


LONG TERM STUDY

Environmental phenology drives spring migration timing

Oleg V. Bourski 

Laboratory of Population Ecology, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

Correspondence

Oleg V. Bourski
Email: obourski@gmail.com

Handling Editor: Davide Dominoni

Abstract

1. Despite the obvious shift in spring bird migration to earlier dates, the mechanism behind this process remains unclear, partly due to inappropriate climate predictors. Information on the influence of climate is not geographically representative, as it comes almost exclusively from the marginal parts of the continents.
2. The objective of this study is to investigate the mechanism for determining the timing of spring terrestrial bird migration based on a new concept of environmental phenology and phenological navigation, using data from Central Siberia as an example.
3. A literature review suggests that migrants follow the phenology of food resources, the dependence on which intensifies towards the end of migration with increasing seasonality of temperature conditions. We propose the concept of environmental phenology as a mediator between the influence of climate and the response of migrants. We defined the environmental phenology index as the average weighted temperature of the preceding days with weights decreasing exponentially in retrospect.
4. Using original data from the first arrival dates of 145 species in Central Siberia from 1976 to 2025, we demonstrated the effectiveness of the environmental phenology index in predicting arrival dates. This indicator reflects the accumulation of climate information by numerous ongoing phenological processes. Due to its high autocorrelation, it predicts future foraging conditions.
5. Despite significant warming at the study site (0.60 degrees per decade), bird arrival dates in the studied community responded to warming with a slight shift towards earlier dates: on average, by -0.91 days per degree annually and by -0.86 days per decade. These estimates are lower than those known for other regions due to the pronounced continental climate and the steep rise in spring temperatures (1 degree in 3 days). We believe the compensated share of this impact (the response to impact ratio) to be a more adequate measure of the organism's response to the impact.
6. Based on the study results, we propose a mechanism of phenological navigation, in which a migrant at each stopover chooses whether to move on or wait for changes based on the relationship between environmental phenology and day length. This simple scheme opens new possibilities for comparing the phenological responses of different groups of organisms.

7. The proposed index of environmental phenology is theoretically and practically substantiated, expands the understanding of the mechanism of phenological navigation and can be used to solve similar phenological issues.

KEYWORDS

climate change, continentality, first arrival date, long-term study, methods, migration timing, phenology, Siberia

1 | INTRODUCTION

The timing of spring migration is an adaptation of the annual cycle, ensuring optimal use of seasonal food abundance for reproduction and survival (Kokko, 1999). With climate warming observed since the 1970s, spring is becoming increasingly earlier and the phenology of the biota is shifting, but to varying degrees (Cohen et al., 2018; Thackeray et al., 2016). Organisms at lower trophic levels, directly dependent on rising temperatures, passively follow warming. Consumers at higher trophic levels are conservative and shift their timing less than their prey. When consumers are closely dependent on resource abundance, a phenological mismatch can arise (Visser & Gienapp, 2019). For example, while the breeding season of the Pied Flycatcher (*Ficedula hypoleuca*) in the Netherlands has changed by 6 days, the maximum of larval abundance has changed by 15 days. This means that the peak of chick food requirements now occurs during periods of reduced prey abundance, leading to a decline in the Pied Flycatcher population (Both et al., 2006). According to monitoring data in Europe, negative trends are more characteristic of those species and populations that have shifted their breeding seasons less (Møller et al., 2008). In some cases, the onset of breeding season shifts closer to the arrival dates, and there is concern that arrival dates from spring migration, as a more conservative element of the annual cycle, may limit the adaptation of breeding seasons to modern conditions (Both & Visser, 2001). Therefore, climate warming is considered one of the main factors affecting the viability of populations and threatening biodiversity (Butchart et al., 2010; Pautasso, 2012).

Despite the abundance of data collected on the shift in migration timing, phenomenology in studies strongly prevails over the analysis of the causes and mechanisms of the phenomenon (Chmura et al., 2019; Knudsen et al., 2011). In general, experts' opinions only agree that migration timing has a genetic basis and represents a broad reaction norm to various climatic factors that precede each phase of migration and influence its progression (Knudsen et al., 2011). Data from meta-analyses (Bitterlin & Van Buskirk, 2014; Lehikoinen et al., 2004; Lehikoinen & Sparks, 2010; Rubolini et al., 2007; Usui et al., 2017) correlate poorly with each other. While advances are common, changes vary in magnitude and direction among species and regions, and the basis for this variation is relatively unknown (Chmura et al., 2019). Many of the inconsistencies stem from repeatedly noted methodological problems, such as distinguishing

between long-term and short-term effects, specifying appropriate explanatory variables and linking them to response date (Møller & Merilä, 2004; Gordo, 2007; Lehikoinen & Sparks, 2010; Lindström & Forchhammer, 2010). The response is typically attributed to general warming, so it is unclear to what extent it reflects local effects within the narrow confines of a season important for the species. The causes of long-term changes should manifest itself in responses to annual climatic fluctuations, but this information is far from always provided. Available indirect indicators, such as the mean monthly temperature, are considered as drivers of phenological responses, even when the month ends later than the phenological event.

Chmura et al. (2019) made significant progress in understanding the phenological mechanisms in their review of factors that are hypothesized to influence bias. They demonstrated the multiple nature of phenological responses and proposed distinguishing two categories of mechanisms: environmental mechanisms, related to the external agent, and organismal mechanisms, related to the traits of the subject of the impact and its physiological and ecological capabilities for a response. This distinction allows for the magnitude of the impact and estimates the response as a compensated fraction of the impact, which can be compared between species groups under different conditions to study organismal mechanisms. However, the key question remains the driver. Here, we see the following prerequisites and a path to a solution.

1.1 | The concept of environmental phenology

The goal of seasonal migration is to follow the distribution of resources (Berthold, 1996; Newton, 2008; Thorup et al., 2017). Given the diversity of extreme examples of migratory behaviour, one must recognize the very strong ability of birds to move and the low cost of mobility as such (Berthold, 1996; Newton, 2008). In this case, the progress of migrants should depend mainly on the abundance of food available at stopover sites, rather than on flight conditions (Nilsson et al., 2013). This is supported by the relationship between migratory movements and the vegetation productivity index (Thorup et al., 2017), as well as in a feeding experiment (Bridge et al., 2010). Therefore, to explain the timing of migration, it is necessary to find an environmental variable that most accurately reflects the availability of food.

Migration timing is controlled by a hereditary endogenous programme that responds to day length (photoperiod) and ensures

optimal environmental adaptation in years with average conditions (Bauer et al., 2020; Gwinner, 1996). When conditions deviate from the average, the migration timing can vary within the reaction norm. This requires additional external information in an accessible form (Bauer et al., 2020; Winkler et al., 2014), that is, cues that are present always and everywhere. The phenological environment, a set of noticeable phenological phenomena along the migration route, possesses this quality.

In temperate climates, temperature determines seasonality and limits biological processes; therefore, all phenological phenomena depend primarily on temperature (Cohen et al., 2018; Gordo, 2007), as well as on the duration of its influence (Tuhkanen, 1980). Seasonal development in insects is determined by temperature conditions, such that each developmental phase strictly corresponds to the sum of accumulated temperatures above a species-specific threshold (Jarošík et al., 2011). Therefore, the timing of initial stages depends more on spring phenology, while subsequent stages depend more on the onset of development (Emmenegger et al., 2014). Consequently, if temperature is the cause of seasonality, then a spring temperature increase predicts a summer peak in biological resource abundance. Studies of phenotypic plasticity (reviewed by Bonamour et al., 2019) have established that multiple cues are selected to match the spring development of prey items. Since each bird species specializes not on a single prey species but on a fairly diverse group, the overall seasonal dynamics of these prey items are important, and this reflects the local course of spring temperatures. This provides information for the development of an effective predictor.

