Int J Biometeorol (2017) 61:1279–1289
DOI 10.1007/s00484-017-1305-5

ORIGINAL PAPER

Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries

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Received: 2 May 2016 / Revised: 15 December 2016 / Accepted: 3 January 2017 / Published online: 31 January 2017

Abstract Long-term phenological data have been crucial at documenting the effects of climate change in organisms. However, in most animal taxa, time series length seldom exceeds 35 years. Therefore, we have limited evidence on animal responses to climate prior to the recent warm period. To fill in this gap, we present time series of mean first arrival dates to Central Europe for 13 bird species spanning 183 years (1828–2010). We found a uniform trend of arrival dates advancing in the most recent decades (since the late 1970s). Interestingly, birds were arriving earlier during the cooler early part of the nineteenth century than in the recent warm period. Temperature sensitivity was slightly stronger in the warmest 30-year period (−1.70 ± SD 0.47 day $°C^{-1}$) than in the coldest period (−1.42 ± SD 0.89 day $°C^{-1}$); however, the difference was not statistically significant. In the most recent decades, the temperature sensitivity of both short- and long-distance migrants significantly increased. Our results demonstrate how centennial time series can provide a much more comprehensive perspective on avian responses to climate change.

Keywords First arrival date · Migratory birds · Phenology · Temperature · Temperature sensitivity

Introduction

Given the rapidity of current climatic changes, long-term observational time series are highly valuable. They can document phenological responses to contrasting climate conditions and provide a broad perspective on the current rapid changes of climate. However, studies with more than a few decades of uninterrupted data are rare, especially for animals. The mean length of published phenological time series is only around 35 years (Bitterlin and van Buskirk 2014; Parmesan and Yohe 2003; Root et al. 2003; Rubolini et al. 2007, but see e.g. Ahas 1999; Askeyev et al. 2009; Lehikoinen et al. 2004; Sparks and Carey 1995) which might bias the detected trends (Hovestadt and Nowicki 2008). Furthermore, several studies already demonstrated spatially variable responses of organisms to temperature (spatial component; Gordo et al. 2007; Parmesan 2007; Saino and Ambrosini 2008). But there is no a priori reason to assume that temperature sensitivity of the species is constant and that the strength of the relationship remains unchanged through time (temporal component). This was proved to be true for plants (Fu et al. 2015; Quansheng et al. 2014; Rutishauser et al. 2008; Rutishauser et al. 2009; Schleip et al. 2008; Wang et al. 2015) and insects (Kharouba et al. 2014). But despite some studies which studied the temperature sensitivity (Askeyev et al. 2009; Gordo

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Electronic supplementary material The online version of this article (doi:10.1007/s00484-017-1305-5) contains supplementary material, which is available to authorized users.

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and Doi 2012; Gordo et al. 2013), a comprehensive long-term study which would investigate the course of temperature sensitivity in vertebrates is still lacking. Yet, an assessment of temporal variability in temperature sensitivity is critical for forecasting their responses to climate change.

The issue of variable temperature sensitivity is especially pressing in organisms at higher trophic levels in which species-specific cues trigger the onset of phenophases (Stenseth and Mysterud 2002; van Ash et al. 2007; Visser and Holleman 2001). In spite of that, temperature is generally accepted to be the main factor driving shifts in phenology (including for example chilling effect and growing degree days), but other mechanisms such as photoperiod, humidity and nutrients were also identified to play a role in triggering of phenophases (Chambers et al. 2013; Ellwood et al. 2012; Heide and Prestrud 2005; Jochner et al. 2013; Körner and Basler 2010; Laube et al. 2014; Tooke and Battey 2010; Zhang et al. 2007). In addition, as the temperature signal pervades from primary producers to top consumers, the number of trophic interactions increases. This results in weaker temperature signals and makes the temporal match of the phenophases less likely (Both et al. 2009; Ellwood et al. 2012; Gordo and Sanz 2005; Naef-Daenzer et al. 2012; Nakazawa and Doi 2012; Schwartzberg et al. 2014). Despite numerous studies about the phenological shifts due to changing climate, it is unclear which mechanisms vertebrates employ to respond to temperature change across a long time period.

Migratory birds represent an ideal system to enlighten this issue. Commonly, they fit into one of two migratory strategies which differ in response to temperature. Short-distance migrants are usually more influenced by temperature due to a strong spatial autocorrelation of climate between the breeding and wintering sites. On the other hand, the onset of long-distance migrants' migration is believed to be under endogenous control (Berthold 1996; Halkka et al. 2011; Lehikoinen et al. 2004; Marra et al. 2005; Mitrus et al. 2005; Sparks et al. 2007; Zalakevicius et al. 2006). Therefore, it is assumed that long-distance migrants are not able to perceive climatic conditions in the distant breeding sites as accurately as short-distance migrants. As a consequence, they are not able to adequately track the speed of the advanced spring phenology (Both and Visser 2001; Both et al. 2010; Møller et al. 2008; Sanz et al. 2003). In contrast to this, only two studies have shown that especially in the last decades the long-distance migrants have advanced their arrivals more than short-distance migrants, which might imply a strong evolutionary pressure on them (Jonzén et al. 2006; Stervander et al. 2005). However, other authors hypothesised that such as rapid advancement could be attributed to improved conditions en route and due to mixture of birds which come from different populations with different timing of migration (Both 2007). In addition, because birds represent top consumers, they are under strong selection to optimise the timing of their arrival to breeding grounds and the onset of nesting with the phenophases of insects (Jonzén et al. 2007). Several multi-trophic-level studies showed that the response of birds to temperature is less strong than their prey and that this can lead to temporal phenological mismatch across the food chain (Both et al. 2009; Thackeray et al. 2010).

To address these issues, we present one of the longest time series of bird arrivals ever analysed dating back to the beginning of the nineteenth century and spanning 183 years. First, we reconstruct the historical avian first arrivals and assess their temporal shifts. Next, we investigate the strength of the relationship between arrival and temperature and how it has been changing throughout such an extensive time period. Finally, we examine the hypothesis that short- and long-distance migrants show different patterns in the strength of the response to the changing temperature (Knudsen et al. 2011).

