corrected bootstrap 95% CI
<b>Continent</b>				
Year	North America	170	-0.1597	-0.1940 to -0.1299
	Europe	49	-0.1359	-0.2115 to -0.0563
	Australia	16	-0.2769	-0.4311 to -0.1275
Temperature	North America	129	-0.2827	-0.3375 to -0.2457
	Europe	29	-0.3799	-0.4894 to -0.3088
<b>Migration distance</b>				
NAO	Short distance	21	-0.2057	-0.2887 to -0.1183
	Long distance	19	-0.2922	-0.3955 to -0.2008
<b>Age at first reproduction</b>				
Temperature	AFR 1	105	-0.3326	-0.3968 to -0.2983
	AFR 2	20	-0.1632	-0.2753 to -0.0644

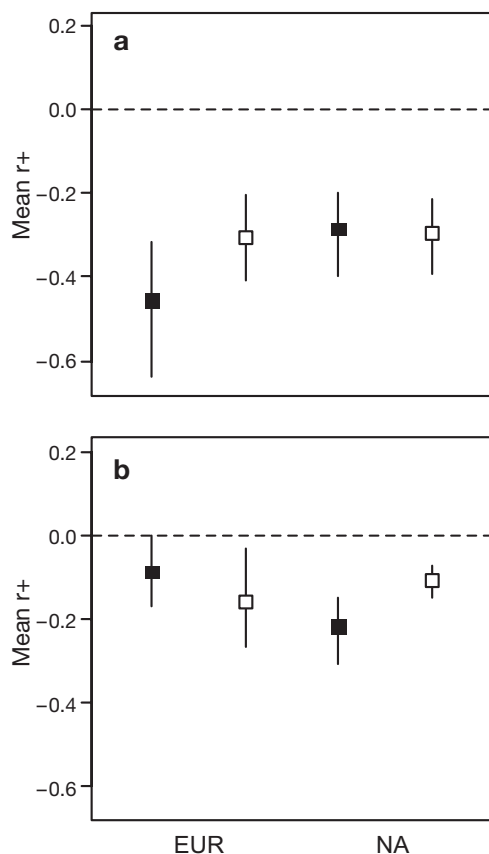


Fig. 2. Mean correlations ( $r+$ ) between arrival date and (a) temperature or (b) year for European (EUR) and North American (NA) short-distance (■) and long-distance (□) migrants. Whiskers indicate bias-corrected 95% confidence intervals

negative association between temperature and arrival date was found to be stronger for European short-distance migrants compared to long-distance migrants ( $Q_b = 3.58$ ,  $df = 1$ ,  $p = 0.07$ ; Fig. 2), whereas no significant differences were found for North American species ( $Q_b = 0.02$ ,  $df = 1$ ,  $p = 0.89$ ; Fig. 2). Again, formal testing of the interaction was not possible. No significant differences were found in the strength of the association of NAO with arrival date between European short- and long-distance migrants ( $Q_b = 1.79$ ,  $df = 1$ ,  $p = 0.19$ ; Table 1).

The age at first reproduction (AFR) for most species in our dataset was either 1 or 2 yr, and, thus, only a comparison between these 2 cases could be reliably done. We found no significant differences in the strength of the association between year and arrival date, depending on the AFR ( $Q_b = 0.16$ ,  $df = 1$ ,  $p = 0.68$ ). For North American species, which showed a greater variation in AFR, we ran a continuous model including all data, but found no evidence for a stronger association in species with earlier reproduction (slope  $[\pm SE]$  of  $r$  vs. AFR =  $0.04 \pm 0.03$ ,  $Q_b = 1.74$ ,  $df = 1$ ,  $p = 0.19$ ). The

negative association between temperature and arrival date was significantly stronger for species that reproduced during their first year compared to those that reproduced during their second year ( $Q_b = 8.65$ ,  $df = 1$ ,  $p = 0.004$ ; Table 1). In the continuous model for the North American species this pattern, however, disappeared (slope of  $r$  vs. AFR =  $0.006 \pm 0.023$ ,  $Q_b = 0.06$ ,  $df = 1$ ,  $p = 0.81$ ).

The strength of the association between year and arrival date of both the European and North American species was not influenced by the time of observations (mean point of observation year: North America:  $Q_b = 0.15$ ,  $df = 1$ ,  $p = 0.70$ ; Europe:  $Q_b = 0.53$ ,  $df = 1$ ,  $p = 0.46$ ). The strength of the association between temperature and arrival date was, in turn, significantly related to the time when the observations were done irrespective of the continent (North America:  $Q_b = 17.73$ ,  $df = 1$ ,  $p < 0.001$ ; Europe:  $Q_b = 4.70$ ,  $df = 1$ ,  $p = 0.03$ ). The later the data were collected (or the closer to present day), the stronger was the response to temperature.