At a transit point along its route, a migrant, having replenished its energy reserves, must decide whether to move on or wait. It has (approximate) knowledge of the calendar date (based on day length) and the phenological conditions (based on its surroundings), which, however, are inseparable. Consequently, the migrant can only choose the ratio of the two: either trust phenology more, but set off on the return journey when cold weather returns, or trust photoperiod more, but miss the opportunity to benefit from warming.

Migration timing is thought to depend on conditions along the entire flyway (see, e.g. Gordo, 2007). However, as the target is approached, the movement slows down (Marra et al., 2005; Schmaljohann, 2019; Youngflesh et al., 2021), and the dependence of timing on spring conditions increases (Emmenegger et al., 2014; Youngflesh et al., 2021). Spring migration is characterized by increased seasonality, such that suitable conditions at the destination appear later than along the flyway, limiting the timing of the end of migration, which in turn determines the onset and progress of migration (Schmaljohann, 2019). Climatic (meteorological) processes span large regions (Di Cecco & Gouhier, 2018), so conditions at the destination can be assessed from afar through spatial autocorrelation and in advance through temporal autocorrelation.

Given these premises, we propose the concept of environmental phenology (EP) as a hypothesis for the complex influence of the environment on the arrival date. Temperature is known to be the main component of boreal climate, limiting the duration of the season favourable for the development of organisms (Cohen et al., 2018;

Gordo, 2007). Consequently, temperature is ultimately responsible for both changes in the timing of bird arrival and the phenology of other natural processes, that is, EP. However, birds are quite resistant to changes in temperature per se (Gavrillov, 2012). Consequently, they respond not so much to temperature as to EP: to those spring abiotic processes and the state of organisms at lower trophic levels that are more directly related to heat accumulation (snow melting, vegetation greening, insect activity, etc.). To assess the development of these processes, we propose an EP index (see Section 2) based on heat accumulation. Each index value marks a specific spring phase associated with the onset of the season's food supply and can thus serve as a cue for optimizing timing. The high autocorrelation of the EP index throughout the season allows migrating birds to anticipate the limits of the food-abundant period and adjust their annual cycle accordingly.

Here, we analyse for the first time original long-term data on terrestrial bird arrival in Central Siberia, a vast, pristine and poorly studied region in the interior of the largest continent. The first spring registration of any migratory species was recorded as the first arrival date (FAD). We define an index of environmental phenology as a driver of migration timing and evaluate its effectiveness under varying parameters. We decompose it into components characterizing environmental forcing mechanisms on daily, annual and multi-year scales and use them to model the arrival dates of each species. Interspecies comparison reveals changes in response to forcing strength and allows us to estimate the average level of compensation for climate change. A general multispecies model evaluates the contribution of environmental phenology components to determining arrival dates. Based on our results, we discuss the mechanism by which environmental phenology influences migration timing, as well as the advantages of the proposed method. The specifics of the organismal responses in the migrant groups will be discussed elsewhere.

2 | METHODS

2.1 | Observations

The materials were collected between 1976 and 2025 in Central Siberia, at the Yenisei Ecological Station in Mirnoye (A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences) (62°20'N, 89°00'E). No special ethical permission is required to conduct field research at the station. Most of the first spring arrival dates (FADs) of the species were obtained during observations along a daily 3-km route through several habitats. Due to logistical difficulties, the observations were not conducted in some years or were limited in time and habitat coverage, resulting in missing the correct FAD of less conspicuous species (Figure S1). Therefore, from the entire sample (2955 records of 145 species), we excluded years with fewer than 60 records (species) and species with fewer than 17 records (years), leaving 2030 records of 95 species. However, we reviewed the entire sample at key locations to ensure that there were no principal differences that disturbed any solution. When we

consider migration timing, we refer to arrival dates, as we recorded the first appearance of both local breeding and transient species.

2.2 | Climate and the environmental phenology

Data on average daily temperature at the nearest Bakhta weather station, 20 km north of the observation site, were obtained from the websites <https://rp5.ru> and <https://data.giss.nasa.gov>. The series of average daily temperatures of each year, starting from January 1, were sequentially converted into a series of daily indices of environmental phenology EP_d according to the recurrent formula

$$EP_d = \alpha \times T_d + (1 - \alpha) \times EP_{d-1},$$

where d is the day of the year, T_1 is the temperature on January 1, $EP_1 = T_1$ and α is the 'oblivion rate'.

As a result, for example, with $\alpha = 0.20$, for each day we obtained a history of the previous development of spring, in which the current day (d) is 100% important, the previous day ($d-1$) is 20% 'forgotten' and therefore 80% important, the day before last ($d-2$) is $0.20 + 0.80 \times 0.20 = 36\%$ 'forgotten' and is 64% important, etc. Therefore, the summary of such a history EP_d is an exponentially weighted average of daily air temperatures for the days preceding day d (inclusive), where the last day has the highest weight as a driver of future changes, and the contribution of each previous day is less than the contribution of the next day by a fraction α (oblivion rate).

EP exhibits long-term, annual and daily variations. Using the regression of EPs by year, we divided the EP series for each date from 1976 to 2025 into two variables: the long-term linear warming trend (L) and the annual deviation from it (A). The daily variation (D) was expressed as the residuals of the regression of the daily temperature T_d in EP_d over the years of observations. Variable D reflects the role of the weather as a driver of phenology, which can increase or decrease the phenological deviation in the environment each day. The resulting variables were centred by subtracting the mean long-term value for each spring date. This yielded three independent phenological variables: L , A and D , expressing the deviation of the state of the environment from the seasonal norm on three time scales. Their units are degrees Celsius. Given the nearly linear increase in average spring temperatures of 0.291°C per day (see below), these variables can also be expressed in days ahead/behind the norm for each observation day.

We examined seasonal variations in the strength of these factors as SDs of the multiyear series to compare the strength of responses. To assess the predictability of the conditions, the autocorrelation A was calculated for each day in May with the values for the following 30 days (averaged over years using the Fisher z -transform).

2.3 | Efficiency of phenological predictors

To assess the influence of phenological deviations on arrival dates, we also converted arrival dates into annual deviations from the

long-term trend in a species-specific linear regression by year of observation. The effect was evaluated in a multispecies linear model of FAD deviations as a function of annual deviations in environmental phenology (A) on the exact day of arrival of each species in a given year. Both variables were prestandardized by dividing by the standard deviation within the species. Next, for comparison, we constructed the same models for each date between 40 days before and 10 days after arrival. To find the best oblivion rate for EP, we constructed the same models with different α values ranging from 0.01 to 1.00 (in increments of 0.01). For comparison, we also calculated the degree-day index (DDO) of the accumulated sum of temperatures above 0°C (Saino et al., 2011) for each day in the same range and substituted it into the regression instead of A . The quality of the models was compared using the adjusted coefficient of determination.

2.4 | Response of species to phenological factors

In subsequent analyses, we used only factors constructed based on the most effective oblivion rate and only models associated specifically with the arrival date. The phenological linear regression model for each species included arrival date deviations as the dependent variable and deviations in three independent factors, L , A and D , as predictors.

The results of species-specific models were used to assess the dependence of responses on the magnitude of the impact. The magnitude of the impact was defined as the standard deviation of the factor over the years of observation. To express the response in the same units, the magnitude of the impact was multiplied by the dependence, that is, the regression coefficient. For example, if the impact deviates by an average of 10 days and the regression coefficient is 0.3, then the response under this impact is 3 days. The scatterplot of species responses to factor magnitude was then assessed to see which kind of model fits best (with species weighted by their sample size). The intercept-only model indicated a constant response regardless of factor size. The proportional interspecific regression model through the origin assumed an increase in the response with increasing magnitude of the factor. The slope of the proportional regression line was considered a measure of compensation for external influence to maintain the constancy of the annual cycle. The Akaike information criterion (AIC) was used to compare the models.

To more accurately assess the extent of compensation, we combined the primary data for all species in a single analysis and constructed a general phenological model with FAD deviation as the response variable, L , A and D as predictors and the slope of the species-specific dependences on L and A as random effects (lme4 package, Bates et al., 2015). We then standardized all variables within species and repeated the calculations to determine the sensitivity of migrants to phenological perturbations on different time scales.