Materials and methods

Phenological data

We compiled first arrival dates (FAD) of birds in the Czech Republic for the period 1828–2010. Data on FAD from the Czech Hydrometeorological Institute, which covered most of the database, were supplemented by data from various societies, networks and grey literature. For a detailed overview of the data sources and their time spans, see Table S1 and Fig. S1. Archival records were converted into digital format as day of the year (where January 1 = day 1), and all nomenclature was updated (see Kolářová and Adamík 2015). Due to the discrepancy between the calendar and astronomical year, we expressed arrival dates in each year as deviations from the vernal equinox (Sagarin 2001). When more than one record of the same species from the same locality was available in a given year, the earliest record was retained in the database.

We visualised the data distribution and detected outliers (mostly mistyped values in old printed records) by inspection of Cleveland dotplots and boxplots; Zuur et al. 2009), and they were subsequently excluded from the analyses. We restricted this study to species for which we had $n \geq 900$ records spanning the period 1828–2010. Barn swallow *Hirundo rustica* arrivals spanned a shorter time period (1853–2010), but its observations were very numerous and had a balanced distribution through time. Three other species (chiffchaff *Phylloscopus collybita*, serin *Serinus serinus*, blackcap *Sylvia atricapilla*) had ≥900 records, but their data distribution was markedly imbalanced through time which would have hampered data analysis and therefore were omitted from analyses. We ended up with 13 species with 80,489 observations of FAD from 3480 sites across the Czech Republic (Fig. 1).

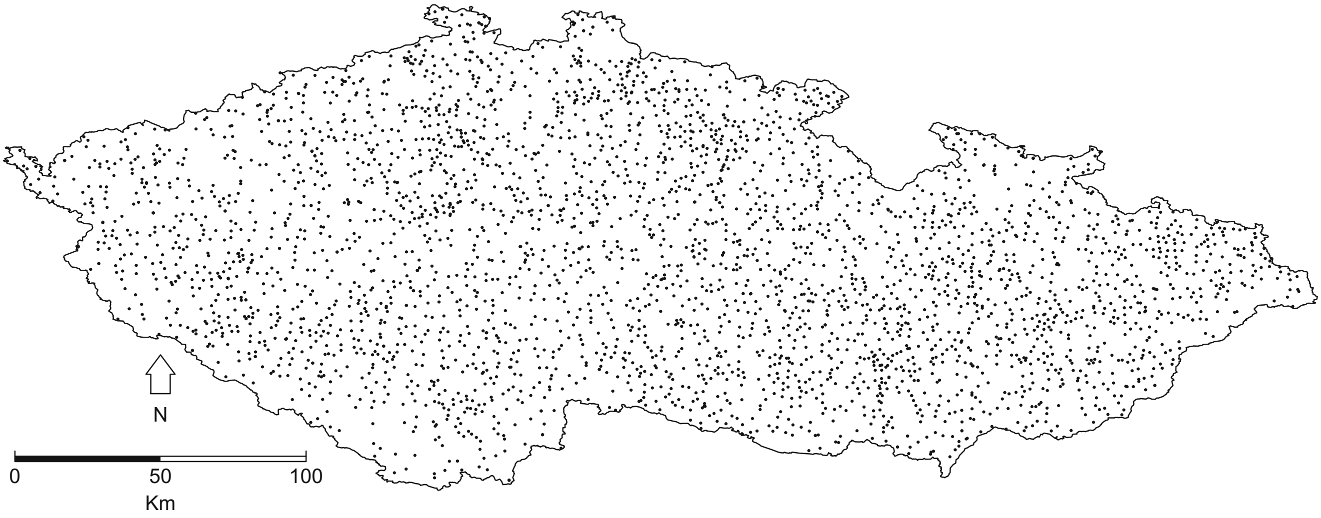


Fig. 1 Map of the Czech Republic with the sites (n = 3480) where first arrival dates were recorded

Out of the 13 species, 7 were short-distance migrants (winter grounds in Europe or Northern Africa) and 6 were long-distance migrants which winter in sub-Saharan Africa (see Table 1).

Reconstruction of arrival dates

For each of the 13 species, we reconstructed annual mean FAD time series within a mixed-effects modelling framework with year as fixed effect and site as random effect (Häkkinen et al. 1995; Schaber et al. 2010; Table S2). Multi-site combined arrival time series were estimated in R-package "pheno" for each species. This package provides functions which enable to deal with estimations of combined phenological time series (Schaber 2012). We used linear mixed effects model (LMM, R-package "lme4") to compare timing of arrivals during the first and last 30-year period with year and species as random effects. Barn swallow arrivals were not included in this model as records of its arrival start later.

Temporal trends in reconstructed arrivals were assessed by generalised additive models (GAM) for the period 1828–2010 and by weighted linear regressions for the period 1978–2010. As weights for linear regression, we used the square root of the number of observations per year and species (Table S3). Similarly, weighted linear regression was used to assess temperature sensitivity. Mean FADs were associated to Czech

Table 1 Weighted linear regression estimates of the relationship between mean first arrival date (FAD) and mean monthly temperature during 1828–2010

Species name	Common name	ms	Arrival	Month	Number	TS (d °C^{-1})	SE	t	R^2	P
Alauda arvensis	Skylark	S	Mar 1	Feb	156	−1.424	0.161	−8.87	0.34	**<0.001**
Sturnus vulgaris	Starling	S	Mar 6	Feb	155	−1.145	0.135	−8.49	0.32	**<0.001**
Vanellus vanellus	Lapwing	S	Mar 13	Mar	131	−2.008	0.265	−7.58	0.31	**<0.001**
Motacilla alba	White wagtail	S	Mar 14	Mar	166	−1.162	0.197	−5.89	0.17	**<0.001**
Columba palumbus	Woodpigeon	S	Mar 19	Mar	127	−1.411	0.329	−4.28	0.13	**<0.001**
Turdus philomelos	Song thrush	S	Mar 23	Mar	151	−0.856	0.389	−2.20	0.03	**0.029**
Phoenicurus ochruros	Black redstart	S	Mar 28	Mar	143	−1.503	0.190	−7.93	0.31	**<0.001**
Phoenicurus phoenicurus	Common redstart	L	Apr 11	Apr	153	0.871	0.390	2.23	0.03	**0.027**
Hirundo rustica	Barn swallow	L	Apr 16	Apr	140	−1.066	0.192	−5.55	0.18	**<0.001**
Delichon urbicum	House martin	L	Apr 22	Apr	155	−0.713	0.224	−3.19	0.06	**0.002**
Cuculus canorus	Cuckoo	L	Apr 26	Apr	167	−0.833	0.172	−4.86	0.13	**<0.001**
Apus apus	Swift	L	May 3	Apr	149	−0.801	0.206	−3.88	0.09	**<0.001**
Coturnix coturnix	Quail	L	May 15	Apr	148	−1.384	0.377	−3.67	0.08	**<0.001**

