Science of the Total Environment 926 (2024) 171945

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Responses in the breeding parameters of the collared flycatcher to the changing climate

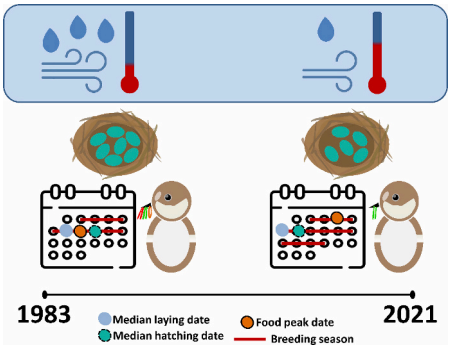
Miklós Laczi [a,b,c,*], Fanni Sarkadi [b,d,1], Márton Herényi [b,e,1], Gergely Nagy [b,f,1], Gergely Hegyi [a,b,1], Mónika Jablonszky [b,f,1], Réka Könczey [g,1], Katalin Krenhardt [b,f,1], Gábor Markó [h,1], Balázs Rosivall [b,1], Eszter Szász [b,1], Eszter Szöllősi [b,1], László Tóth [i,1], Sándor Zsebők [b,f,1], János Török [a,b]

[a] HUN-REN–ELTE–MTM Integrative Ecology Research Group, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary
[b] Behavioural Ecology Group, Department of Systematic Zoology and Ecology, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary
[c] The Barn Owl Foundation, Temesvári út 8., H-8744 Orosztony, Hungary
[d] Doctoral School of Biology, Institute of Biology, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary
[e] Department of Zoology and Ecology, Institute for Wildlife Management and Nature Conservation, Hungarian University of Agriculture and Life Sciences, Páter Károly utca 1, H-2103 Gödöllő, Hungary
[f] Evolutionary Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány út 4., H-2163 Vácrátót, Hungary
[g] Hungarian Institute for Educational Research and Development, Eszterházy Károly University, Rákóczi út 70, H-1074 Budapest, Hungary
[h] Department of Plant Pathology, Institute of Plant Protection, Hungarian University of Agriculture and Life Sciences, Ménesi út 44., H-1118 Budapest, Hungary
[i] Institute for Rural Development and Landscape Management, Faculty of Agricultural and Rural Development, Eszterházy Károly University, Mátrai út 36., H-3200 Gyöngyös, Hungary

HIGHLIGHTS

- Previous climate change studies on birds mostly explored the effects of temperature.
- We considered changes and reproductive effects of a broad range of weather variables.
- Four decades of data from a wild population were analyzed using sliding time windows.
- Temperature, precipitation and wind conditions all shift and predict reproduction.
- Novel pathways are suggested by which climate change can threaten wild populations.

GRAPHICAL ABSTRACT



* Corresponding author at: HUN-REN–ELTE–MTM Integrative Ecology Research Group, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary.
E-mail addresses: miklos.laczi@ttk.elte.hu (M. Laczi), fanni.sarkadi@ttk.elte.hu (F. Sarkadi), herenyi.marton.farkas@uni-mate.hu (M. Herényi), nagy.gergely@ecolres.hu (G. Nagy), gergely.hegyi@ttk.elte.hu (G. Hegyi), jablonszky.monika@ecolres.hu (M. Jablonszky), krenhardt.katalin@ecolres.hu (K. Krenhardt), marko.gabor@uni-mate.hu (G. Markó), balazs.rosivall@ttk.elte.hu (B. Rosivall), szasz.eszter@ttk.elte.hu (E. Szász), eszter.szollosi@ttk.elte.hu (E. Szöllősi), toth.laszlo@uni-mate.hu (L. Tóth), zsebok.sandor@ecolres.hu (S. Zsebők), janos.torok@ttk.elte.hu (J. Török).
[1] These authors share second authorship.

https://doi.org/10.1016/j.scitotenv.2024.171945
Received 27 November 2023; Received in revised form 6 March 2024; Accepted 22 March 2024
Available online 24 March 2024

ARTICLE INFO

Editor: Anastasia Paschalidou

Keywords:
Migratory bird
Weather change
Breeding phenology
Temperature
Precipitation
Wind speed