We performed calculations in R 4.2.2 (R Core Team, 2022) and used STATISTICA 12 (StatSoft, Inc., 2014) for plotting.

3 | RESULTS

3.1 | Efficiency of phenological predictors

To test the proposed concept, we investigated arrival date deviations as a function of annual deviations in environmental phenology by varying two parameters: the day of condition assessment and the rate of

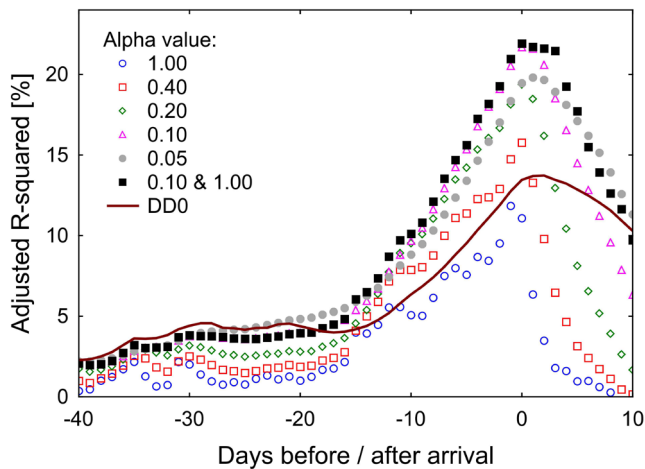


FIGURE 1 Performance of models explaining the deviation of the first arrival date (FAD) as a function of the deviation of the environmental phenology (EP, annual component A) in the date range around the arrival date. Each point represents a multispecies regression model in which both variables are represented by annual deviations from a long-term linear trend and standardized within the species sample. The EP index is constructed as a weighted average of past daily temperatures, the contribution of which decreases by a fraction of α each day in retrospect. For comparison, the thin line represents the dependence on the degree-day index with a zero threshold (DDO).

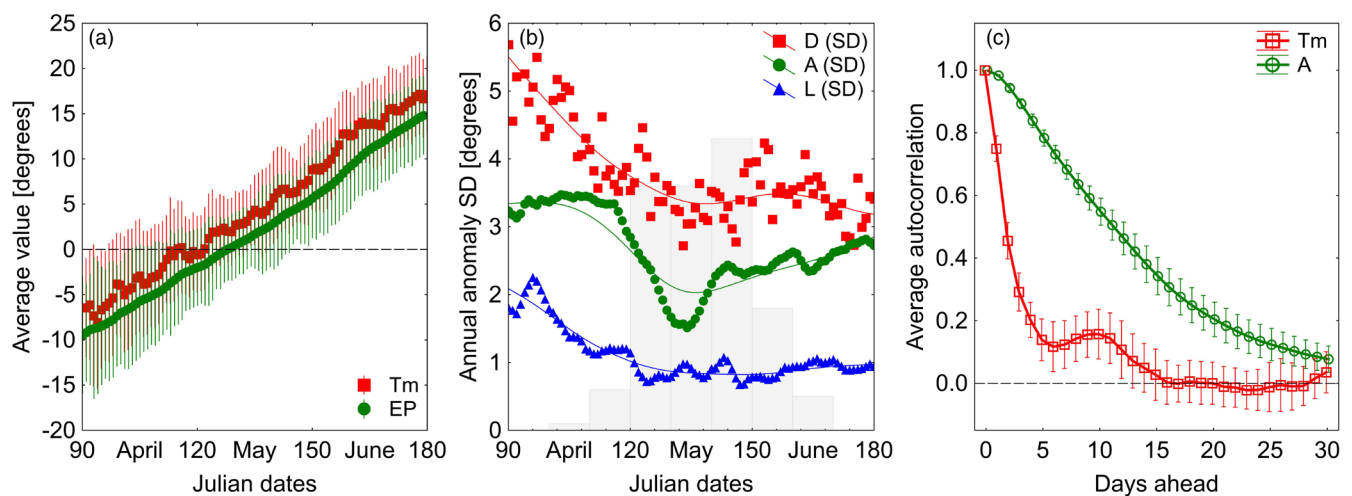


FIGURE 2 Phenological characteristics of spring from 1976 to 2025 at the study site. (a) Mean course of temperature and annual environmental phenology (\pm SD); note the constant slope of $0.291^{\circ}\text{C day}^{-1}$. (b) Variability of spring phenology; note the unstable conditions for early migrants. (c) Autocorrelation of anomalies during May: mean correlation \pm 95% prediction interval between any day and k days ahead; note that phenological conditions can be successfully predicted for much longer time than temperature. Tm is daily air temperature; EP is an index of environmental phenology with an oblivion rate $\alpha=0.10$ (see text); L, A and D are long-term, annual and daily components of EP. The background histogram shows the seasonal distribution of mean FADs of the observed species.

estimated phenological change (Figure 1). The effect of environmental phenology increased rapidly 2–3 weeks before arrival, reached a maximum on the day of arrival and then declined. The greatest effect was exerted by the annual phenological component A with an oblivion rate of $\alpha=0.10$, at which EP is updated by half in 7 days. No second index added to the model improved this effect, except for the index at $\alpha=1.00$, that is, the temperature on the day of arrival. The independent effect of this variable is equivalent to the daily phenological component D. Fitting models with the degree-day index (DDO in Figure 1) instead of A resulted in significant losses ($\Delta\text{AIC}=174.4$ between the top models). Moreover, its estimates turned out to be unreasonably high for the early phase of spring, when DDO is determined only in years with the most advanced phenology.

3.2 | Seasonal variability of phenological factors

The phenology index of the environment, measured with an oblivion rate of 0.10, increased almost linearly during the spring season, in parallel with the increase in air temperature, on average at a rate of $0.291^{\circ}\text{C per day}$ (Figure 2a). Over the years of observation, the long-term component of environmental phenology (L) during the spring migration season increased by an average of $0.6^{\circ}\text{C per decade}$, but for early migrants, it was sufficiently larger (Figure 2b). The interannual variations (SD) of environmental phenology (A) averaged 2.2°C ($=7.5$ days), although for early migrants, the phenological uncertainty was twice as large as for mid-May migrants. The interannual variations (SD) of the daily component of phenology (D) during the season were large and relatively constant: they changed no more than one and a half times. Autocorrelation of weather conditions (using daily temperature as an example) did not allow us to confidently (95%) expect the anomaly's sign to persist for more than a few days

(Figure 2c). At the same time, spring deviations in environmental phenology (A) persisted with a high probability (95%) for more than a month after arrival.

3.3 | Responses of species to phenological factors

For each species, an FAD model with three predictors (L, A and D) was constructed using $\alpha=0.10$ (Table S1). Most responses to warming conditions were directed towards early arrival (Figure 3). The highest number of significant relationships was found with annual deviations, while the fewest were with daily deviations. More than a quarter of the species list responded significantly to long-term warming.

Given the variability of the components of environmental phenology, we sought to determine to what extent birds are able to withstand this uncertainty and reduce (compensate) for its impact on their annual cycle (Table 1). The daily component (D), under the greatest weather uncertainty, had a minimal effect: The species responses varied greatly without regard to the level of environmental variability. The main contribution to the determination

of the migration timing (SD=2.0 days) was made by responding to significant annual deviations (SD=7.5 days) in environmental phenology (A), compensating for them by 25%. The directional changes in the environment (L) during the observation period were 2.5 times smaller, but were compensated more completely, by 43%.

