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# Bird arrival dates in Central Europe based on one of the earliest phenological networks

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ABSTRACT: Recording arrival dates of migratory birds to their breeding grounds has been one of the most popular activities among naturalists for more than 2 centuries. However, we know extremely little about the timing of birds' annual cycles when systematic field observations were still in their infancy, before the current warming period. Here we aim at filling this gap for bird arrival dates of 35 species for one of the earliest phenological networks, run by the Bohemian Patriotic-Economic Society during 1828-1847 in the present day Czech Republic. We retrieved station-based archival data and present the arrival dates correlated with local temperature prior to species-specific arrival. The mean slope of arrival advancement with monthly temperature across all species was  $-1.4 \text{ d} \circ \text{C}^{-1}$  in our study, which is remarkably similar to a recent dataset from the same region. The strength of this relationship depended on species-specific timing of migration. Early migrating species showed stronger negative relationships with temperature than later arriving, long-distance migrants. Cross-correlations in arrival dates among stations were positive and high for well-known species such as skylark, common quail and common cuckoo. Stationbased data also showed strong relationships with temperature. For most species, comparisons with recent arrivals (1991–2010) show later arrivals in recent years, and we suggest that changes in population sizes might also play a role in explaining bird phenology.

KEY WORDS: Bird arrival  $\cdot$  Long-distance migrant  $\cdot$  Phenology  $\cdot$  Short-distance migrant  $\cdot$  Temperature

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### 1. INTRODUCTION

The 18th century was a period of great interest in endeavouring to explain natural phenomena. In an atmosphere of the development of natural sciences, many academic institutions were established and the foundations of numerous scientific disciplines were laid (Inkster & Morrell 2007, Alcoforado et al. 2012). This was also the case for phenological observations. The first organised networks for observing plants, birds and insects were established across the European continent. The Swedish and Finnish phenological networks were initiated by von Linné and Leche in the 1750s (von Haartman & Söderholm-Tana 1983, Terhivuo et al. 2009). Beginning in 1846, the Finnish Society of Sciences and Letters set up a regular phenological network which is still running (Lehikoinen et al. 2004, Kubin et al. 2008). Another phenological series originated from Norfolk in the UK. Here the Marsham family recorded the phenological events of over 20 plants and animals over a period of more than 200 yr during 1736 to 1947 (Sparks & Carey 1995). The oldest systematic European network was operated by the Societas Meteorologica Palatina in Mannheim between 1781 and 1792 (Menzel 2003). As well as meteorological data, they also collected phenological records on plants and animals. The data regarding avian phenology consisted of arrivals and departures, and included migratory species such as white stork *Ciconia ciconia*, barn swallow *Hirundo*  *rustica*, common nightingale *Luscinia megarhynchos*, and common cuckoo *Cuculus canorus*. After the first International Ornithological Congress in 1884, interest in avian phenology was awakened in other countries, and especially during the 20th century many national phenological networks were established (Menzel 2003, Nekovář et al. 2008).

The first sporadic notes on avian phenology in the Czech lands were made by J. Stepling, A. Strnad, T. Haenke and M. David in the second half of the 18th century (Nekovář & Hájková 2010). However, the first regular network was created by members of the Imperial Royal Patriotic-Economic Society of Bohemia. This society was originally established as the Society of Agriculture and Liberal Arts in the Kingdom of Bohemia (Gesellschaft des Ackerbaues und den freien Künste im Königreich Böhmen) by Empress Maria Theresa in 1767. The main aim of this society was to enhance the agricultural and industrial production in the Czech lands (Krška & Šamaj 2001). In 1789 the society was reorganised and renamed as the Imperial Royal Patriotic-Economic Society of Bohemia (K. K. Patriotisch-ökonomische Gesellschaft im Königreich Böhmen) (Volf 1967). Among other topics, the members focussed on meteorology, plant and animal phenology. In 1835, a series of books about the topography of Moravia (Die Markgrafschaft Mähren, topographisch, statistisch und historisch geschildert) was published by the Benedictine T. Wolný (Wolný 1835, Krška 2003). As well as plant phenology, he also described the usual arrival of some common bird species such as skylark Alauda arvensis, white wagtail Motacilla alba and corncrake Crex crex (Wolný 1835). In 1861 the Natural Science Society in Brno (Naturforschender Verein in Brünn) was established (Krška 2003). The society organised meteorological and phenological observations in the areas of Moravia and Silesia. The phenological records of birds were published regularly until 1906. Since 1853 phenological observations, including bird arrival data, were organised from Vienna by the newly established Zentralanstalt für Meteorologie und Geodynamik. Another network based on observations, initiated by Rudolf, the Crown Prince of Austria, was temporarily run by Comité für Ornithologische Beobachtungs-Stationen in Österreich during the 1880s. Since 1923, a national scheme of phenological stations has been run by the present-day Czech Hydrometeorological Institute.