ABSTRACT

Global climate change involves various aspects of climate, including precipitation changes and declining surface wind speeds, but studies investigating biological responses have often focused on the impacts of rising temperatures. Additionally, related long-term studies on bird reproduction tend to concentrate on breeding onset, even though other aspects of breeding could also be sensitive to the diverse weather aspects. This study aimed to explore how multiple aspects of breeding (breeding onset, hatching delay, breeding season length, clutch size, fledgling number) were associated with different weather components. We used an almost four-decade-long dataset to investigate the various aspects of breeding parameters of a collared flycatcher (*Ficedula albicollis*) population in the Carpathian Basin. Analyses revealed some considerable associations, for example, breeding seasons lengthened with the amount of daily precipitation, and clutch size increased with the number of cool days. Parallel and opposing changes in the correlated pairs of breeding and weather parameters were also observed. The phenological mismatch between prey availability and breeding time slightly increased, and fledgling number strongly decreased with increasing mistiming. Our results highlighted the intricate interplay between climate change and the reproductive patterns of migratory birds, emphasizing the need for a holistic approach. The results also underscored the potential threats posed by climate change to bird populations and the importance of adaptive responses to changing environmental conditions.

1. Introduction

Global warming causes systematic changes and anomalies in local weather events (Easterling et al., 2000; Stott, 2016), globally altering the patterns of natural climate (Timmermann et al., 1999; Houghton, 2009). However, climate change exhibits spatial differences (Walther et al., 2002; Bathiany et al., 2018) even within a smaller geographical region (Khan et al., 2019; Szabó et al., 2019). As local-scale meteorological variables can change more rapidly and more irregularly than large-scale events, one might presume that they are less predictive of the long-term biological changes in response to the changing climate (Hallett et al., 2004), but this is not necessarily true (Knape and de Valpine, 2011). Numerous studies attempting to explore the far-reaching ecological consequences of climate change have often focused on examining how locally rising temperatures affect phenological synchronization between different trophic levels (Thackeray et al., 2010; Nakazawa and Doi, 2012) and the timing of seasonal life-cycle activities (Gordo and Sanz, 2009; Richardson et al., 2018), and these are indeed key components of the biological responses.

There are many studies of weather effects focusing on birds (see, e.g. Dunn and Møller, 2019) because birds are relatively easy to observe and they are susceptible to changes in their environment. Hence, their population distributions, migratory patterns, and breeding behaviours can provide valuable insights into how climate change is impacting wildlife. Concerning long-term changes, a growing mountain of evidence supports that warming over time may impact the actual timing of arrival dates at the breeding grounds and the onset of reproduction (e.g. Crick et al., 1997; Carey, 2009; Møller, 2013a), as well as cause disruption in the synchronization of breeding and the peak availability of prey (Stenseth and Mysterud, 2002; Sanz et al., 2003).

However, climate change manifests not only in an increase of average temperatures but also in alterations in other aspects of weather, for example the occurrence and duration of extreme temperatures (Lorenz et al., 2019) or seasonal changes in precipitation patterns (Trenberth, 2011). Additionally, it has recently been demonstrated that average terrestrial surface wind speed also shows a long-term decrease in Europe and other regions due to increasing temperatures (Wu et al., 2018; Zha et al., 2021). There is a growing number of studies on the impacts of these other aspects of climate change on long-term shifts in the reproductive phenology of birds, for example, on how rainfall could be a driving force in such shifts (Rubolini et al., 2007; Senapathi et al., 2011; McDermott and DeGroote, 2016), and on how the precipitation conditions could be a driving force of other overlooked aspects of bird reproduction (short-term studies, e.g. Hidalgo Aranzamendi et al., 2019; Martin and Mouton, 2020; Smart et al., 2021; Boersma et al., 2022), but we still have relatively less knowledge about this in a global change context. Similarly, wind conditions are even less often taken into account in long-term studies of bird reproduction (Møller, 2013b).

Long-term studies on the reproduction of birds often pay attention to the breeding onset. Fortunately, more and more studies are investigating other principal aspects of breeding phenology previously usually out of focus, such as, incubation time (Cresswell and McCleery, 2003; Matthysen et al., 2011; Kwon et al., 2018), seasonal distribution of clutches (Solís et al., 2023), breeding season length (Jankowiak et al., 2014; Halupka and Halupka, 2017; Hällfors et al., 2020; Halupka et al., 2021; Mingozzi et al., 2022; Murphy et al., 2022), and reproductive output (e.g. clutch size, number of fledglings) (Kwon et al., 2018; Laczi et al., 2019; Halupka et al., 2020; Murphy et al., 2022). It is important to pay more attention to these less studied breeding parameters, and analyze multiple parameters in parallel. If we look at one breeding parameter only, for example, the onset of reproduction (see Both et al., 2004), in the absence of a phenological shift in this parameter, we may erroneously conclude the complete lack of biological responses, though another breeding parameter may have changed significantly.