The species differed in their arrival conditions, which made it possible to assess the nature of the influence of each component with changing levels of uncertainty (Table 1). The long-term response was stronger for species whose migration period was subject to greater warming. Therefore, the interspecific differences were described more accurately using the proportional model than using the constant model ($\Delta AIC=3.0$). They were even better described by the quadratic model ($\Delta AIC=6.3$), suggesting an accelerated increase in response as the warming intensifies. The opposite trend was observed for the annual response: interspecific differences were more consistent with the constant model than with the proportional model ($\Delta AIC=10.4$). With a range of environmental variability (SD) from 5 to 12 days, the range of response (SD) remained constant at about 2 days. Consequently, compensation for annual deviations decreased from 0.40 in relatively stable conditions to 0.17 in a less

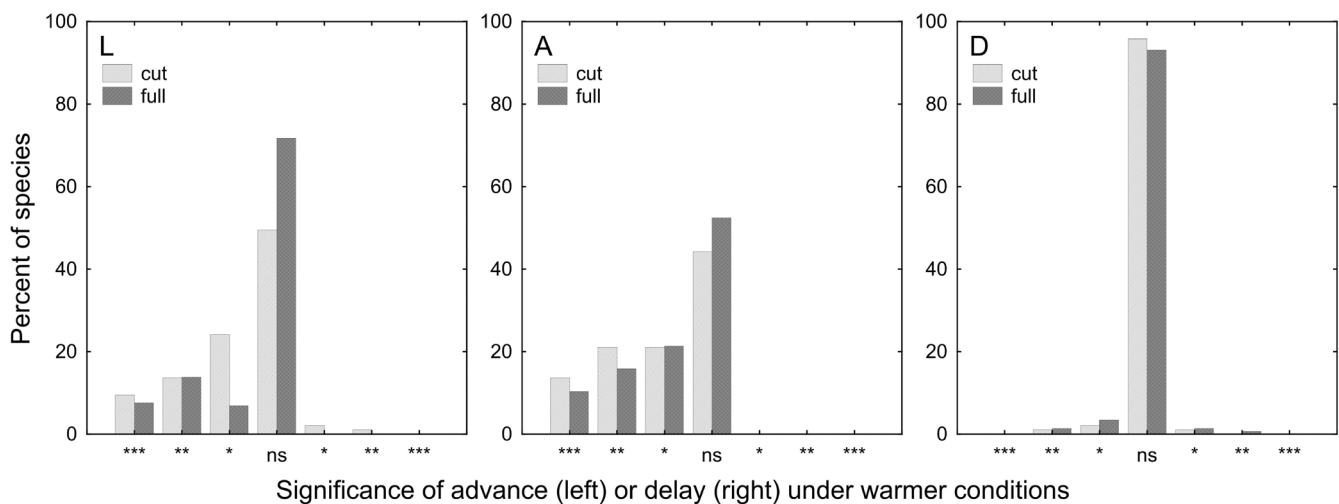


FIGURE 3 Distribution of species by the significance of responses to phenological factors. L, long-term warming; A, annual environmental phenology deviation; D, daily deviation. Sample size: Cut, 2030 observations of 95 species; full, 2948 observations of 145 species. Significance levels: ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

TABLE 1 Response of species to the impact of components of environmental phenology.

EP components	Environ. impact Mean SD (days)	Constant response		Proportional response		
		Mean \pm SE	AIC	Mean \pm SE	AIC	R^2_{adj}
L (long-term linear advance)	3.00	-1.24 \pm 0.21	412.6	-0.43 \pm 0.07	409.6	27.9
A (annual deviation)	7.45	-1.96 \pm 0.14	328.2	-0.25 \pm 0.02	338.6	64.5
D (daily change)	11.88	-0.24 \pm 0.11	294.0	-0.02 \pm 0.01	294.5	2.9

Note: The constant response is a model of type $Y=a+\epsilon$, where a is the same response for any species. The proportional response is a model of type $Y=bX+\epsilon$, where b is the same proportion of compensation for the impact for any species. Model quality: AIC—Akaike information criterion, R^2_{adj} —adjusted coefficient of determination (%).

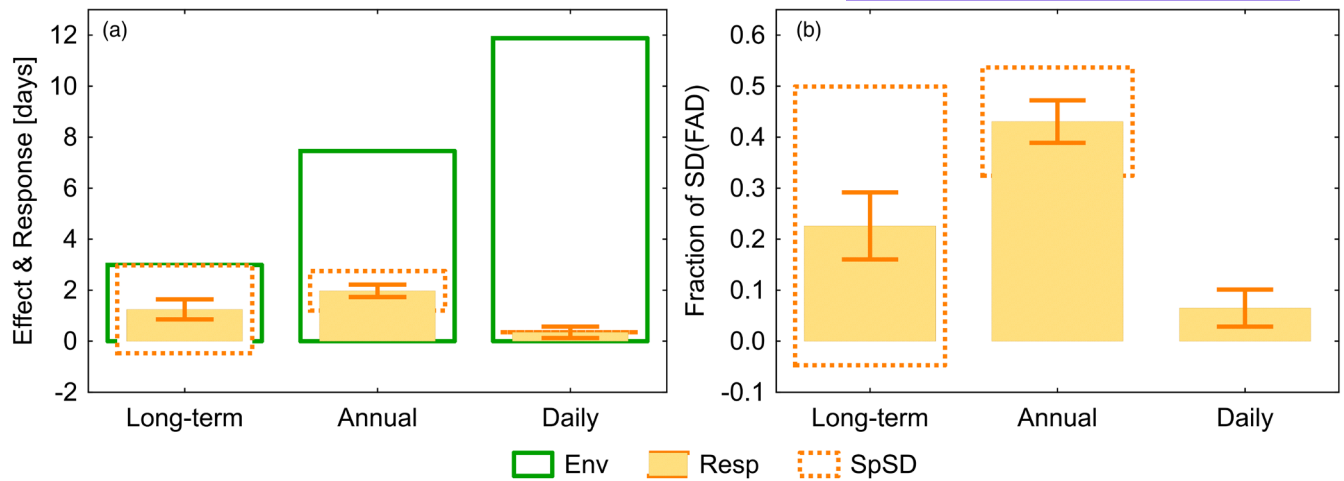


FIGURE 4 General phenological model. (a) Mean absolute response of species versus strength (SD) of environmental influences. (b) Distribution of the absolute response between environmental phenology components (after standardization of variables). Env, environmental variability; Resp, response; SpSD, random effect of interspecific slope differences; whiskers indicate 95% confidence interval.

TABLE 2 Average response of species from the general phenological model.

	Model slope \pm se	<i>p</i>	Compensation \pm se	Env. impact	Response	Species SD
<i>L</i> *	-0.86 ± 0.27 d	<0.001	-0.42 ± 0.07 d d ⁻¹	2.05 d	-0.86 d	1.18 d
<i>L</i>	-1.44 ± 0.23 d°C ⁻¹	<0.001	-0.42 ± 0.07 d d ⁻¹	3.00 d	-1.25 d	1.72 d
<i>A</i>	-0.91 ± 0.06 d°C ⁻¹	<0.001	-0.27 ± 0.02 d d ⁻¹	7.45 d	-1.98 d	0.78 d
<i>D</i>	-0.10 ± 0.03 d°C ⁻¹	<0.01	-0.03 ± 0.01 d d ⁻¹	11.88 d	-0.35 d	not defined

Note: *L*—long-term warming (*L**—shift per 10 years), *A*—annual deviation, *D*—daily weather change. Species SD—random effect of interspecific slope differences. Explanation power: $R^2_{\text{marg}} = 21.2\%$, $R^2_{\text{cond}} = 34.7\%$.

predictable environment. As the determination coefficient showed, the species responded similar to annual phenological deviations but diverged significantly in the long-term trend.

A general phenological model assessed the dependence of arrival dates on three components and yielded similar results (Figure 4a and Table 2). The weather change had a weak but significant effect, explaining 3% of the FAD variance. The main predictor of migration timing was annual fluctuations during spring, which changed arrival by 2 days off 7.4. A linear warming trend over the years of observation shifted the spring timing by 10 days and the arrival timing by 4 days; that is, by 2 standard deviations of the annual response. Species-specific differences (SD) exceeded the mean long-term change and accounted for approximately one-third of the annual variance.