Species are listed in ascending order according to their mean FAD

ms migratory strategy (*S* short-distance migrant, *L* long-distance migrant), *Month* focal month used for temperature-arrival relationship, *Number* number of years with available data, *TS* temperature sensitivity, regression estimates of mean FAD against mean monthly temperature, *SE* standard error of the TS estimate, significant P values (≤0.05) are in bold mean monthly temperature series spanning 1828–2010 (Fig. S2) reconstructed from station-based meteorological observations (Brázdil et al. 2012) and weighted by the square root of the number of observations per year (Table 1). The focal month for temperature was selected individually for each species based on the temporal overlap with its arrival. To describe the temporal changes in temperature-arrival relationship, we estimated linear regressions as 30-year moving windows with the shift by 1 year starting in 1828 (for barn swallow in 1853). Again, all regressions were weighted by the square root of the number of observations per year. We chose a period of 30 years since this was the most commonly reported length of published time series with FAD (see "Introduction" section).

Next, we assessed whether the species' temperature-arrival relationship differed during cold and warm periods. For that, we detected the warmest and the coldest periods by averaging the mean monthly temperature of the focal month for arbitrarily set 30-year time intervals (the last one having 33 years) 1828–1857, 1858–1887, 1888–1917, 1918–1947, 1948–1977 and 1978–2010. The 1978–2010 period was the warmest for all the months, while the coldest periods were 1828–1857 for February and March and 1888–1917 for April. Species-specific differences in slopes of the temperature-arrival relationship between the warmest and coldest periods were assessed according to Zar (1999; slope test).

For an assessment of temporal changes in the mean temperature sensitivity between short- and long-distance migrants, we averaged the species-specific estimates of temperature sensitivity weighted by the square root of the number of observations per year for 30-year moving windows at the beginning (1857–1886), in the middle (1919–1948) and at the end (1981–2010) of the 1828–2010 time series. Differences in mean responses (average temperature sensitivity estimates) were assessed by GLM where we used a model that included interaction between the three time periods and migratory strategy.

Results

Bird arrival dates 1828–2010

The temporal trends for majority of the species showed strong non-linearity in arrivals during the period 1828–2010 (Fig. S3). Usually, the arrivals were most pronounced at the beginning of the nineteenth century. Between beginning and ca. second half of the nineteenth century, the arrivals were delaying and then again advancing which lasted until the first half of the twentieth century. From then, the arrivals were constantly delaying until the 1970s. Afterwards, there is a clear pattern in rapid advancement which lasts up to now (Figs. 2 and S3).

During the most recent period, 1978–2010, all species advanced their arrivals (mean advancement was −0.35 day year^{-1}, SD = 0.27; Table S3). The mean shift for short-distance migrants was −0.35 day year^{-1} (SD = 0.36) and for long-distance migrants −0.35 day year^{-1} (SD = 0.15). Despite these advancements, most species are still arriving later today (LMM effect for period 5.25 ± 1.32 days, $t = 3.9$, $P < 0.001$) than in the early half of the nineteenth century (e.g. house martin *Delichon urbicum* and cuckoo *Cuculus canorus*, Figs. 2 and S3).

Relationship between arrival and temperature

Across all species (except for the common redstart *Phoenicurus phoenicurus*), mean FADs were negatively associated with temperature during the period 1828–2010 (mean response for all 13 species −1.03 day °C^{-1}, SD = 0.68, without common redstart −1.19 day °C^{-1}, SD = 0.37, Table 1). The mean response to temperature was −1.36 day °C^{-1} (SD = 0.36) in short-distance migrants and −0.65 day °C^{-1} (SD = 0.79) in long-distance migrants (without common redstart −0.96 day °C^{-1}, SD = 0.27). The positive temperature responses were rare and appeared in periods with poor data coverage, i.e. early part of the twentieth century (Fig. 3). The strongest variation in responses was detected in lapwing *Vanellus vanellus*. Early arriving species such as skylark *Alauda arvensis* and starling *Sturnus vulgaris* had very similar patterns of the temperature-arrival relationship. Strong temperature sensitivity in the second half of the nineteenth century was followed by a moderate relationship from the late 1920s onwards. Four long-distance migrants (barn swallow, house martin, cuckoo and swift *Apus apus*) showed, with various intensities, a strengthening of the relationship around the 1950s and then a steep weakening prior to 2000 followed by a slight strengthening in the last decade. In contrast to other species, common redstart showed an unusually long period of strengthening of the temperature-arrival relationship from the 1920s until today (Fig. 3).

The mean temperature sensitivity across all species was slightly stronger in the warmest period (−1.70 day °C^{-1}, SD = 0.47) than in the coldest period (−1.42 day °C^{-1}, SD = 0.89; Table 2). However, the species-specific differences in the temperature-arrival relationship between these two contrasting periods were significant only for common redstart (Table 2).

Differences between short- and long-distance migrants in variation of temperature sensitivity

Temperature sensitivity of short- and long-distance migrants varied considerably during the study period, but the responses