Previously, a comparative study described that breeding phenology in terms of breeding onset had advanced in the face of rising temperatures in a Hungarian population of the collared flycatcher (*Ficedula albicollis*) (Samplonius et al., 2018). Similarly, it has been revealed that the timing of the peak abundance of phytophagous caterpillars had shifted back by almost a week per decade, at the very same location (Laczi et al., 2019). These are one of the main diet sources of nestlings (Chaplyhina et al., 2022), and it have been found that caterpillar biomass influenced the reproductive success (Veen et al., 2010). In line with these, it is also known that across the area of Hungary, the degree of dryness and the spring temperatures have markedly increased during the last century (Breuer et al., 2017; Izsák and Szentimrey, 2020), and the higher altitudes, including the region where the studied collared flycatchers breed, are more strongly affected (Breuer et al., 2017). In light of these previous findings, we aimed to explore the responses of collared flycatchers to climate change. For this, we used breeding and weather data from an almost four-decade-long period to investigate how different aspects of local weather parameters covary with certain population-level breeding characteristics. More specifically, our central goal was the investigation of the year-to-year variations of breeding season length, deviation from the expected hatching date, and primary reproductive investment in relation to different measures of temperature, precipitation, and wind speed. Analyses investigating the responses of population-level breeding traits to weather conditions have typically used a time window of meteorological parameters selected in a quasi-arbitrary way (e.g. Both et al., 2004; Goodenough et al., 2011; Laczi et al., 2019), but this method may fail to capture variation in biological responses to changing climate because the arbitrary period may be too short, too long or misplaced. To assess the connection of breeding biology with weather, we performed a sliding window approach (van de

Pol et al., 2016), designed to overcome the latter limitation.

2. Materials and methods

2.1. Study site and study species

We collected data between 1982 and 2021 in the Pilis-Visegrádi Mountains, Duna-Ipoly National Park, Hungary (centered at 47.725 N 19.006E). Our study plots where we collected the present data are situated at 550 m above sea level. The study sites are covered by oak-dominated (*Quercus cerris*, *Q. petraea*) deciduous forests (trees were approximately 50 years old in 1981). The B-type wooden nest boxes are arranged in a grid system with an average distance of 30.7 m, and are principally used by the collared flycatcher and to a lesser degree by great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). The collared flycatcher is a long-distance migratory species (Cramp and Perrins, 1993). The first birds arrive in early to mid-April. Females mostly lay 4–8 eggs (but typically 5–7) on consecutive days, one egg per day, and laying gaps are extremely rare in our population. Females raise only one brood within a reproductive season, but re-nesting events are possible in the case of previous failures. The global abundance estimate of mature individuals of this species is relatively high (Callaghan et al., 2021). Based on the standardized data collection of the Hungarian Monitoring of Common Birds (MMM) (Szép and Gibbons, 2000), the number of breeding collared flycatchers specifically in Hungary was estimated at 70–150 thousand pairs in the 1990s and 2005–2007, and 75–80 thousand pairs in 2014–2018, which could be indicative, and local trends suggest a regionally mixed picture of abundance changes (Szép et al., 2022). Importantly, the country was covered to different extents in different survey periods (Szép et al., 2012), and these estimates could be uncertain due to methodological and logistical constraints (Bibby et al., 2000; Pomeroy et al., 2018).