During the last 2 decades a renaissance in phenological research has occurred as a consequence of ongoing climatic changes, which have affected plants and animals at different trophic levels and in

various ecosystems (Rosenzweig et al. 2008). Changes in the timing of bird migration have been reviewed by Lehikoinen et al. (2004), Rubolini et al. (2007), Knudsen et al. 2011, Pearce-Higgins & Green (2014). However, nearly all the studies use time series of no more than a few recent decades (for rare exceptions see Sparks & Carey 1995, Ahas 1999, Lehikoinen et al. 2004, Ellwood et al. 2010, Gordo et al. 2013). This is in contrast to climatology or plant phenology where detailed studies on the reconstruction of past events are widely available. Here we aim to fill this gap for bird arrival dates for one of the earliest phenological networks which ran during 1828 to 1847 in Bohemia, Austrian Empire (nowadays the western part of the Czech Republic). We present an analysis of the archival records, link them to local climate and assess the reliability of data, both from a local, station-based, and regional perspective.

## 2. DATA AND METHODS

## 2.1. Historical data

During 1828 to 1847 the members of the Imperial Royal Bohemian Patriotic-Economic Society contributed their phenological observations to annual reports in the society's journal Neue Schriften. The final 2 years appeared in Verhandlugen und Mittheilungen. Both migratory and resident bird species were recorded. The data were restricted to Bohemia and involved 33 phenological stations (see Fig. 1, see Table S1 in the Supplement at www.int-res.com/ articles/suppl/c063p091\_supp.pdf). They consisted of records on the first arrival and the last departure dates of 35 bird species (3594 arrival and 2174 departure records). The reports distinguished between true migratory species (i.e. those with non-overlapping distributions during breeding and wintering periods) and resident species for which peaks in spring and autumn movements were observed (e.g. tits, treecreepers and crossbills). In this study we considered arrival data only.

We expressed the dates of observations as days of the year (DOY; where January 1 = Day 1). The original scientific names were converted into present-day form (see Table 1) and the data were then checked for outliers and incorrect dates caused by mistakes in the original printed records. All incorrect data and scattered outliers (detected by inspection of boxplots and Cleveland dotplots; Zuur et al. (2010) were excluded from analysis (71 records on arrivals). In those cases where there was a clear mistake in listing the arrival date as the departure date and vice versa, the data were assigned to the right category. For the sites Klášterec nad Ohří, Český Krumlov and Želiv there were 2 first arrivals of birds observed: one at low and another at high altitudes. In these cases, the earlier arrival was chosen and included in the analyses. In a few cases where a range of dates was provided, the earlier date was considered as the first arrival. For the fieldfare *Turdus pilaris* and pine grosbeak *Pinicola enucleator* the autumn arrival data to central Europe actually represented their arrival to wintering sites. In the 19th century the fieldfare was still spreading south from northern Europe and it was only later when it extended its breeding range into the central European region.

For each species we set a lower limit of 50 records for inclusion in analyses (see Table 2); 27 species met this criterion. For each of these 27 species we reconstructed the Bohemian arrival time series with linear mixed-effect models where Site was taken as a random effect and Year as a fixed effect (Häkkinen et al. 1995, Schaber et al. 2010). Species-specific multi-site combined arrival time series were estimated in the Rpackage 'pheno' (Schaber 2012; see Table S5 in the Supplement at www.int-res.com/articles/suppl/c063

p091\_supp.pdf). Annual predicted values of arrivals from the fixed part of the model were then used to explain the relationship with climate using linear regressions and Pearson correlations. Species-specific arrivals were compared to mean temperature of the month of arrival or to the month preceding the mean arrival (depending on the temporal overlap of arrivals and the focal month; see Table S2 in the Supplement at www.int-res.com/ articles/suppl/c063p091\_supp.pdf). Mean monthly temperatures are widely used in avian phenological studies (Gordo 2007). The mean monthly temperature data were obtained from a reconstructed homogenized temperature series (1800–2010) for the Czech Republic (Brázdil et al. 2012a,b).