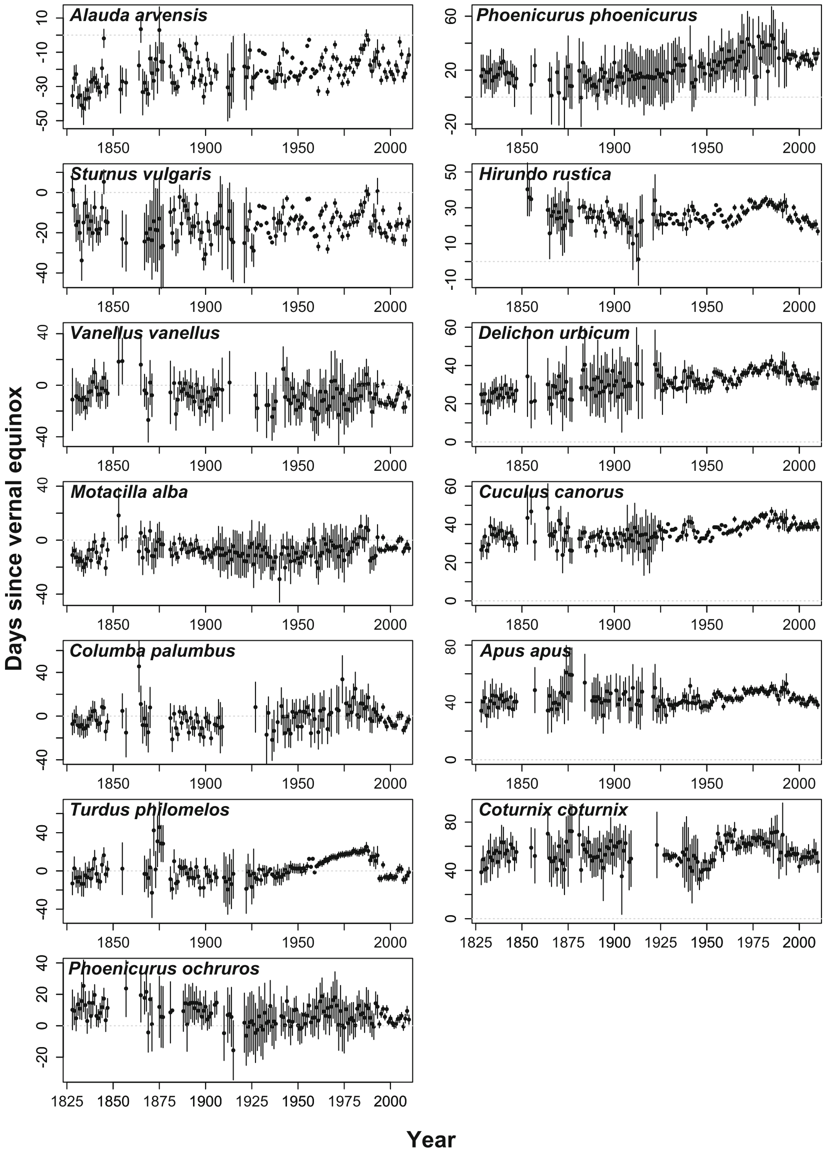


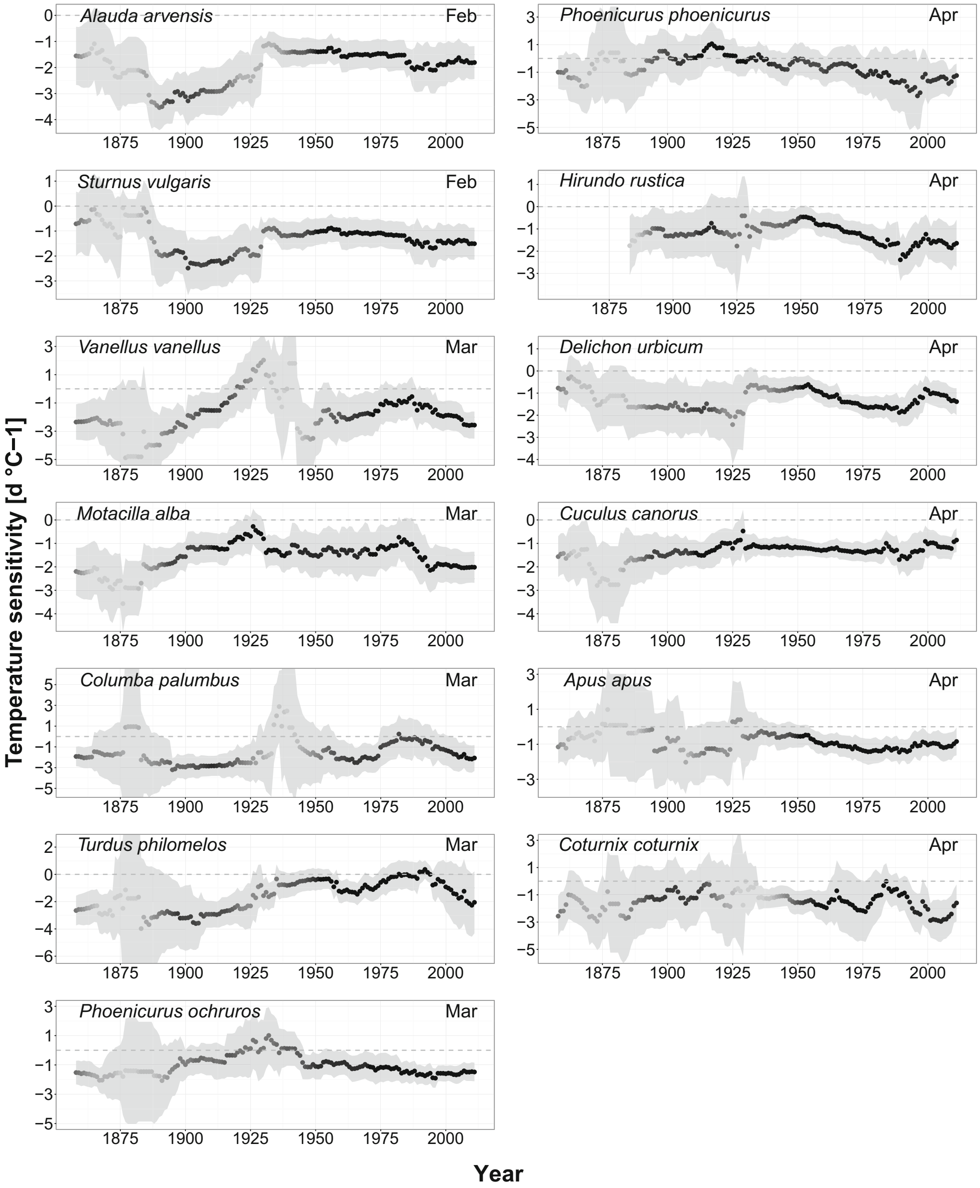
Fig. 2 Reconstructed mean first arrival dates with 95% confidence intervals in the Czech Republic for the period 1828–2010. The arrivals are expressed as annual deviations relative to vernal equinox (zero line). Species are ordered according to their mean first arrival date (FAD). *Left column*: short-distance migrants, *right column*: long-distance migrants

of the two migratory groups did not differ statistically (GLM, factor period $F_{2,35} = 6.00$, $P = 0.006$, factor migratory strategy $F_{1,35} = 1.59$, $P = 0.216$; Fig. 4). While in the first decades (1828–1857) short-distance migrants reacted more strongly to temperature (−1.93 day $°C^{-1}$) than long-distance migrants (−1.22 day $°C^{-1}$), there was no significant difference between these two groups over the three time periods (GLM with period by migratory strategy interaction $F_{2,33} = 1.52$, $P = 0.233$).