2.2. Breeding data

We captured breeding birds when their nestlings were already endothermic, and individually marked them using numbered rings (Aranea, Poland). From the start of nest-building, we checked nest-box plots regularly (typically every five days) in order to determine the laying date of the first egg and the hatching date of the first nestling in each nest. Using these data, we calculated a number of population-level variables for each year that we expected to be affected by weather. On this basis, taking into account the length of the study period, 37 yearly data points were included in the analyses (except for phenological mismatch and fledgling number, see later). To describe the inter-annual shift of the breeding season, we calculated the annual median laying date, which was determined as the median value of the laying dates of the first eggs in each clutch (expressed relative to 1 April). We used the median instead of the arithmetic mean to estimate the central tendency, as the within-year distribution of laying dates was positively skewed. We defined breeding season length as the difference (in number of days) between the 10th and 90th percentiles of individual birds' laying dates. We used these values instead of the very first and last breeding events, as the timing of the first and last events may be very stochastic. Because environmental conditions could cause change in length of the incubation time (our personal observations), we calculated the mean deviation (in days) of the actual hatching date from the expected hatching date (hereafter the hatching deviation). For this purpose, we used only nests with 5–7 eggs, as these are the most typical clutch sizes in our population (78.0 % of clutches) and because we have exact information on the expected hatching timing only regarding these clutch sizes. Namely, expected hatching timing is 12 days after the last egg was laid in 5- or 6-egg clutches and 12 days after the 6th egg was laid in clutches with 7 eggs (Rosivall et al., 2005). Based on this, we calculated the expected hatching date by adding 16 days to the laying date in 5-egg clutches and 17 days in the other two cases. This way we also controlled for the effect of clutch size on incubation time. Furthermore, we analyzed the annual mean clutch size using only nests with successful hatching and no signs of predation on eggs. Finally, we also considered the annual mean fledgling number, i.e. the number of nestlings per nest that reached the fledging age (13 days old). We took into account only such nests that produced at least one fledgling. The correlation matrix of the above-described breeding parameters analyzed in connection with meteorological parameters is detailed in the supplementary data (Table S1). All breeding variables were normally distributed.

As there was a correlation between median hatching date and caterpillar peak date ($r = 0.77$, $p < 0.001$, $N = 34$), we also aimed to investigate the temporal trend through the study period in phenological advancement relative to food availability as a measure of mistiming. Additionally, we also explored whether the reproductive output, i.e. the fledgling number, correlated with the mistiming, as food availability may have a strong influence on fledging success (see, e.g. Vatka et al., 2014). Therefore, we used the relative hatching date as a measure of phenological mismatch, i.e. the median of hatching date delays from the caterpillar peak date, during 1983 and 2018 (as from the last three years of the study period we do not have the exact caterpillar peak data yet). For this, we collected caterpillar frass during the reproductive season, every five days on average (Smith et al., 2011), starting from bud-burst of trees, covering the breeding period of the collared flycatchers. Each collector was placed at standard locations (8–10/year; each 0.25 m^2 square textile canvas, suspended next to the tree trunk, at an average height of 0.5 m above the ground). Frass samples were weighed to the nearest 0.001 g, controlled for collection intervals. Maximum caterpillar availability usually took the form of a peak or plateau. We defined caterpillar peak date as the date half-way between the date of maximum frass mass after the largest increase and the preceding date (Verboven et al., 2001; Laczi et al., 2019).

Before we calculated the variables detailed above, we excluded data of i) the very first year of the study period as this was the establishment date of the study plots (see Both and Visser, 2005), ii) all within-year re-nesting events of the same birds or same pairs (detected by ring-number) that typically resulted from the failure of the first nest, and iii) data of birds involved in such experiments that potentially influenced their breeding schedule and the relevant breeding variables. Because of the latter, we had no data from 1985 and 1986. Furthermore, in the case of the fledgling number, we had to exclude a further 17 years because of nestling-related predation outbreaks (1989–1991, 2004–2005, 2009–2011, 2020), and the high number of experiments specifically affecting the fledgling number (1987–1993, 1997, 2001–2005, 2009–2010). In addition to the scarcity of data from these years, these data could represent a non-random sample of the population, as predation events and experiments followed distinct seasonal patterns. We have to note that, due to the reduced sample sizes, the results of the fledgling number should be treated with caution. As the analyses were based on data aggregated at an annual level, we were unable to account for repeated observations from the same individual(s) across years. However, as calculated with the 'rptR' R package (Stoffel et al., 2017), the individuals showed low repeatability in their breeding parameters, suggesting that using their repeats would not bias the analyses (see the Results). In addition, two breeding bouts made by the same pair of individuals are exceedingly rare, so pair-level pseudoreplication is absent from our data.

2.3. Statistical analyses

To give a brief preliminary overview, the following analyses had three different phases: 1) selection of the most appropriate time window for each meteorological variable in terms of correlation with breeding parameters; 2) analyzing breeding (response) variables in relation to combinations of the verified meteorological (predictor) variables; 3) looking for changes over the years in the predictor and response variables. The analyses were performed in R 4.2.1 (R Core Team, 2022).