The standardized phenological model showed the distribution of the response among independent components of environmental phenology (Figure 4b and Table 3). A small but significant contribution was due to the change in weather. Large annual deviations caused the greatest response. The response to a stable linear warming trend was only half as strong, although it was almost two orders of magnitude weaker than the annual deviations. Furthermore, interspecific differences (SD) exceeded the mean long-term response and represented less than a quarter of the total annual deviations.

TABLE 3 Response to environmental phenology components based on the results of the standardized model.

	Model slope \pm se	<i>p</i>	SpSD
<i>L</i>	-0.226 ± 0.033	<0.001	0.273
<i>A</i>	-0.431 ± 0.021	<0.001	0.106
<i>D</i>	-0.065 ± 0.019	<0.001	not defined

Note: Explanation power: $R^2_{\text{marg}} = 24.4\%$, $R^2_{\text{cond}} = 33.0\%$. The rest are as in Table 2.

4 | DISCUSSION

Following the results of previous studies, we concluded that migration timing depends on food availability rather than flight conditions. Food abundance has a phenological pattern, that is, it depends on preserved traces of weather effects from the recent past. We found an optimal balance between the accumulation of phenological information and its use by migrants along the migration route. For a more precise assessment, we used various methods: linear mixed-effects models, separating the effects by time scale and precise matching of the effect and response over time. This helped us estimate the magnitude of climate impacts and the compensatory responses of birds.

4.1 | Validity of observations

We use the FAD as a measure of migration timing, recognizing the imperfections of this metric. FAD correlates well with long-term changes in the median arrival date (MAD) (Dale et al., 2024; Rubolini et al., 2007; Tøttrup et al., 2006; Vähätalo et al., 2004), but diverges in its response to intraseasonal changes (Goodenough et al., 2015). The latter is inevitable, as the FAD precedes the MAD by 1–4 weeks and, therefore, reflects the phenology of a different period of spring. FAD occurs during more risky phenological conditions and is therefore more dependent on them (Dale et al., 2024; Rubolini et al., 2007; Tøttrup et al., 2006). A disadvantage of the FAD is that it is estimated from a single observation. However, intraspecific variation in FAD over years is only slightly greater than MAD (Dale et al., 2024) or differs insignificantly (Goodenough et al., 2015; Tøttrup et al., 2006). Thus, FAD is neither a proxy for MAD nor an outlier. Rather, it is a natural characteristic of the advanced population group (Kokko, 1999), reflecting future changes in the population majority (Tøttrup et al., 2006; Vähätalo et al., 2004). We compensate for the statistical limitations of FAD by a larger set of species and the duration of observations.

4.2 | Environmental phenology as a key seasonal predictor

Migrants follow changes in vegetation productivity to adjust the timing of migration based on resource availability (Cole et al., 2015; Emmenegger et al., 2014; Thorup et al., 2017; Youngflesh et al., 2021), thus explaining the causal relationship. However, local temperatures have been shown to provide more accurate information about flight path conditions than remote sensors do (Tøttrup et al., 2010), as long as the time window of exposure is chosen correctly (van de Pol et al., 2016). The degree-day (DD) index, which measures the sum of daily temperatures above a certain threshold (Saino et al., 2011), partially helps avoid subjective limits of the time window. Another way to avoid estimating the exposure-time window is an exponential moving average (Gienapp et al., 2005), though it requires the selection of a smoothing parameter. We used the latter method and determined the optimal parameter value (oblivion rate α) directly from the strength of the FAD response. The proposed EP index is similar to the DD agroclimatic indicator, adjusted for the regional and seasonal rate of spring processes. Unlike DDO (the thin line in Figure 1), EP has greater power, a normal distribution of annual deviations and invariant properties independent of spring phases. These characteristics are important for interspecific comparisons and statistical inference.

The EP index is based solely on temperature data because, in boreal climates, the heat deficit limits biological processes, determines seasonality and is the cause of seasonal migrations. In the continental climate of Siberia, this deficit is exacerbated. Many researchers have noted the predominant influence of temperature on the timing of spring migration in the temperate zone (Cohen et al., 2018;

Gordo, 2007; Lehikoinen et al., 2004; Lehikoinen & Sparks, 2010). Where seasonality is determined by precipitation, the EP index should obviously reflect its amount. In boreal climates, moisture is always sufficient, but snow depth could be an additional clarification, as some of the accumulated heat is expended on snowmelt. However, the accuracy of realistic models likely depends more on the quality of arrival observations.

The EP index is not reducible to temperature dependence: It biologically adequately reflects the exponential growth (or degradation) of natural objects with a linear increase in temperature, giving less weight to past processes and emphasizing recent ones, the development of which becomes autonomous and will influence the future. For this reason, the main property of this index is high autocorrelation (Figure 2c). It contains reliable information about the future development of spring, including the timing of summer food abundance. The same is likely true for spatial autocorrelation (Koenig, 1999), which allows migrants to assess conditions along the route (Gordo, 2007; Tøttrup et al., 2010). The EP index made it possible here to separate and correctly assess effects having different time scales: a long-term phenological trend, on the one hand, and daily weather, on the other hand.

4.3 | The general reaction to the strength of a factor

Visser and Both (2005) pointed out the need to find a general measure of how much a species should shift its phenology to assess whether the shift is sufficient or a risk of a mismatch with peak abundance of its prey is possible. For migratory birds whose numbers are limited in their winter range, food abundance in the breeding range may be excessive (Ricklefs, 1980), and climate warming may increase this excess. Therefore, it appears that a more achievable and prioritized task is to estimate the change in migration timing relative to EP, which is fully reflected by regression on EP components on three time scales. Such a criterion will allow researchers to objectively compare shifts in consumer timing and food resource estimates from independent sources, as well as compare different points in the range or moments of the annual cycle within a species.

Currently, despite the abundance of data, even simpler comparisons are difficult. The magnitude of phenological responses can vary between regions (Both & te Marvelde, 2007; Knudsen et al., 2011; Rubolini et al., 2007) and over time (Lehikoinen et al., 2004), generally reflecting differences in the intensity of warming. Unfortunately, authors often either do not specify the magnitude of the effect or provide a generalized estimate, ignoring seasonal differences (Lehikoinen & Sparks, 2010; Cohen et al., 2018, but see Youngflesh et al., 2021). Estimates of a shift of arrival dates from meta-analyses (Bitterlin & Van Buskirk, 2014; Lehikoinen et al., 2004; Lehikoinen & Sparks, 2010; Rubolini et al., 2007; Usui et al., 2017) would seem to converge to a common level, but their results vary widely, from –3.7 to –1.5 days per decade, and weaken in more recent studies, despite increasing global warming (Hurrell & Trenberth, 2010). The slope

of the annual response (the reaction norm) has received less attention, but existing average estimates also vary widely: from -2.90 to -0.93 days per degree (Lehikoinen et al., 2004; Marra et al., 2005; Usui et al., 2017; Van Buskirk et al., 2012), thereby falling outside each other's confidence intervals. Our regional results of -0.91 days per degree between years and -0.86 days per decade (i.e. -1.44 days per degree of warming) fall outside this range, although the reliability of the estimates is not lower than in the mentioned meta-analyses.

There are several methodological and geographic explanations for our 'low' absolute values. The methodological explanations are not new but remain relevant. (i) The long-term dependence tends to flatten out with increasing time-series length (Cohen et al., 2018; Lehikoinen et al., 2004; Usui et al., 2017). (ii) The long-term warming trend is correlated with annual temperature anomalies that are an order of magnitude larger, so statistical separation of these effects is required for a correct assessment (Lehikoinen et al., 2004; Lindström & Forchhammer, 2010; Møller & Merilä, 2004). (iii) The assessment of responses to climate change depends on the choice of variables and the form of their presentation (Gordo, 2007; Lehikoinen et al., 2004; Møller & Merilä, 2004), and a biologically sound choice should change the balance between long-term and annual responses in favour of the annual effect.