Discussion

To the best of our knowledge, we present one of the longest comprehensive time series of mean first arrivals of 13 bird species. We found that birds arrived earlier at the beginning of the nineteenth century than today, although at that time the climate was cooler and more humid (Brázdil et al. 2011). The later arrivals compared to the beginning of the nineteenth century persisted despite an ongoing advancement of arrival dates in recent decades. The sensitivity of bird arrivals to temperature varied considerably throughout the two centuries. However, it did not differ significantly between the coldest and warmest periods (except for common redstart). In accordance with other studies (reviewed in Pearce-Higgins and Green 2014; Rainio 2008; Usui et al. 2016), short-distance migrants responded more strongly to temperature. But in recent decades, long-distance migrants showed similar or even stronger responses than short-distance migrants, although there was no evidence of significant difference. Since the late 1970s, the short-distance migrants showed a clear strengthening of the temperature-arrival relationship, while the

Fig. 3 Temporal changes in temperature sensitivity. Regression slopes of mean first arrival date (FAD) against mean monthly temperature (focal month indicated in the *upper right corner*) based on the estimates of 30-year moving windows during the period 1828–2010. Each data point represents the end-year of the 30-year moving window (starting in 1828) for which the linear regression was estimated. *Grey areas* show 95% confidence intervals. *Dot colour intensity* indicates the number of missing values in the 30-year period from low (*black*) to high (*grey*). Species are ordered based on their mean first arrival dates. *Left column*: short-distance migrants, *right column*: long-distance migrants



relationship for long-distance migrants did not show any directional shift.

At the beginning of the time series, some species were arriving earlier compared to the long-term mean (Fig. 2). This is in contrast to the findings of Brázdil et al. (2011) who found a later onset of plant phenology in Bohemia during the cooler and humid period 1828–1848 compared to the warmer period 1993–2009. One possibility for the past earlier arrivals might be that in the nineteenth century birds were under stronger selection due to more common unfavourable weather events. For example, barn swallows regularly die in large numbers during fall migration in the Alps with consequences for their phenology (Newton 2007). Hence, only the strongest individuals could have survived which were likely to arrive earlier. It could also be the case that our set of species might have been more common in the past than today. Under such scenario, there could be a better detectability of arriving individuals and also a stronger selection for early arriving males. Earlier arrivals in historical datasets were also recorded by Ahas (1999) for white wagtail *Motacilla alba* in Estonia. While other long-term studies showed usually the opposite (Askeyev et al. 2009; Kullberg et al. 2015; Lehikoinen et al. 2004).

The trends in arrivals during the last decades agreed with the general advancement found by other authors (e.g. Gordo 2007; Knudsen et al. 2011; Pearce-Higgins and Green 2014). The advancement of the late-arriving species might be explained by the strong recent increase of April and May mean temperatures in the area of the Czech Republic. The mean temperature in the dataset of Brázdil et al. (2012) increased by 0.08 °C year^{-1} ($P < 0.001$) in April and by 0.06 °C year^{-1} ($P = 0.005$) in May, respectively, during 1970–2010 (Fig. S2). But the lack of significant difference in temperature sensitivity

Table 2 Weighted linear regression statistics of the relationship between mean first arrival dates (FAD) and monthly temperature for the coldest and the warmest 30-year periods

		Coldest period							Warmest period							
Species	Month	Period	Number	TS (d °C^{-1})	SE	t	R^2	P	Period	Number	TS (d °C^{-1})	SE	t	R^2	P	P diff
Alauda arvensis	Feb	1828–1857	23	−1.554	0.569	−2.73	0.26	**0.013**	1978–2010	33	−1.749	0.317	−5.53	0.50	**<0.001**	0.884
Sturnus vulgaris	Feb	1828–1857	22	−0.709	0.657	−1.08	0.06	0.293	1978–2010	33	−1.453	0.311	−4.67	0.41	**<0.001**	0.242
Vanellus vanellus	Mar	1828–1857	21	−2.350	0.638	−3.68	0.42	**0.002**	1978–2010	33	−2.543	0.466	−5.46	0.49	**<0.001**	0.886
Motacilla alba	Mar	1828–1857	23	−2.196	0.516	−4.25	0.46	**<0.001**	1978–2010	33	−2.028	0.323	−6.29	0.56	**<0.001**	0.918
Columba palumbus	Mar	1828–1857	22	−1.923	0.479	−4.01	0.45	**0.001**	1978–2010	33	−2.126	0.656	−3.24	0.25	**0.003**	0.765
Turdus philomelos	Mar	1828–1857	21	−2.653	0.555	−4.78	0.55	**<0.001**	1978–2010	33	−2.072	1.188	−1.75	0.09	0.091	0.615
Phoenicurus ochruros	Mar	1828–1857	21	−1.520	0.411	−3.70	0.42	**0.002**	1978–2010	33	−1.461	0.309	−4.73	0.42	**<0.001**	0.958
Phoenicurus phoenicurus	Apr	1888–1917	30	0.898	0.801	1.12	0.04	0.272	1978–2010	31	−1.411	0.434	−3.25	0.27	**0.003**	**0.006**
Hirundo rustica	Apr	1888–1917	27	−1.160	0.788	−1.47	0.08	0.153	1978–2010	33	−1.794	0.463	−3.88	0.33	**<0.001**	0.449
Delichon urbicum	Apr	1888–1917	25	−1.728	0.657	−2.63	0.23	**0.015**	1978–2010	33	−1.263	0.265	−4.76	0.42	**<0.001**	0.576
Cuculus canorus	Apr	1888–1917	30	−1.285	0.370	−3.48	0.30	**0.002**	1978–2010	33	−0.966	0.226	−4.28	0.37	**<0.001**	0.362
Apus apus	Apr	1888–1917	23	−1.251	0.785	−1.59	0.11	0.126	1978–2010	33	−1.084	0.355	−3.06	0.23	**0.005**	0.949
Coturnix coturnix	Apr	1888–1917	21	−1.037	1.317	−0.79	0.03	0.441	1978–2010	32	−2.187	0.640	−3.42	0.28	**0.002**	0.605