### 3.2. Phenotypic rates of change

The average rate of advancement in arrival times was  $0.23 \text{ d yr}^{-1}$ , which corresponds to an advancement of about 7 d and 0.07 h over the respective study periods (Table 2). Average annual standard deviations for arrival dates were rather large, ranging from 5.4 d in garden warblers *Sylvia borin* at Ottenby (Sweden) to 18.1 d in song thrushes *Turdus philomelos* on Helgoland (Germany).

## 4. DISCUSSION

Our results provide strong support for earlier assertions (e.g. Lehikoinen et al. 2004, Jonzén et al. 2006, Thorup et al. 2007) that avian spring migration has been advancing overall and that there are robust relationships between migration time and large-scale (NAO) and small-scale climatic variables (local temperatures). This has been described several times previously in separate studies (e.g. Forchhammer et al. 2002, Hüppop & Hüppop 2003, Vähätalo et al. 2004, Stervander et al. 2005), but combining all of the data and using a formal meta-analysis framework provide even more certainty that climate change is affecting spring migration in birds.

The fact that migration time was more closely related to local temperature and NAO than year should not be too surprising. Any variable determining migration timing will explain more variation than a linear time trend unless this variable shows a perfect linear time trend. Furthermore, researchers are likely to look for

Table 2. Phenotypic rates of change in avian migration time. Shown are the rates of change expressed in haldanes ( $h$ , SD units generation<sup>-1</sup>), slope of the regression of average passage date against year (d yr<sup>-1</sup>; note that all trends reported here are statistically significant,  $p < 0.05$ ) and advancement (d) over the study period. 1: Jonzén et al. (2006); 2: Spottiswoode et al. (2006); 3: Hüppop & Hüppop (2003); 4: Tøttrup et al. (2006)

Ringling station and species	Slope (d yr <sup>-1</sup> )	No. of study years	Advance-ment (d)	$h$	Source
<b>Falsterbo (Sweden)</b>					
Eurasian reed warbler <i>Acrocephalus scirpaceus</i>	-0.31	21	-7.5	-0.099	1
Chiffchaff <i>Phylloscopus collybita</i>	-0.45	25	-10.9	-0.098	1
Garden warbler <i>Sylvia borin</i>	-0.29	25	-6.9	-0.091	1
<b>Jomfruland (Norway)</b>					
Tree pipit <i>Anthus trivialis</i>	-0.39	20	-9.4	-0.156	1
Chiffchaff <i>P. collybita</i>	-0.51	24	-11.6	-0.161	1
Barn swallow <i>Hirundo rustica</i>	-0.21	20	-5.0	-0.059	1
Red-backed shrike <i>Lanius collurio</i>	-0.33	20	-8.0	-0.126	1
Willow warbler <i>Phylloscopus trochilus</i>	-0.32	25	-7.7	-0.076	1
Blackcap <i>Sylvia atricapilla</i>	-0.37	24	-9.0	-0.069	1
<b>Ottenby (Sweden)</b>					
Chiffchaff <i>P. collybita</i>	-0.39	25	-9.4	-0.083	1
Icterine warbler <i>Hippolais icterina</i>	-0.21	25	-5.0	-0.065	1
Garden warbler <i>S. borin</i>	-0.28	25	-6.7	-0.104	1
<b>Helgoland (Germany)</b>					
Willow warbler <i>P. trochilus</i>	-0.31	22	-6.6	-0.074	2
Eurasian reed warbler <i>A. scirpaceus</i>	-0.20	41	-8.1	-0.046	3
European robin <i>Erithacus rubecula</i>	-0.17	41	-6.7	-0.025	3
Pied flycatcher <i>Ficedula hypoleuca</i>	-0.16	41	-6.2	-0.034	3
Icterine warbler <i>H. icterina</i>	-0.05	39	-1.8	-0.011	3
Spotted flycatcher <i>Muscicapa striata</i>	-0.26	41	-10.4	-0.074	3
Common redstart <i>Phoenicurus phoenicurus</i>	-0.17	41	-6.9	-0.036	3
Willow warbler <i>P. trochilus</i>	-0.23	41	-9.2	-0.051	3
Blackcap <i>S. atricapilla</i>	-0.25	41	-10.0	-0.034	3
Garden warbler <i>S. borin</i>	-0.18	41	-7.2	-0.049	3
Common whitethroat <i>Sylvia communis</i>	-0.17	41	-6.7	-0.034	3
Lesser whitethroat <i>Sylvia curruca</i>	-0.20	38	-8.1	-0.038	3
Winter wren <i>Troglodytes troglodytes</i>	-0.22	39	-8.4	-0.029	3
Redwing <i>Turdus iliacus</i>	-0.17	41	-6.6	-0.028	3
Common blackbird <i>Turdus merula</i>	-0.28	34	-11.3	-0.051	3
Song thrush <i>Turdus philomelos</i>	-0.16	41	-6.4	-0.027	3
<b>Christiansø (Denmark)</b>					
Common blackbird <i>T. merula</i>	-0.59	22	-12.4	-0.102	4
Average	-0.24		-7.2	-0.066	