Geographically, metadata are strongly biased towards regions with a maritime climate (see maps in Gordo, 2007; Usui et al., 2017; Cohen et al., 2018). First, here, populations of many migratory species are able to become partially sedentary with warming. They respond to climate non-linearly, with some probability that the arrival date becomes meaningless. For example, in a study spanning 30 years in Lithuania (Lehikoinen et al., 2004), 19 of 56 species shifted their FAD by more than a month. In a continental climate, this is unlikely due to the sharp contrast between adaptations to the sedentary and migratory lifestyle. The second and main difference is as follows: Each Celsius degree of warming advances the spring phase several days further in a maritime climate than in a continental climate. For example, the difference between Great Britain and Finland reaches three times (nearly 20 and 7 days per degree, respectively). In our continental region, the speed of spring onset is even greater (Figure 2a). Consequently, the trend and deviation expressed in days (per year or per degree)—both in the environment and in the responses of the organisms—are consistently reduced with increasing continentality and do not reflect the actual situation. For these reasons, the estimates in days are not informative for geographic comparison. An ecologically meaningful metric should reflect the extent of compensation of a factor in proportion to its strength in the environment.

Meta-analyses often use a standardized model as an estimate of the robustness of factor effects. While the simple model compares the response with the exposure, the standardized model compares the response with other responses. It accounts only for sensitivity (the correlation as the ability of organisms to distinguish between treatments) but does not account for the magnitude of the response. Our data demonstrate high robustness of the response to environmental phenology across three scales compared to simple temperature indicators (Gienapp et al., 2007). The long-term response varies

greatly between species in sensitivity and is inferior to the annual response since, at low impact strengths, stochastic fluctuations that do not correlate with the impact predominate in many species.

4.4 | How much is enough?

Assuming that the response is proportional to the impact, we estimate that the long-term shift in migration timing compensates for warming by 42%. Over 49 years, the onset of spring has shifted by 9.6 days, and arrival dates have shifted by an average of 4.0 days, meaning that they remain closer to the old date than to the new date, which maintains the same conditions. Annual deviations compensate for environmental fluctuations even less, by 27%, that is, if spring arrives 8 days earlier than usual, birds arrive 2 days earlier. In other words, migrants rely more on endogenous timing control than exogenous control. They change the annual arrival date only by one-fourth of the change in environmental phenology, while by three-fourths, they follow the average calendar dates, which are determined by the length of the day. Youngflesh et al. (2021) obtained similar results for North America, where arrival date variations compensate for annual plant phenology variations by an average of 13%, with an increase from 0% in Florida to 27% at 60°N.

Comparison of species (Table 1) showed that, as the impact increases, the amplitude of the annual phenological response remains similar between species and may therefore be close to the plasticity limit. Under less predictable conditions, the annual dependence has a flatter slope and likely provides a basis for selection. On the contrary, the long-term shift increases with some acceleration. Consequently, the long-term response to climate warming is lagged, as it must be mediated by natural selection and/or dispersal: the response begins and gains strength several generations after warming has moved beyond annual fluctuations. In our sample, the long-term response during the observation period is on average more than twice the annual response, consistent with the genetic variation in the trait. If a delay in the long-term response occurs, then compensation for warming should increase over time, even without further increases in impact.

The daily effect of the weather, expressed as an increase or decrease in current temperature, causes a significant but weak response. The unique role of weather is in creating conditions for a migration surge (Alerstam, 1993). Weather can further accelerate or delay the decision depending on internal stimuli and food availability (Nilsson et al., 2013), but it cannot significantly influence arrival timing without taking into account environmental phenology.

Aligning breeding with the seasonal peak in food abundance increases fitness, and the timing of arrival should be consistent with this objective (Both & te Marvelde, 2007). However, the annual compensatory response deviates from the mean date only by $SD = 2$ days, which may seem insufficient. At the same time, if the objective is to match the future phenology of the breeding season, the response to current phenology should not be stronger than the autocorrelation in the environment: following a deviation makes sense for a migrant if the deviation lasts long enough. Our estimate (Figure 2c) indicates

that the (sign of) phenological deviation in the environment will persist with 95% probability for a month after arrival, but its magnitude will decrease several times. The ability to assess the phenology of the environment should persist after arrival, which will provide the opportunity to adjust the prediction later by shifting the onset of clutch laying and extending it until hatching. Thus, the compensation of one-fourth is close to optimal to meet breeding conditions and allows avoiding unnecessary risks.

Direct evidence for the microevolution of migration timing has recently been obtained (Helm et al., 2019; Moiron et al., 2024). In the latter case, timing shifted by 5% per year, that is, over 20 years, by an amount comparable to the annual deviation due to phenotypic plasticity. In our case (Table 2), the annual shift in the reaction norm averaged 4.3% of the standard deviation of the annual response across 95 species, and over the years of observation, it exceeded it by 2.13 times. Such an excess is impossible due to phenotypic plasticity and suggests a genetic basis.

4.5 | Phenological navigation

Based on our research, we propose a framework that a migrant should use as a 'phenological compass' to assess its phenological position and adjust it to the current spring conditions (Figure 5). While in a stopover, it perceives two material signals suitable for reading: the calendar date (based on the length of the day) and the phenology of the environment (based on the surrounding). Using these, it assesses the situation in terms of 'late' or 'early', and waits if it is early, or makes a migratory leap if it is late. The boundary between 'late' and 'early' is determined by the isoline of phenological tolerance to deviations in timing and conditions (thin dotted line options in Figure 5).

The research task is to determine this boundary based on the timing of migration through the observation site in different years. Day length and environmental phenology are interrelated variables, since each date (i.e. day length) corresponds to a specific phenology value. A migrant can select only one variable or the ratio between their deviations. In long-term observations, day length and phenology behave as independent variables, so their relationship will then be expressed by the regression slope, which we call compensation, since the abscissa measures the effect and the ordinate measures the response. Several consequences follow from this understanding of phenological navigation.

1. The migrant position in the photoperiod and environmental phenology coordinates is uniquely determined by the observation date and current phenology conditions. Using the day length as a regressor in models explaining the arrival date is redundant.
2. Under the described continental conditions, spring processes occur rapidly and with great intensity. The same processes in a temperate maritime climate proceed much more slowly and last longer. Accordingly, the oblivion rate decreases, and an

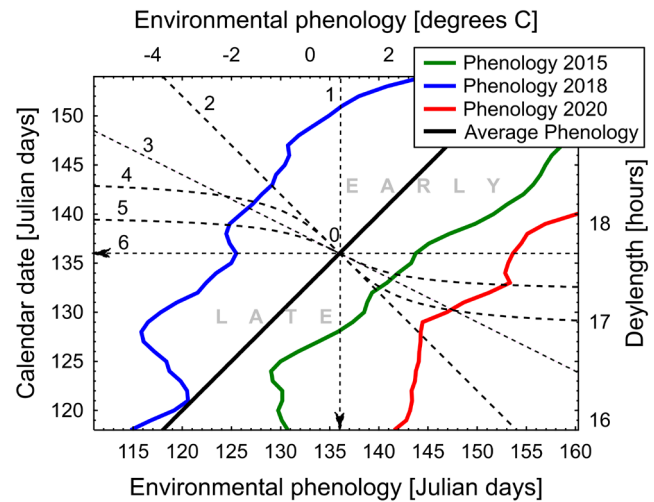


FIGURE 5 Variations of the migrant's response to environmental phenology and daylength in its own coordinate system at the observation site. In year with average phenology, environmental conditions change linearly in accordance with calendar dates (black line). The migrant adheres to point 0, where the optimal phenology for it (0.7°C) coincides with the calendar (daylength 17 h 40 min). In some years, reality deviates significantly from the norm and forces the migrant to choose a position on the coloured line far from the optimum for both parameters, through migratory bursts or waiting at stops. Depending on species preferences, the migrant adheres to the intersection with one of the dotted lines. Line 1 maintains the optimal environment, line 6 maintains the optimal daylength, line 2 maintains an equal deviation for both parameters and line 3 prioritizes daylength. A phenological anomaly can generate a false signal and cause untimely migration, so deviations from optimal day length may be limited to a certain 'light corridor'. In this case, a position on lines 4 or 5, asymptotically bounded by a wide or narrow corridor, is more likely.

environmental phenology index with a smaller exponential coefficient should better explain phenological processes. A long-memory signal is suitable for longer range forecasts.