For those sites where reliable time series ( $\geq$ 14 yr of data) were available for particular bird species (Hradec Králové, Loket, Velké Dvorce and Vyšší Brod), we assessed the local relationship between arrivals and temperature. For an assessment of between-site similarity in annual first arrivals, we cross-correlated the time series of these 4 stations. Paired *t*-tests were used to compare the slopes of arrival–climate relationships both at a regional (Bohemian) and site scale.

### 2.2. Recent data

To compare the historical arrivals with recent data we used a dataset for the period 1991-2010. We collated data on bird arrivals from various sources, but the majority of the records were collected from the phenological network of the Czech Society for Ornithology and supplemented by data from various personal diaries and grey literature. We tried to match the observations to spatially overlap with those of the Bohemian Patriotic-Economic Society. For some species (e.g. Ardea cinerea, Upupa epops, etc.) we did not have enough records to reconstruct the arrival dates. Therefore the recent dataset consisted of only 17 species: true migrants for which we had sufficiently large sample sizes. We checked for outliers and used mixed effect modelling as for the historical times series.



Fig. 1. Overview of available station-based arrival data from the network of the Bohemian Patriotic-Economic Society, 1828–1847. In parentheses: number of years with data for each site

Original scientific name	Original	Current valid	Common English name Common skylark		
	German name	scientific name			
Alauda arvensis	Feldlerche	Alauda arvensis			
Anas anser canorus	Wildgans	Anser spp. <sup>a</sup>	Geese		
Anas anser ferus	Wildgans	Anser spp.	Geese		
Ardea cinerea	Fischreiher	Ardea cinerea	Grey heron		
Ardea minuta	Kleine Rohrdommel	Ixobrychus minutus	Little bittern		
Ardea stellaris	Gemeine Rohrdommel	Botaurus stellaris	Great bittern		
Certhia familiaris	Baumkletterer	Certhia spp. <sup>b</sup>	Treecreeper		
Ciconia alba	Gemeiner Storch	Ciconia ciconia	White stork		
Columba oenas	Holztaube	Columba oenas	Stock dove		
Columba palumbus	Ringeltaube	Columba palumbus	Wood pigeon		
Columba turtur	Turteltaube	Streptopelia turtur	Turtle dove		
Colymbus cristatus	Großer Haubentaucher	Podiceps cristatus	Great crested grebe		
Cuculus canorus	Kukuck	Cuculus canorus	Common cuckoo		
Hirundo apus	Mauerschwalbe	Apus apus	Common swift		
Hirundo riparia	Uferschwalbe	Riparia riparia	Sand martin		
Hirundo urbica	Hausschwalbe	Delichon urbicum	House martin		
Larus	Möwen	<i>Larus</i> spp.	Gulls		
Loxia cocothraustes	Dickschnabel	Coccothraustes coccothraustes	Hawfinch		
Loxia enuncleator	Fichtenkernbeißer	Pinicola enucleator	Pine grosbeak		
Motacilla alba	Gemeine Bachstelze	Motacilla alba	White wagtail		
Motacilla erithacus	Hausrothschwänzchen	Phoenicurus ochruros <sup>c</sup>	Black redstart		
Motacilla hortensis	Grasmücke	Sylvia spp. <sup>d</sup>	_		
Motacilla luscinia	Nachtigall	Luscinia megarhynchos	Common nightingale		
Motacilla phoenicurus	Gartenrothschwänzchen	Phoenicurus phoenicurus	Common redstart		
Oriolus galbula	Goldamsel	Oriolus oriolus	Golden oriole		
Parus ater	Schwarzmeise	Periparus ater	Coal tit		
Parus coeruleus	Blaumeise	Cyanistes caeruleus	Blue tit		
Parus major	Kohlmeise	Parus major	Great tit		
Scolopax rusticola	Waldschnepfe	Scolopax rusticola <sup>e</sup>	Eurasian woodcock		
Sturnus vulgaris	Star	Sturnus vulgaris	Common starling		
Tetrao coturnix	Wachtel	Coturnix coturnix	Common quail		
Turdus musicus	Singdrossel	Turdus philomelos	Song thrush		
Turdus pilaris	Kronowetvogel	Turdus pilaris	Fieldfare		
Turdus viscivorus	Misteldrossel	Turdus viscivorus	Mistle thrush		
Upupa epops	Wiedehopf	Upupa epops	Eurasian hoopoe		
Vanellus cristatus	Kiebitz	Vanellus vanellus	Northern lapwing		