the temperature variable that explains most variation in their data, which could explain the closest association with local temperature (Fig. 1).

If the timing of spring migration is a heritable trait—not an unreasonable assumption given what we know about the genetics of autumn migration (Pulido et al. 2001, Pulido & Widmer 2005) and most other phenological and life-history traits (e.g. van der Jeugd & McCleery 2002, Réale et al. 2003, Sheldon et al. 2003, Charmantier et al. 2006)—then selection for advanced arrival time caused by climate change would lead to evolutionary responses. Furthermore, species with shorter generation times should show faster responses than species with longer generation times, simply because of time lags experienced by the long-lived species with overlapping generations. We did not, however, find any evidence for the expected trend that the

migration of species with an earlier AFR would have advanced more strongly. This supports the contention that the observed advancements are not evolutionary responses, but rather, plastic responses. If so, we would expect to find differences between long- and short-distance migrants in their response to (local) climatic variables, since the migration schedules of long-distance migrants are thought to be determined mainly by endogenous factors linked to photoperiod (Berthold 1996, Gwinner 1996). In accordance with this, we found that European short-distance migrants responded more strongly to (local) temperatures than did long-distance migrants, while no difference in the response to NAO was observed (see Rainio et al. 2006). The NAO is a large-scale climatic phenomenon, and, consequently, the association of any ecological parameter with the NAO is expected to be comparably weak (but see

Hallett et al. 2004, Stenseth & Mysterud 2005); thus any differences between long- and short-distance migrants may have been obscured.

Since temperatures have generally increased over the last 2 decades and migration time in short-distance migrants is more closely related to local temperatures than it is in long-distance migrants, one may expect that short-distance migrants have advanced their migration time at a faster rate. In contrast with some studies (e.g. Tryjanowski et al. 2002, Tøttrup et al. 2006, Rubolini et al. 2007), but in accordance with others (e.g. Hüppop & Hüppop 2003), our meta-analysis did not find a difference in the advancement of long- and short-distance migrants for European species, while there was a difference among the North American species. The migration speed of pied flycatchers *Ficedula hypoleuca* in Europe is related to weather conditions during migration: the birds are able to migrate faster in warmer springs (Ahola et al. 2004, Hüppop & Winkel 2006). Climatic conditions at the wintering grounds also influence the timing of migration and arrival in Italy (Saino et al. 2004, 2007, this issue). The migration schedule of long-distance migrants may, thus, not be as tightly determined by endogenous factors and photoperiod as previously thought. Long-distance migrants may also have some opportunity to adjust their arrival at the breeding grounds to environmental conditions. In contrast to this, Jonzén et al. (2006) found that the migration time of long-distance migrants also advanced in southern Europe (Italy). Thus, the birds would have to depart earlier from their trans-Saharan breeding grounds or migrate faster through Africa. However, Jonzén et al. (2006) failed to identify climatic variables that could explain a faster migration through Africa, and concluded that the observed advancement in migration time is the result of a genetic change in their departure time controlled by endogenous factors and photoperiod (but see Both 2007).