3. Interannual variations in arrival dates, to a first approximation, are inversely linearly related to environmental phenology: the warmer, the earlier. However, winter thaws do not induce migration and prolonged springs do not cancel it. Consequently, photoperiodic control determines the range of variations in arrival dates, and therefore, the relationship has a sigmoidal shape, for example, $FAD \sim A \sqrt{1+A^2}^{-1}$ (Figure 5, lines 4 and 5). Indeed, this model significantly improves the explanation of our data ($\Delta AIC = 29.8$). Compared to the general model (Table 2), it predicts a 1.5-fold steeper slope for the annual dependence for small and medium impacts. For strong impacts, the response deviation does not exceed ± 4 days on average.

5 | CONCLUSIONS

We demonstrate that EP is more effective, both theoretically and practically, than other known methods for predicting migration

timing. This approach can be recommended for use in combination with other methods (measuring conditions precisely on the day of arrival, identifying three time scales and separating sensitivity and responsiveness). Its effectiveness comes from the fact that EP reflects the accumulation of climatic information important for a variety of ongoing processes that determine future foraging conditions.

Central Siberian migrant populations change their arrival dates less than is known in other regions, despite higher rates of warming in Siberia. This difference is due to the continental climate and pronounced seasonality. A more adequate measure of the response to warming may be the compensation level: the response-to-impact ratio. We showed that EP explains a significant portion of the variation in FAD across three scales, but the FAD response is far from completely compensating for these effects. Reasons for this include the limited range of phenological prediction, the limit of the reaction norm and life-history priorities. In addition to the general trends described, we discovered a number of group-specific environmental and organismal mechanisms that modify phenological responses; these deserve separate consideration elsewhere.

Despite the high stochasticity of FAD and systematic differences from the timing of the main migration wave (Rubolini et al., 2007; Tøttrup et al., 2010), we hope that our general conclusions can be extended to the timing of migration in general. They differ in many ways from previous generalizations, but are built on a robust foundation. A similar approach to analysing data from other regions is needed to test our conclusions. The concept of phenological navigation may be useful to verify the proposed hypotheses about the mechanisms of responses to climate change.

ACKNOWLEDGEMENTS

The author thanks A.I. Panaiotidi for help with organizing the work and N.V. Anzigitova, B.I. Sheftel, E.A. Kuznetsov, M.A. Tarkovsky, I.V. Rebrova, W. Forstmeier, A. Kessler, O.N. Batova, V.N. Lunevsky, E.Y. Demidova and A.A. Morkovin for participation in the observations. Shevchuk Editing Company edited English in the manuscript. A major part of the work was supported by Russian Foundation for Basic Research grants no. 11-04-01614, 15-04-08491 and 18-04-00269.

CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.msbcc2gc8> (Bourski, 2026).

ORCID

Oleg V. Bourski  <https://orcid.org/0000-0002-2483-0063>

REFERENCES

Alerstam, T. (1993). *Bird migration*. Cambridge University Press.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>

Bauer, S., McNamara, J. M., & Barta, Z. (2020). Environmental variability, reliability of information and the timing of migration. *Proceedings of the Royal Society B: Biological Sciences*, 287(1926), 20200622. <https://doi.org/10.1098/rspb.2020.0622>

Berthold, P. (1996). *Control of bird migration*. Springer Science & Business Media.

Bitterlin, L. R., & Van Buskirk, J. (2014). Ecological and life history correlates of changes in avian migration timing in response to climate change. *Climate Research*, 61(2), 109–121. <https://doi.org/10.3354/cr01238>

Bonamour, S., Chevin, L. M., Charmantier, A., & Teplitsky, C. (2019). Phenotypic plasticity in response to climate change: The importance of cue variation. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 374(1768), 20180178. <https://doi.org/10.1098/rstb.2018.0178>

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(7089), 81–83. <https://doi.org/10.1038/nature04539>

Both, C., & te Marvelde, L. (2007). Climate change and timing of avian breeding and migration throughout Europe. *Climate Research*, 35(1–2), 93–105. <https://doi.org/10.3354/cr00716>

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, 411(6835), 296–298. <https://doi.org/10.1038/35077063>

Bourski, O. V. (2026). Data from: First Arrival Dates on spring bird migration in Mirnoye, Central Siberia. Dryad Digital Repository. <https://doi.org/10.5061/dryad.msbcc2gc8>

Bridge, E. S., Kelly, J. F., Bjornen, P. E., Curry, C. M., Crawford, P. H., & Paritte, J. M. (2010). Effects of nutritional condition on spring migration: Do migrants use resource availability to keep pace with a changing world? *Journal of Experimental Biology*, 213(14), 2424–2429. <https://doi.org/10.1242/jeb.041277>

Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P., Almond, R. E., Baillie, J. E., Bomhard, B., Brown, C., Bruno, J., & Carpenter, K. E. (2010). Global biodiversity: Indicators of recent declines. *Science*, 328(5982), 1164–1168. <https://doi.org/10.1126/science.1187512>

Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecological Monographs*, 89(1), e01337. <https://doi.org/10.1002/ecm.1337>

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8(3), 224–228. <https://doi.org/10.1038/s41558-018-0067-3>

Cole, E. F., Long, P. R., Zelazowski, P., Szulkin, M., & Sheldon, B. C. (2015). Predicting bird phenology from space: Satellite-derived vegetation green-up signal uncovers spatial variation in phenological synchrony between birds and their environment. *Ecology and Evolution*, 5(21), 5057–5074. <https://doi.org/10.1002/ece3.1745>

Dale, V. R., Bolton, M., Dornelas, M., Magurran, A. E., Dennis, R., Broad, R., & Reid, J. M. (2024). Among-species variation in six decades of changing migration timings explained through ecology, life-history and local migratory abundance. *Global Change Biology*, 30(7), e17400. <https://doi.org/10.1111/gcb.17400>

Di Cecco, G. J., & Gouhier, T. C. (2018). Increased spatial and temporal autocorrelation of temperature under climate change. *Scientific Reports*, 8(1), 14850. <https://doi.org/10.1038/s41598-018-33217-0>

Emmenegger, T., Hahn, S., & Bauer, S. (2014). Individual migration timing of common nightingales is tuned with vegetation and prey phenology at breeding sites. *BMC Ecology*, 14(1), 9. <https://doi.org/10.1186/1472-6785-14-9>

Gavrillov, V. M. (2012). Fundamental energetics of birds: 1. The maximum ability of birds to change their thermal conductance and the efficiency of metabolic energy transformation into mechanical work. *Biology Bulletin*, 39(7), 569–578. <https://doi.org/10.1134/S1062359012070047>