Table 1. Bird species recorded by the members of the Bohemian Patriotic-Economic Society and current valid classification of species names

<sup>a</sup>Geese were not well recognized to species level at that time. <sup>b</sup>At that time Eurasian treecreeper and short-toed treecreeper were not separately recognized, therefore data may refer to both species. <sup>c</sup>Misidentification of robin and black redstart was very common. <sup>d</sup>M. hortensis is now garden warbler but at that time several Sylvia warbler species were labelled under this name. <sup>e</sup>This could be any species of the genus Scolopax, Gallinago and Lymnocryptes

## 3. RESULTS

## 3.1. General pattern of bird arrivals to Bohemia

We retrieved data on 35 bird species (27 species with >50 records) from 33 sites (Fig. 1, Table 1, see Table S1 in the Supplement). For an overview of mean first arrival dates to Bohemia and sample sizes see Table 2. In general the mean first arrival dates correlated negatively with mean monthly temperatures (see Table S2 in the Supplement). The mean slope of arrival advancement with temperature across all species was -1.43 d °C<sup>-1</sup> for both the 1828–1847 and the 1991–2010 periods. The mean slope of the 17 species for the 1828–1847 period was -1.52 d °C<sup>-1</sup>. Slope estimates for the arrival–temperature relationship between these 2 time periods were highly correlated (r = 0.61, n = 17, p = 0.010). While some early arriving species such as skylark or song thrush showed strong negative responses to temperature (-1.8 to -2.5 d °C<sup>-1</sup>), other species, especially the later arriving ones, did not. The strength of the

Table 2. List of the 35 species whose arrivals were observed by the members of the Bohemian Patriotic-Economic Society in 1828–1847, and a comparison with recent (1991–2010) arrival dates. Migratory categories (mc): short- (S) or long-distance (L) migrant; n: number of records; Mean first arrival day of the year (DOY) for species with n < 50 was taken as a simple arithmetic mean of all observations (marked with <sup>a</sup>), and for species with n > 50 an arrival time series was reconstructed from a linear mixed-effects model (see 'Data and methods'). Significance of comparisons of arrival dates between the 2 periods (2-tailed *t*-test): ns = non-significant difference, \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001

Species	mc		1828-1847				– Difference	
		n	DOY	SE	n	DO	Y SE	p-value
Alauda arvensis	S	211	50	8.5	48	0 62	2 9.8	***
Anser spp.	S	120	66	9.3				
Apus apus	L	113	119	9.3	45	6 12	3 5.1	ns
Ardea cinerea	S	83	93	9				
Botaurus stellaris <sup>a</sup>	S	15	94					
Certhia spp.	S	81	77	13.2				
Ciconia ciconia <sup>a</sup>	L	49	98					
Coccothraustes coccothraustes <sup>a</sup>	S	35	78					
Columba oenas	S	166	74	11.8	92	2. 81	L 7.3	*
Columba palumbus	S	162	78	10.1	34	3 75	5 9.9	ns
Coturnix coturnix	L	145	132	10.3	19	5 13	4 12	ns
Cuculus canorus	L	197	113	5.5	48	4 12	0 6.4	***
Cyanistes caeruleus	S	67	71	9.5				
Delichon urbicum	L	210	106	7.4	39	1 11	3 6.5	***
Ixobrychus minutus ª	L	2	87					
Larus spp. <sup>a</sup>		48	81					
Luscinia megarhynchos	L	58	117	3.5	20	6 11	8 4.8	ns
Motacilla alba	S	185	71	7.8	53	3 76	6 9	**
Oriolus oriolus	L	69	105	13.9	19	7 12	8 6.5	***
Parus major	S	85	72	11.7				
Periparus ater	S	61	68	11.2				
Phoenicurus ochruros	S	116	94	11.2	52	7 86	6 8.6	***
Phoenicurus phoenicurus	L	100	96	11.1	27	0 10	9 8.5	***
Pinicola enucleator <sup>a</sup>	S	21	289					
Podiceps cristatus <sup>a</sup>	S	14	89					
Riparia riparia ª	L	2	183					
Scolopax rusticola	S	176	88	10.9				
Streptopelia turtur	L	90	113	11.3	18	8 11	9 10.5	***
Sturnus vulgaris	S	139	68	10.6	54	9 61	l 9.1	***
Sylvia spp.		127	112	11				
Turdus philomelos	S	151	74	8.8	40	0 73	8 8.9	ns
Turdus pilaris	S	101	297	18.9				
Turdus viscivorus	S	88	55	14.3	13	2 62	2 10.1	ns
Upupa epops	L	52	104	11.2				
Vanellus vanellus	S	94	76	11.6	38	0 70	) 11.8	***