Species are listed in ascending order according to their mean FAD

Month the focal month linked to the bird arrival, *Number* number of years with available data in the 30-year period, *TS* temperature sensitivity, estimate of FAD against mean monthly temperature, *SE* standard error of the estimate, *P diff* significance of comparisons of the slopes of temperature sensitivity between the coldest and the warmest periods, significant *P* values (≤0.05) are in bold

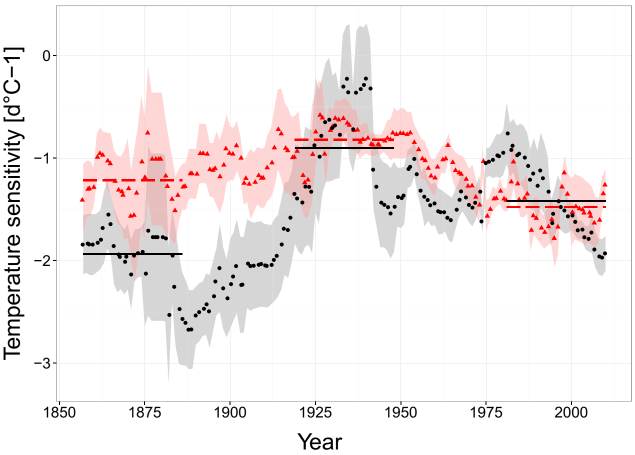


Fig. 4 Averaged linear regression estimates of mean first arrival date (FAD) against monthly temperatures during 1828–2010 for short- (*black dots*) and long-distance (*red triangles*) migrants (for classification see Table 1). Each data point represents the end-year of the 30-year moving window (starting in 1828) for which the linear regression was estimated. The *shadow area* shows ±1SE of the regression estimate. The *horizontal lines* indicate the mean of the regression coefficients for a given 30-year period for short- (*solid line*) and long-distance migrants (*dashed line*, colour figure online)

between the coldest and warmest periods precludes us from a conclusion that the migratory strategy matters more than the need to adjust the species' arrival during specific climatic conditions. Spatial replicates of arrival times series from other areas outside of Central Europe would help to reach a definitive conclusion on this topic.

According to several studies, population density affects the ability to detect the first arrived individuals. Thus, higher population densities can overestimate the real shift in arrivals (Dunn and Møller 2014; Miller-Rushing et al. 2008; Sparks 1999). This might be the case also for this study since some species were likely to be much more numerous in the nineteenth century than today (for a detailed discussion, see Kolářová and Adamík 2015). We are also aware of potential biases caused by the use of FADs which might be sensitive to outliers (Goodenough et al. 2015; Tryjanowski et al. 2005). On the other hand, we used mean FADs across multiple sites which are likely to reduce any potential bias. We also would like to emphasise that FADs are often the only available data for old time series. For the common redstart, we got positive temperature-arrival relationship which does not match the conventional negative pattern. We do not know whether this could be a result of misinterpreted observations with black redstart *Phoenicurus ochruros*, especially in the nineteenth century. For the most recent period, the relationship was in line with the other species (Table 2). Another potential source of bias might come from different source of data over time. Obviously, the knowledge on bird life histories and identification skills was different in 1828 and 2010. Also, spatial variability in locations could lead to different estimates. To overcome this issue, we collated data from throughout Czechia. However, for the earliest period, 1828–1847, we only have data from Bohemia, i.e. the western area (Kolářová and Adamík 2015). But due to the landscape configuration and spatial scale of the study area, there is little latitudinal and longitudinal variation in arrival dates (Beklová 1975; Beklová et al. 1983).

It is usually assumed that long-distance migrants are unable to shift their timing of arrival to breeding sites sufficiently due to constraints of their migratory triggers (especially photoperiod; Berthold 1996; Gwinner 1996). However, we showed that during the last decades long-distance migrants strengthened the temperature-arrival relationship equally to short-distance migrants (Fig. 4). This has led to advanced arrivals in both migratory groups. Among the numerous phenological studies, only Stervander et al. (2005) and Jonzén et al. (2006) found markedly stronger responses in the arrivals of long-distance compared to short-distance migrants. They both suggested that microevolution can play a role in the mechanism of changing migration. But as Both (2007) argued, the advanced arrival can be caused by faster migration due to better conditions en route and that the birds can come from mixed populations which differ in onset of migration. In our study, we cannot fully exclude the issue of mixed origin of populations even though our data were intentionally collected as arrivals to breeding grounds. In addition, climatic teleconnections between breeding and non-breeding grounds or improved environmental conditions north of the Sahara Desert might also lead to shorter stopovers and advanced arrivals (Finch et al. 2014; Saino and Ambrosini 2008).

Short-distance migrants have consistently strengthened the temperature-arrival relationship since the late 1970s (Fig. 4). We hypothesise that this might be a consequence of changed environmental conditions which result in rapid modifications of migratory routes such as decreasing migratory distances between breeding and non-breeding residency grounds (Berthold et al. 1992; Sutherland 1998). This was recently documented for several short-distance migrants (Pulido and Berthold 2010; Smallegange et al. 2010; Visser et al. 2009) and a long-distance migrant, the barn swallow (Ambrosini et al. 2011). This probably leads to better climatic teleconnections of residency sites of birds over their annual cycle. One consequence of this might be that short-distance migrants will always show stronger relationship in arrivals when linked to breeding site temperature.

By reconstructing one of the longest avian phenological time series, we analysed the course of temperature sensitivity across nearly two centuries. We showed that the strength of the temperature-arrival relationship has been changing throughout time but independently of cold or warm periods. Our results show that time series of sufficient length provide a more complex perspective on avian responses to climatic variability than studies with short time series. Centennial time series with bird arrivals are rare (e.g. Ahas 1999; Ellwood et al. 2010; Lehikoinen et al. 2004; Sparks and Carey 1995; Sparks 1999). Thus, a comprehensive synthesis of such long records from various sites with different patterns of climatic trends would be highly desirable as this would help us to better understand vertebrate responses to climatic variability.

Acknowledgements Thousands of volunteers have contributed with their observations. Without their input, it would be impossible to reconstruct bird arrivals over two centuries. We thank the reviewers for constructive comments on an earlier version of the paper. EK was supported by Palacký University internal grant for graduate students (IGA PrF).