- Gienapp, P., Hemerik, L., & Visser, M. E. (2005). A new statistical tool to predict phenology under climate change scenarios. *Global Change Biology*, 11(4), 600–606. <https://doi.org/10.1111/j.1365-2486.2005.00925.x>
- Gienapp, P., Leimu, R., & Merilä, J. (2007). Responses to climate change in avian migration time—Microevolution versus phenotypic plasticity. *Climate Research*, 35(1–2), 25–35. <https://doi.org/10.3354/cr00712>
- Goodenough, A. E., Fairhurst, S. M., Morrison, J. B., Cade, M., Morgan, P. J., & Wood, M. J. (2015). Quantifying the robustness of first arrival dates as a measure of avian migratory phenology. *Ibis*, 157(2), 384–390.
- Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, 35(1–2), 37–58. <https://doi.org/10.3354/cr00713>
- Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology*, 199(1), 39–48. <https://doi.org/10.1242/jeb.199.1.39>
- Helm, B., Van Doren, B. M., Hoffmann, D., & Hoffmann, U. (2019). Evolutionary response to climate change in migratory pied flycatchers. *Current Biology*, 29(21), 3714–3719. <https://doi.org/10.1016/j.cub.2019.08.072>
- Hurrell, J. W., & Trenberth, K. E. (2010). Climate change. In A. P. Møller, W. Fiedler, & P. Berthold (Eds.), *Effects of climate change on birds* (pp. 9–29). Oxford University Press.
- Jarošík, V., Honěk, A., Magarey, R. D., & Skuhrovec, J. (2011). Developmental database for phenology models: Related insect and mite species have similar thermal requirements. *Journal of Economic Entomology*, 104(6), 1870–1876. <https://doi.org/10.1603/ec11247>
- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., & Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86(4), 928–946. <https://doi.org/10.1111/j.1469-185X.2011.00179.x>
- Koenig, W. D. (1999). Spatial autocorrelation of ecological phenomena. *Trends in Ecology & Evolution*, 14(1), 22–26. [https://doi.org/10.1016/S0169-5347\(98\)01533-x](https://doi.org/10.1016/S0169-5347(98)01533-x)
- Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68(5), 940–950. <https://doi.org/10.1046/j.1365-2656.1999.00343.x>
- Lehikoinen, E., & Sparks, T. H. (2010). Changes in migration. In A. P. Møller, W. Fiedler, & P. Berthold (Eds.), *Effects of climate change on birds* (pp. 89–112). Oxford University Press.
- Lehikoinen, E. S. A., Sparks, T. H., & Zalakevicius, M. (2004). Arrival and departure dates. *Advances in Ecological Research*, 35, 1–31. [https://doi.org/10.1016/S0065-2504\(04\)35001-4](https://doi.org/10.1016/S0065-2504(04)35001-4)
- Lindström, J., & Forchhammer, M. C. (2010). Time-series analyses. In A. P. Møller, W. Fiedler, & P. Berthold (Eds.), *Effects of climate change on birds* (2nd ed., pp. 57–66). Oxford University Press.
- Marra, P. P., Francis, C. M., Mulvihill, R. S., & Moore, F. R. (2005). The influence of climate on the timing and rate of spring bird migration. *Oecologia*, 142(2), 307–315. <https://doi.org/10.1007/s00442-004-1725-x>
- Moiron, M., Teplitsky, C., Haest, B., Charmantier, A., & Bouwhuis, S. (2024). Micro-evolutionary response of spring migration timing in a wild seabird. *Evolution Letters*, 8(1), 8–17. <https://doi.org/10.1093/evlett/grad014>
- Møller, A. P., & Merilä, J. (2004). Analysis and interpretation of long-term studies investigating responses to climate change. *Advances in Ecological Research*, 35, 111–130. [https://doi.org/10.1016/S0065-2504\(04\)35006-3](https://doi.org/10.1016/S0065-2504(04)35006-3)
- Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, 105(42), 16195–16200. <https://doi.org/10.1073/pnas.0803825105>
- Newton, I. (2008). *The migration ecology of birds*. Elsevier.
- Nilsson, C., Klaassen, R. H., & Alerstam, T. (2013). Differences in speed and duration of bird migration between spring and autumn. *The American Naturalist*, 181(6), 837–845. <https://doi.org/10.1086/670335>
- Pautasso, M. (2012). Observed impacts of climate change on terrestrial birds in Europe: An overview. *Italian Journal of Zoology*, 79(2), 296–314. <https://doi.org/10.1080/11250003.2011.627381>
- R Core Team. (2022). *R version 4.2.2: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org/>
- Ricklefs, R. E. (1980). Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk*, 97(1), 38–49.
- Rubolini, D., Møller, A. P., Rainio, K., & Lehikoinen, E. (2007). Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research*, 35(1–2), 135–146. <https://doi.org/10.3354/cr00720>
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M., & Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 278(1707), 835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Schmaljohann, H. (2019). The start of migration correlates with arrival timing, and the total speed of migration increases with migration distance in migratory songbirds: A cross-continental analysis. *Movement Ecology*, 7(1), 25. <https://doi.org/10.1186/s40462-019-0169-1>
- StatSoft, Inc. (2014). STATISTICA (data analysis software system), version 12.
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241–245. <https://doi.org/10.1038/nature18608>
- Thorup, K., Tøttrup, A. P., Willemoes, M., Klaassen, R. H., Strandberg, R., Vega, M. L., Klaassen, R. H. G., Dasari, H. P., Araújo, M. B., Wikelski, M., & Rahbek, C. (2017). Resource tracking within and across continents in long-distance bird migrants. *Science Advances*, 3(1), e1601360. <https://doi.org/10.1126/sciadv.1601360>
- Tøttrup, A. P., Rainio, K., Coppack, T., Lehikoinen, E., Rahbek, C., & Thorup, K. (2010). Local temperature fine-tunes the timing of spring migration in birds. *Integrative and Comparative Biology*, 50(3), 293–304. <https://doi.org/10.1093/icb/icq028>
- Tøttrup, A. P., Thorup, K., & Rahbek, C. (2006). Patterns of change in timing of spring migration in north European songbird populations. *Journal of Avian Biology*, 37(1), 84–92. <https://doi.org/10.1111/j.0908-8857.2006.03391.x>
- Tuhkanen, S. (1980). Climatic parameters and indices in plant geography. Sv. växtgeografiska sällsk.
- Usui, T., Butchart, S. H., & Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: A phylogenetic meta-analysis. *Journal of Animal Ecology*, 86(2), 250–261. <https://doi.org/10.1111/1365-2656.12612>
- Vähätalo, A., Rainio, K., Lehikoinen, A., & Lehikoinen, E. (2004). Spring arrival of birds depends on the North Atlantic oscillation. *Journal of Avian Biology*, 35(3), 210–216. <https://doi.org/10.1111/j.0908-8857.2004.03199.x>
- Van Buskirk, J., Mulvihill, R. S., & Leberman, R. C. (2012). Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing. *Ecology and Evolution*, 2(10), 2430–2437. <https://doi.org/10.1002/ece3.367>
- Van de Pol, M., Bailey, L. D., McLean, N., Rijdsdijk, L., Lawson, C. R., & Brouwer, L. (2016). Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution*, 7(10), 1246–1257. <https://doi.org/10.1111/2041-210x.12590>

- Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2561–2569. <https://doi.org/10.1098/rspb.2005.3356>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3(6), 879–885. <https://doi.org/10.1038/s41559-019-0880-8>
- Winkler, D. W., Jørgensen, C., Both, C., Houston, A. I., McNamara, J. M., Levey, D. J., Partecke, J., Fudickar, A., Kacelnik, A., Roshier, D., & Piersma, T. (2014). Cues, strategies, and outcomes: How migrating vertebrates track environmental change. *Movement Ecology*, 2(1), 10. <https://doi.org/10.1186/2051-3933-2-10>
- Youngflesh, C., Socolar, J., Amaral, B. R., Arab, A., Guralnick, R. P., Hurlbert, A. H., LaFrance, R., Mayor, S. J., Miller, D. A. W., & Tingley, M. W. (2021). Migratory strategy drives species-level variation in bird sensitivity to vegetation green-up. *Nature Ecology & Evolution*, 5(7), 987–994. <https://doi.org/10.1038/s41559-021-01442-y>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Species attributes and estimates of the dependence on phenological variables.

Figure S1. Distribution of numbers of FAD observations by years and expected arrival dates.

How to cite this article: Bourski, O. V. (2026). Environmental phenology drives spring migration timing. *Journal of Animal Ecology*, 00, 1–13. <https://doi.org/10.1111/1365-2656.70230>