2.4. Meteorological parameters and sliding window analyses

We acquired weather data from the *E*-OBS daily gridded dataset v25.0e with 0.25°x0.25° spatial resolution (Haylock et al., 2008; Cornes et al., 2018) at the ECAD website (European Climate Assessment and Dataset, http://www.ecad.eu), using the 'ncdf4' package (Pierce, 2021). From the dataset, we separated the gridcell representing our study area by averaging the respective daily meteorological values extracted from the four combinations of the relevant coordinates (47.649 N, 47.749 N, 18.949 E, 19.049 E). We extracted the following four parameters at daily resolution: maximum temperature (°C), minimum temperature (°C), precipitation sum (mm), and average wind speed (m/s).

At first, to find out whether there is any link between the weather and breeding variables, we performed sliding window analyses using the 'climwin' package (Bailey and van de Pol, 2016; van de Pol et al., 2016). This method compares models fitting the same meteorological variable with different time windows, representing different models. These models are compared to each other by Akaike's information criterion corrected for small sample sizes (AICc, see Burnham and Anderson, 2004). We could identify the best time window for a given meteorological variable (see below) as the one giving the best model, i.e. the model with the lowest negative ΔAICc value, based on the difference between the AICc value of a given model and the baseline model, which was a null model with an intercept but without entering any fixed effect in our case. Using this approach, we extracted climate windows that explain the most variation in the breeding variables. Furthermore, because the sliding window approach is characterized by an enormous number of tests, we checked for Type 1 error in each best model by running ten randomizations of the given meteorological variable for the respective dataset in order to assess the probability of selecting the same top model by chance (van de Pol et al., 2016). We considered the best model verified if it significantly differed ($\alpha = 0.05$) from the output of the randomized analyses based on the highly sensitive Pc metric developed specifically for such comparisons with a low number of randomizations (van de Pol et al., 2016). Pc values represent the probability that the best climate signal is a false positive. For very short time windows, there could be a higher probability of false-positive detections (see Capilla-Lasheras et al., 2021), so we considered sliding windows only at least of >7 day-length. With this criterion, and considering both the width of the investigated time interval and the resolution (see below), the procedure consists of 2145 tests per dependent variable.

We used the sliding window approach with linear models, allowing linear effects between the given meteorological variable (predictor variable) and the breeding variable (response variable). More specifically, we searched for 'absolute time windows' (i.e. the same window for all years) as we were interested in making the years comparable, and 'relative time windows' (i.e. different windows allowed for each year) are not suitable for this purpose. The reference date was May 31, and we searched time windows going back 70 days. We chose this time interval because the earliest observation of collared flycatchers during the study period was dated April 4, and we added a few days backwards as the detection of the very first arrivals may be very uncertain. We ran 'climwin' in daily resolution with respect to changing time window lengths in sliding steps.

For each of the raw meteorological parameters, we considered different derived variables. Other than the mean values (i.e. mean daily maximum temperature, mean daily minimum temperature, mean daily precipitation sum, and mean daily average wind speed), we also considered that the number of days below or above a particular threshold of a given meteorological parameter could be a limiting factor shaping year-to-year breeding patterns. In these analyses, we used the 'binary' function in 'climwin', which assigns each day a 0 or 1, depending on whether the value of the meteorological parameter for that day is above or below the threshold. We considered the number of cool days (if the daily maximum temperature did not reach a certain threshold, considering each integer temperature from 15 to 20 °C as threshold), the number of cold days (if the daily minimum temperature did not reach a certain threshold, with each integer temperature between 0 and 5 °C as threshold), the number of rainy days (if the daily precipitation sum was larger than each integer precipitation from 2 to 8 mm as threshold), and the number of windy days (if the daily average wind speed was >1.5 to 3.5 m/s as threshold, considering each integer and half value). Finally, we also considered the slope of the relationship between date and temperature within-season (degrees per day).