relationship between arrival and temperature was, in part, explained by species-specific arrival dates, i.e. a stronger relationship in early arriving species and vice versa (Fig. 2, linear regression:  $b = 0.016 \pm 0.006$  SE,  $F_{1,24} = 7.09$ , p = 0.013, R<sup>2</sup> = 0.23) for the period 1828–1847. For the recent dataset the arrival-temperature relationship was slightly stronger ( $b = 0.029 \pm 0.005$ ,  $F_{1,15} = 32.36$ , p < 0.001, R<sup>2</sup> = 0.66). There was no significant relationship between mean arrival day and SE in the datasets for 1828–1847 ( $b = -0.03 \pm 0.02$ ,  $F_{1,24} = 0.94$ , p = 0.178, n = 26 excluding the field-fare) or 1991–2010 ( $b = -0.03 \pm 0.02$ ,  $F_{1,15} = 3.21$ , p = 0.093, n = 17).

#### 3.2. Local magnitude of arrivals

Station-based first arrival dates from the 4 sites with the most reliable datasets were generally positively cross-correlated (mean  $r = 0.41 \pm 0.23$  SD, n = 33 pairwise comparisons), with the highest correlation in arrival in the common cuckoo and skylark (see Table S4 in the Supplement at www.int-res.com/articles/suppl/c063p091\_supp.pdf).

Comparisons of site-based arrival-temperature slopes with those from Bohemian regional data showed a significantly stronger relationship at the regional scale for Loket and Velké Dvorce, but not for



Fig. 2. Relationship between species-specific mean first arrival date and the slopes of the relationship between arrival and mean monthly temperature (1828–1847). Fieldfare data is not included since it represents autumn arrival to wintering sites

Hradec Králové; Bohemia versus Loket (paired *t*-test;  $t_{12} = 3.27$ , p = 0.001), Bohemia versus Velké Dvorce ( $t_{10} = 3.29$ , p = 0.008) and Bohemia versus Hradec Králové ( $t_{12} = -2.08$ , p = 0.059). Mean slope estimates with monthly temperature were -2.40 in Loket (n = 13), -2.04 in Velké Dvorce (n = 11), -0.91 in Hradec Králové (n = 13), and -1.16 in Vyšší Brod (n = 3; see Table S3 in the Supplement at www.int-res.com/ articles/suppl/c063p091\_supp.pdf).