References

Ahas R (1999) Long-term phyto-, ornitho- and ichthyophenological time-series analyses in Estonia. Int J Biometeorol 42:119–123

Ambrosini R, Rubolini D, Møller AP, Bani L, Clark J, Karcza Z, Vangeluwe D, du Feu C, Spina F, Saino N (2011) Climate change and the long-term northward shift in the African wintering range of the barn swallow *Hirundo rustica*. Clim Res 49:131–141

Askeyev OV, Sparks TH, Askeyev IV (2009) Earliest recorded Tatarstan skylark in 2008: non-linear response to temperature suggests advances in arrival dates may accelerate. Clim Res 38:189–192

Beklová M (1975) Ankuft und Abzug der tschechoslowakischen Population *Hirundo rustica, Delichon urbica* und *Apus apus*. Folia Zool 24:21–42

Beklová M, Pikula J, Šabatka L (1983) Phenological maps of bird migration. Acta Sc Nat Brno 17:1–47

Berthold P (1996) Control of bird migration. Chapman & Hall, London

Berthold P, Helbig AJ, Mohr G, Querner U (1992) Rapid microevolution of migratory behaviour in a wild bird species. Nature 360:668–670

Bitterlin LR, van Buskirk J (2014) Ecological and life history correlates of changes in avian migration timing in response to climate change. Clim Res 61:109–121

Both C (2007) Comment on "Rapid advance of spring arrival dates in long-distance migratory birds". Science 315:598

Both C, Van Asch M, Bijlsma RG, Van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constrains or adaptations? J Anim Ecol 78:73–83

Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc R Soc B 277:1259–1266

Both C, Visser ME (2001) Adjustment of climate change is constrained by arrival date in a long-distance migrants. Nature 411:296–298

Brázdil R, Bělínová M, Rožnovský J (2011) Phenological observations made by the I. R. Bohemian Patriotic–Economic Society, 1828–1847. Theor Appl Climatol 105:71–81

Brázdil R, Bělínová M, Dobrovolný P (2012) Temperature and precipitation fluctuations in the Czech lands during the instrumental period. Masarykova Univerzita, Brno

Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont L, Crawford R, Durrant JM, Hughes L, Keatley MR, Low M, Morellato LPC, Poloczanska E, Ruoppolo V, Vansteels R, Woehler E, Wolfaardt A (2013) Changes in southern hemisphere phenology. PLoS One 8:e75514

Dunn PO, Møller AP (2014) Changes in breeding phenology and population size of birds. J Anim Ecol 83:729–739

Ellwood ER, Primack RB, Talmadge ML (2010) Effects of climate change on spring arrival times of birds in Thoreau's Concord from 1851 to 2007. Condor 112:754–762

Ellwood ER, Diez JM, Ibáñez I, Primack RB, Kobori H, Higuchi H, Silander JA (2012) Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming? Oecologia 168:1161–1171

Finch T, Pearce-Higgins JW, Leech DI, Evans KL (2014) Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. Biodivers Conserv 23(10):2427–2444

Fu YH, Zhao H, Piao S, Peaucelle M, Peng S, Zhou G, Ciais P, Huang M, Menzel A, Peñuelas J, Song Y, Vitasse Y, Zeng Z, Janssens IA (2015) Declining global warming effects on the phenology of spring leaf unfolding. Nature 526:104–107

Goodenough AE, Fairhurst SM, Morrison JB, Cade M, Morgan PJ (2015) Quantifying the robustness of first arrival dates as a measure of avian migratory phenology. Ibis 157:384–390

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, Doi H (2012) Drivers of population variability in phenological responses to climate change in Japanes birds. Clim Res 54:95–112

Gordo O, Sanz JJ (2005) Phenology and climate change: a long-term study in a Mediterranean locality. Oecologia 146:484–495

Gordo O, Sanz JJ, Lobo JM (2007) Environmental and geographical constraints on common swift and barn swallow spring arrival patterns throughout the Iberian Peninsula. J Biogeogr 34:1065–1076

Gordo O, Tryjanowski P, Kosicki JZ, Fulín M (2013) Complex phenological changes and their consequences in the breeding success of a migratory bird, the white stork *Ciconia ciconia*. J Anim Ecol 82:1072–1086

Gwinner E (1996) Circadian and circannual programmes in migratory birds. J Anim Ecol 75:1119–1127

Häkkinen R, Linkosalo T, Hari P (1995) Methods for combining phenological time-series - application to bud burst in birch (*Betula pendula*) in central Finland for the period 1896–1955. Tree Physiol 15:721–726

Halkka A, Lehikoinen A, Velmala W (2011) Do long-distance migrants use temperature variations along the migration route in Europe to adjust the timing of their spring arrival? Boreal Environ Res 16:35–48

Heide OM, Prestrud AK (2005) Low temperatures, but not photoperiod, controls the growth cessation and dormancy induction and release in apple and pear. Tree Physiol 25:109–114

Hovestadt T, Nowicki P (2008) Process and measurement errors of population size: their mutual effects on precision and bias of estimates for demographic parameters. Biodivers Conserv 17(14):3417–3429

Jochner S, Ankerst D, Beck GA, Hoefler J, Traidl-Hofmann C, Menzel A (2013) Nutrient status—the missing factor in phenological research. J Exp Bot 64:2081–2092

Jonzén N, Lindén A, Ergon T, Knudsen E, Vik OJ, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsonn L, Stervander M, Andersson A, Walderström J, Lehikoinen A, Edvardsen E, Solvang R, Stenseth NC (2006) Rapid advance of spring arrival dates in long-distance migratory birds. Science 312:1959–1961

Jonzén N, Hedenström A, Lundberg P (2007) Climate change and the optimal arrival of migratory birds. Proc R Soc B 274:269–274

Kharouba H, Paquette SR, Kerr JT, Vellend M (2014) Predicting the sensitivity of butterfly phenology to temperature over the past century. Glob Chang Biol 20:504–514

Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N, Sutherland WJ, Bach LA, Coppack T, Ergon T, Gienapp P, Gill JA, Gordo O, Hedenström A, Lehikoinen E, Marra PP, Møller AP, Nilsson ALK, Péron G, Ranta E, Rubolini D, Sparks TH, Spina F, Studds CE, Sæther SA, Tryjanowski P, Stenseth NC (2011) Challenging claims in the study of migratory birds and climate change. Biol Rev 86:928–946

Kolářová E, Adamík P (2015) Bird arrival dates in Central Europe based on one of the earliest phenological networks. Clim Res 63:91–98