2.5. Interplays of the climatic signals

At the end of the sliding window analyses, if we found that a certain breeding variable was correlated with multiple, verified variables of the same principal axis (i.e. temperature, precipitation, wind speed) of weather (e.g. mean temperature maximum and slope of temperature minimum), we selected one 'overall best' signal for that axis of weather based on the lowest negative ΔAICc value (Lv et al., 2020), as these 'close relative' variables were highly intercorrelated (see supplementary data Table S2–3). Thereafter, in case we got 'overall best' signals from more than one different axis of weather (e.g. a rain and a wind variable) for a breeding variable, then we tested for whether a given weather signal (verified formerly by the sliding window and randomization approach) remains supported when another weather signal is taken into account, and we also tested for the potential interaction between these signals. For this purpose, using the lm() function from the R 'stats' package (R Core Team, 2022), we performed linear models (LMs) by entering each breeding variable as a response variable, and adding the meteorological variables and their one-way interactions as predictor variables. In the case of median laying date and clutch size, the predictors of the initial models also included density (breeding pairs/ha) because these parameters may be affected by density (Ahola et al., 2012; Both et al., 2000). We used backward stepwise model selection (e.g. Hegyi and Laczi, 2015). In our analyses, the inverse of the variance of each breeding variable was used as a weighting factor. We assessed the severity of collinearity of the main predictors by variance inflation factor (VIF) analyses, using the vif() function from the 'car' package (Fox and Weisberg, 2018). All VIF indices for main effects stayed below 1.46 suggesting small effects of multicollinearity on our regression coefficients. Importantly, when we repeated the statistics with detrended predictor variables, we obtained very similar results (see details in the supplementary material).

2.6. Analyses of temporal trends and phenological mismatch

Before the analyses of temporal changes, we checked our variables for temporal autocorrelation by Durbin–Watson test using the durbinWatsonTest() function from the 'car' package (Fox and Weisberg, 2018). None of the investigated breeding parameters or meteorological variables was temporally autocorrelated (all $p > 0.09$, D—W statistics were between 1.53 and 2.33).

As biological responses and weather variables often show non-linear relationships with time (e.g. Charmantier et al., 2008; Laczi et al., 2019), we performed backward stepwise polynomial regressions to analyze the relationships of breeding variables and the meteorological variables (each as response variable) resulting from the final best climate windows with year (as predictor variable, centred before analyses). Similarly to the above GLMs, the inverse of the variance of each breeding variable was used as a weighting factor. We considered second- and third-order polynomials. All model residuals were normally distributed, and showed no patterns with the independent variables, making generalized additive models (GAMs) unnecessary.

Additionally, we analyzed if the fledgling number (as a response variable) was associated with the relative hatching date (as a predictor variable), weighting the data by the inverse of the variance of the fledgling number.

These analyses were performed using the lm() function from the R

'stats' package (R Core Team, 2022).

3. Results

3.1. Data selection

According to the selection criteria, we used data from 8290 breeding events in total (see details for year-to-year sample sizes at https://doi.org/10.6084/m9.figshare.24564373). The Lessells–Boag's repeatability estimates of breeding variables were generally low (repeatability R and 95 % confidence intervals for laying date: 0.197 (0.158, 0.236) and 0.071 (0.029, 0.114); hatching deviation: 0.11 (0.066, 0.155) and 0.017 (0.00, 0.07); clutch size: 0.196 (0.158, 0.233) and 0.072 (0.03, 0.115); fledgling number: 0.054 (0.000, 0.244) and 0.002 (0.000, 0.095) in females and males, respectively). This is in concordance with findings in another population (from the Czech Republic) of this species where the breeding schedules of two consecutive years were not correlated (Briedis et al., 2018).

3.2. Sliding window analyses

Table 1 shows the verified weather signals identified by sliding window analyses (detailed results are shown in the supplementary data, Table S4). Based on these, the median laying date was associated with a time window of the number of rainy days (>2 mm), the number of cool days (<17 °C), the mean temperature maximum and minimum, the mean wind speed, and the number of windy days (>2 m/s). The breeding season length was associated with the number of rainy days (>7 mm), the mean daily rain sum, and the slope of temperature maximum. The hatching deviation was associated with the number of rainy days (>7 mm), the number of cool days (<16 °C), the mean temperature maximum and minimum, the slope of temperature maximum and minimum. The clutch size was associated with the slope of temperature maximum, and the number of cool days (<20 °C). Finally, the fledgling number was not associated with the local weather variables.

3.3. Interplays of the climatic signals

The LMs (results are detailed in Table 2) revealed that the median laying date was delayed by an increasing number of cool days and an increasing mean wind speed (Fig. 1A-B). Breeding season length was negatively correlated with the slope of the daily maximum temperature and positively to the mean daily precipitation sum (Fig. 2A-B). Hatching deviation increased with the number of cool days and rainy days (Fig. 3A-B). Finally, clutch size was positively correlated with the number of cool days (Fig. 4A). An AIC-based model selection approach using the stepAIC function from the 'MASS' package (Venables and Ripley, 2002) also confirmed the above results obtained with backward stepwise model selection; in the case of the breeding season length, the ΔAIC is only 0.285 between the two models with or without the interaction term, hence, considering parsimony, the less complex model was preferred (see details in the supplementary data, Table S5). If we

Table 2
Relationships of density and weather parameters of the best climate windows with population-level breeding parameters in the collared flycatcher.