In the meta-analysis presented above, we used differences in the advancement of migration time that would be correlated with AFR, to test whether the observed changes in avian migration are due to phenotypic plasticity or 'rapid evolution'. In our second, indirect approach, we compared the observed rates of phenotypic changes in arrival times with rates reasonable in light of theoretical models (e.g. Lynch & Lande 1993, Lynch 1996). Any selection imposes a demographic load, i.e. reduction in average reproduction or survival, on a population, since not all individuals can reproduce or survive optimally. If the environmental change becomes sufficiently strong and persistent, the resulting selection can lead to a substantial reduction in population mean fitness, which, in turn, increases the probability of extinction. There is thus a 'critical rate of environmental change' beyond which extinction becomes

more likely or even certain (Lynch & Lande 1993). Making a few simplifying assumptions (e.g. constant genetic variance [see Bürger & Gimelfarb 1999, Zhang & Hill 2005] and a spatially homogenous environment), theoretical models predict a critical rate of about 0.1 phenotypic standard deviations per generation for medium-sized (i.e.  $N_e \approx 500$ ) sexual populations. Including demography and stochastic environmental processes in similar models (Bürger & Lynch 1995, Gomulkiewicz & Holt 1995) yields similar values. The maximum rate of sustainable evolution is hence unlikely to be larger than a few percent of  $1 h$  (i.e. change expressed in phenotypic standard deviations per generation), even in large populations. In Table 2 we have compiled several phenotypic trends of migration time and transformed the phenotypic rates to haldanes using the species-specific phenotypic standard deviations and generation times. The spring migration time advanced, on average, by 0.07 standard deviations per generation. This is on the same order of magnitude as the suggested rate of 'sustainable evolution'. A similar analysis for avian breeding time yielded a much larger value (0.19; Gienapp et al. 2007), which would be inconsistent with a 'sustainable evolution' scenario. While the observed phenotypic rates in avian breeding time are thus likely phenotypically plastic responses to warming spring temperatures, the observed rates for the timing of migration could be evolutionary responses to selection induced by climate change.

Unfortunately, the results of our 2 approaches to disentangle phenotypic plasticity and a microevolutionary response are inconsistent. While we found no effect of AFR on the rate of advancement, the observed rates are consistent with a sustained response to selection. However, there are possible caveats with such *en gros* approaches. It is unclear how the observed phenotypic standard deviation of migration time compares with the phenotypic standard deviation of other traits, and, thus, how comparable obtained haldane estimates are. Variation in migration time may have a (very) large environmental component, since it is the sum of several traits and is likely to be influenced by many factors at the wintering grounds and en route (e.g. Ahola et al. 2004, Saino et al. 2004, Both et al. 2005). All data in Table 2 come from ringing stations, since annual standard deviations are only available for such data. It is possible—and even likely—that several populations pass through any given ringing station, which would inflate the inferred variation in arrival time if the populations differ in the timing of their migration. Furthermore, it is unknown how the variation in passage time (at a ringing station) is related to variation in arrival date (at the breeding area), which is the variable ultimately related to reproductive success, a major component of fitness. An additional problem



with passage dates obtained from ringing stations may be the quality of the data. The standard deviation is somewhat sensitive to outliers. Fitting a parametric seasonal distribution curve (Knudsen et al. 2007, this issue) and using the standard deviation from these curves may lead to different results. Accurate data on generation time require good estimates of adult survival rates, which are not easily obtainable for many species. We therefore had to use AFR, which is more easily determined, as a proxy. Although the two are highly correlated, the variation in AFR is necessarily lower, since generation time is also affected by adult survival rates (Charlesworth 1994). Furthermore, low variation in generation time in migratory birds, because the majority are small passerines with similar life histories, may influence this comparison.

Hence, to sum up, at this point we are not in a position to judge whether climate-related changes in spring migration are reflections of phenotypic plasticity or evolutionary responses to selection. Given the evidence from the case studies of avian breeding time, in which heritability and selection intensities were known and sizeable (Sheldon et al. 2003, Gienapp et al. 2006), but no evolutionary response was observable, the scales may just tip in favour of phenotypic plasticity.

## 5. CONCLUSIONS

There is now very good evidence that spring migration of most bird species on a worldwide scale is advancing and affected by both small- (local temperature) and large-scale (NAO) climatic variables. Although some patterns between continents and long- and short-distance migrants are not clear, and may call for further analyses, we think that the focus should shift away from correlative analyses of large-scale patterns in many species. As pointed out above, distinguishing whether an observed change is a phenotypically plastic response to a warmer climate or a genetic change as a response to selection—or possibly both at the same time—is important for our ability to predict potential impacts of climate change. We therefore need detailed field studies of the fitness consequences of the timing of migration, preferably also addressing the causal link between the two, e.g. climatic factors imposing a fitness cost on early arrival and food availability, and thus affecting reproductive success. In addition, studies on individual phenotypic plasticity and quantitative genetics of migration timing would be necessary. This would require tracking the migration and arrival time of single individuals and their offspring over >1 season—a gargantuan undertaking. However, as we have demonstrated here, other approaches are unlikely to succeed in answering the questions posed.

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