Körner C, Basler D (2010) Phenology under global warming. Science 327:1461–1462

Kullberg C, Fransson T, Hedlund J, Jonzén N, Langvall O, Nilsson J, Bolmgren K (2015) Change in spring arrival of migratory birds under era of climate change, Swedish data from the last 140 years. Ambio 44(1):69–77

Laube J, Sparks TH, Estrella N, Menzel A (2014) Heat or humidity, which triggers tree phenology? New Phythol 202(2):350–355

Lehikoinen E, Sparks TH, Zalakevicius M (2004) Arrival and departure dates. Adv Ecol Res 35:1–31

Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307–315

Miller-Rushing A, Lloyd-Evans TL, Primack RB, Satzinger P (2008) Bird migration times, climate change, and changing population sizes. Glob Chang Biol 14:1959–1972

Mitrus C, Sparks TH, Tryjanowski P (2005) First evidence of phenological change in a transcontinental migrant overwintering in the Indian sub-continent: the Red-breasted Flycatcher *Ficedula parva*. Ornis Fennica 82:13–19

Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. Proc Natl Acad Sci U S A 42:16195–16200

Naef-Daenzer B, Luterbacher J, Nuber M, Rutishauser T, Winkel W (2012) Cascading climate effects and related ecological consequences during past centuries. Clim Past 8:1527–1540

Nakazawa T, Doi H (2012) A perspective on match/mismatch of phenology in community contexts. Oikos 121:489–495

Newton I (2007) Weather-related mass-mortality events in migrants. Ibis 149:453–467

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob Chang Biol 13:1860–1872

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pearce-Higgins JW, Green RE (2014) Birds and climate change: impacts and conservation responses. Cambridge University Press

Pulido F, Berthold P (2010) Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. Proc Natl Acad Sci U S A 107:7341–7346

Quansheng G, Huanjiong W, Jingyun Z, Rutishauser T, Junhu D (2014) A 170 year spring phenology index of plants in eastern China. J Geophys Res-Biogeo 119:301–311

Rainio K (2008) Climate change effects on avian migration. Dissertation, University of Turku

Root TL, Price JT, Hall KR, Schneider SH, Rozenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Rubolini D, Møller AP, Rainio K, Lehikoinen E (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. Clim Res 35: 135–146

Rutishauser T, Luterbacher J, Defila C, Frank D (2008) Swiss spring phenology 2007: extremes, a multi-century perspective, and changes in temperature sensitivity. Geophys Res Lett 35:L05703. doi:10.1029/2007GL032545

Rutishauser T, Schleip C, Sparks TH, Nordli Ø, Menzel A, Wanner H, Jeanneret F, Luterbacher J (2009) Temperature sensitivity of Swiss and British plant phenology from 1753 to 1958. Clim Res 39:179–190

Sagarin R (2001) False estimates of the advance of spring. Nature 414: 600

Saino N, Ambrosini R (2008) Climatic connectivity between Africa and Europe may serve a basis for phenotypic adjustment of migration schedules of trans-Saharan birds. Glob Chang Biol 14:250–263

Sanz JJ, Potti J, Moreno J, Merino S, Frías O (2003) Climate change and fitness components of migratory bird breeding in the Mediterranean region. Glob Chang Biol 9:461–472

Schaber J, Badeck F, Doktor D, von Bloh W (2010) Combining messy phenological time series. In: Hudson IL, Keatley MR (ed) Phenological Research, Springer, pp 147–158

Schaber J (2012) Pheno: auxiliary functions for phenological data analysis. R package version 1:6 Available at: http://CRAN.R-project.org/package=pheno

Schleip C, Rutishauser T, Luterbacher J, Menzel A (2008) Time series modelling and central European temperature impact assessment of phenological records over the last 250 years. J Geophys Res 113: G04026. doi:10.1029/2007/JG000646

Schwartzberg EG, Jamieson MA, Raffa KF, Reich PB, Montgomery RA, Lindroth RL (2014) Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. Oecologia 3:1041–1049

Smallegange IM, Fiedler W, Köppen U, Geiter O, Bairlein F (2010) Tits on the move: exploring the impact of environmental change on blue and great tit migration distance. J Anim Ecol 79:350–357

Sparks TH (1999) Phenology and the changing pattern of bird migration in Britain. Int J Biometeorol 42:134–1938

Sparks TH, Carey PD (1995) The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736−1947. J Ecol 83:321–329

Sparks TH, Huber K, Bland RL, Crick HQP, Croxton PJ, Flood J, Loxton RG, Mason CF, Newnham JA, Tryjanowski P (2007) How consistent are trends in arrival (and departure) dates of migrant birds in the UK? J Ornithol 148:503–511

Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. Proc Natl Acad Sci U S A 99:13379–13381

Stervander M, Lindström Å, Jonzén N, Andersson A (2005) Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. J Avian Biol 36:210–221

Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. J Avian Biol 29:441–446

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliot JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16:3304–3313

Tooke F, Battey NH (2010) Temperate flowering phenology. J Exp Bot 61:2853–2862

Tryjanowski P, Kuźniak S, Sparks TH (2005) What effects the magnitude of change in first arrival dates of migrant birds? J Ornithol 146:200–205

Usui T, Butchart SHM, Phillimore AB (2016) Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. J Anim Ecol. doi:10.1111/1365-2656.12612

Van Ash M, Van Tienderen P, Holleman LJM, Visser ME (2007) Predicting adaptation of phenology in response to climate change, an insect herbivore example. Glob Chang Biol 13:1596–1604

Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. Proc R Soc B 268:289–294

Visser ME, Perdeck AC, van Balen JH, Both C (2009) Climate change leads to decreasing bird migration distances. Glob Chang Biol 15: 1859–1865

Wang H, Dai J, Zheng J, Ge Q (2015) Temperature sensitivity of plant phenology in temperate and subtropical regions of China from 1850–2009. Int J Climatol 35:913–922

Zalakevicius M, Bartkeviciene G, Raudonikis L, Janulaitis J (2006) Spring arrival response to climate change in birds: a case study from eastern Europe. J Ornithol 147:326–343

Zhang X, Tarpley D, Sullivan JT (2007) Diverse responses of vegetation phenology to warming climate. Geophys Res Lett 34:L19405. doi:10.1029/2007GL031447

Zar JH (1999) Biostatistical analysis. Prentice Hall

Zuur AF, Ieno EN, Elphick CS (2009) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14