## 4. DISCUSSION

The Bohemian Patriotic-Economic Society organised a network of observations of bird arrivals for 20 yr. This is one of the earliest and most comprehensive networks on avian phenology in central Europe. We confirmed with more recent datasets that warmer weather was associated with earlier spring arrivals. The mean slope of arrival advancement with temperature across all species was -1.43 d  $^{\circ}C^{-1}$  for both periods in our study. But the strength of this relationship depended on species-specific timing of migration. Early migrating species showed much stronger and negative relationship with temperature than later arriving (mostly long-distance) migrants. This is in line with the comprehensive overviews of Lehikoinen et al. (2004) and Pearce-Higgins & Green (2014). The mean response fits into the range (-1.11)d  $^{\circ}C^{-1}$  for long-distance and -1.87 d  $^{\circ}C^{-1}$  for shortdistance migrants, see Table S2 in the Supplement for source data) based on studies from the second half of the 20th century ( $-2.9 \text{ d} \circ \text{C}^{-1}$  in Lehikoinen et al. 2004; and ca. –0.35 and –1.3 d  $^{\circ}\mathrm{C}^{-1}$  in long- and short-distance migrants, respectively, in PearceHiggins & Green 2014). Few studies have analyzed 18th and 19th century time series on bird arrivals. Data on 3 species from Finland show responses between -1.02 to -2.34 d °C<sup>-1</sup> in 1749-1762 (Lehikoinen et al. 2004). The Marsham family records from the east of England and 2 other shorter British time series show a slightly stronger relationship with temperature; e.g. the common cuckoo: -1.5 to -2.8 d  $^{\circ}C^{-1}$ , which in our study was -1.2 d  $^{\circ}C^{-1}$  in the regional dataset (but see also the variable station-based data, Sparks & Carey 1995, Sparks 1999). Spatial heterogeneity in local adaptations could result in this pattern (Sparks et al. 2007). The Bohemian Patriotic-Economic Society also recorded data on plant phenology. An assessment of these records shows very strong negative relationships with local temperature (Brázdil et al. 2011). Although, the members of the Society were mostly professionals, e.g. foresters and teachers, it is possible that their knowledge on identification of species was not sufficient. For example, some well-known species such as white wagtail, skylark, wood pigeon Columba palumbus or common cuckoo show reasonable associations with temperature. In contrast, the song of starlings Sturnus vulgaris was likely confused with that of the golden oriole Oriolus oriolus since there are several records of golden oriole from February and March (very unlikely arrival dates for a long-distance migrant that is among the latest species to appear in central Europe). This suggests that arrivals for well-known and easily recognized species are more reliable than for the less well-known ones. Judging from the magnitude of temperature-arrival relationships of the 2 Czech datasets, we conclude that these historical records are as reliable as the recent arrival data.

The period 1828–1847 in Bohemia was characterized by a monthly temperature in March and April that was ~2°C lower than in the 1991–2010 period (Brázdil et al. 2012a). We know extremely little on how birds tuned their timing of migration at times when climate was cooler (cf. Sparks 1999, Lehikoinen et al. 2004). Studies on plants show much later onset of phenophases in the first half of the 19th century than today (Brázdil et al. 2011, Možný et al. 2012, Kolářová et al. 2014). In contrast, comparison with the more recent data on bird arrivals to Bohemia shows that timing of migration was in general earlier by 4.1 d (2.9 d when excluding the golden oriole) in 1828–1847. Of the 17 species available for comparisons, 12 arrived later in the recent period. We do not know why so many species in the 19th century dataset arrived earlier than today. The temperaturearrival relationships are similar in these 2 datasets,

indicating their reliability. From 1983 to 2003, arrival dates to western Poland were on average 2.3 d earlier (for 12 species in common) than our historical dataset. When excluding the golden oriole the difference is 4.9 d (Tryjanowski et al. 2005). This discrepancy could be attributed to changes in population sizes, which in declining species may result in apparent delayed arrival (Tryjanowski & Sparks 2001, Miller-Rushing et al. 2008). Especially farmland species such as skylark or quail are currently suffering from severe population declines (Reif et al. 2008). On the other hand, a wide range of species were hunted for food (e.g. skylark, starling, thrushes and tits) or trapped for their song (e.g. blackcap, nightingale), which could locally lead to significant declines of their populations at that time (Baum 1955). We can-

their populations at that time (Baum 1955). We cannot rule out also the possible role of dynamic changes in migratory routes or wintering areas that could be also mirrored in different timing of arrivals (Berthold et al. 1992, Sutherland 1998).

We also showed that station-based first arrival dates were positively cross-correlated. Given the high variability in first arrival dates, which makes this variable often criticized for its stochastic component (Moussus et al. 2010), we perceive this as a sign of reliability of these records. A detailed view on station-based associations with climate shows a much stronger relationship than at regional scales for 2 stations, and a tendency towards weaker a relationship at 1 station. It might be that the observer effect plays a major role in the quality of station-based data. For this reason we suggest that the regional reconstructions provide more reliable estimates of arrival dates than the station-based data. The latter may be confounded by the observer effect, population trends, predation pressure and skills of individual observers, or the length of the time series might be too short to detect a true relationship with climate (von Haartman & Söderholm-Tana 1983, Sparks 1999, Hušek et al. 2009, 2012, Lehikoinen & Sparks 2010).

Phenological data are a good indicator of the response of biota to climate change (Parmesan 2007). Therefore, reconstructing historical time series broadens our understanding of how both plants and animals reacted to climate at times that preceded the current warming period (Amano et al. 2010, Naef-Daenzer et al. 2012, Primack & Miller-Rushing 2012, this study).

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