Response variable	Predictor variable	F(df1, df2)		Effect size R	95 % CI
Median laying date	Density	9.06 (1,35)	**	−0.46	−0.69/ −0.16
	No. cool days (<17 °C)	28.55 (1,34)	***	0.68	0.46/ 0.82
	No. rainy days (>2 mm)	1.54 (1,32)		0.21	−0.12/ 0.50
	Mean wind speed	9.19 (1,33)	**	0.47	0.17/ 0.69
	No. rainy days x no. cool days	0.84 (1,31)		−0.16	−0.46/ 0.17
	No. rainy days x wind speed	0.07 (1,32)		−0.05	−0.37/ 0.28
	Wind speed x no. cool days	0.25 (1,31)		−0.09	−0.4/ 0.24
Breeding season length	Tmax slope	32.45 (1,35)	***	−0.70	−0.83/ −0.48
	Mean daily rain sum	8.98 (1,34)	**	0.46	0.16/ 0.68
	Tmax slope x mean daily rain sum	2.10 (1,33)		−0.24	−0.53/ 0.09
Hatching deviation	No. cool days (<16 °C)	21.19 (1,34)	***	0.62	0.37/ 0.79
	No. rainy days (>7 mm)	24.69 (1,35)	*	0.65	0.41/ 0.80
	No. rainy days x no. cool days	0.28 (1,33)		0.09	−0.24/ 0.40
Clutch size	Density	0.06 (1,34)		0.04	−0.29/ 0.36
	No. cool days (<20 °C)	23.36 (1,35)	***	0.63	0.39/ 0.79

CI refers to lower/upper boundaries of confidence interval.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$

Table 1
Weather variables predicting year-to-year variation in population-level breeding parameters of the collared flycatcher. These weather signals as best climate windows were obtained from sliding window analyses. Best windows, selected as best models based on ΔAICc values, explain the most variance in the response variables and used for statistical analyses. Due to the day-to-day temporal autocorrelations of weather, they represent the usually wider window (with less explained variance) where the weather is presumably actually acting. The latter can be assessed, for example, using median windows (see details in Bailey and van de Pol, 2016, van de Pol et al., 2016). Additionally, the % refers to what percent of models fall within the 95 % confidence interval of total models, higher values may be possible if there is a stronger temporal autocorrelation for the given meteorological parameter within the allowed time frame for sliding windows.

Response variable	Predictor variable	Pc	ΔAICc	Best window	Median window	%
Median laying date	No. rainy days (>2 mm)	0.033	−10.4	24/03–25/04	02/04–07/05	55 %
	No. cool days (<17 °C)	0.00061	−28.62	30/03–30/05	30/03–19/05	20 %
	Mean temperature maximum	0.00071	−25.34	30/03–30/04	30/03–16/05	19 %
	Mean temperature minimum	0.0013	−20.25	19/05–29/05	09/04–26/05	24 %
	Mean wind speed	0.0063	−14.8	02/05–11/05	23/04–22/05	39 %
Breeding season length	Mean daily rain sum	0.0019	−14.36	21/05–31/05	29/04–23/05	32 %
	Slope of temperature maximum	0.00016	−19.74	07/04–30/05	10/04–23/05	8 %
Hatching deviation	No. rainy days (>7 mm)	0.0040	−14.02	06/05–13/05	20/04–24/05	31 %
	No. cool days (<16 °C)	0.00021	−27.52	27/04–31/05	29/04–26/05	9 %
	Mean temperature maximum	0.0013	−17.81	27/04–29/05	27/04–22/05	20 %
	Slope of temperature maximum	0.020	−10.12	05/04–11/05	04/04–11/05	45 %
	Mean temperature minimum	0.0051	−13.21	27/04–29/05	26/04–21/05	31 %
	Slope of temperature minimum	0.011	−10.61	09/04–16/04	03/04–11/05	38 %
Clutch size	No. cool days (<20 °C)	0.004	−13.42	22/03–10/05	05/04–07/05	33 %

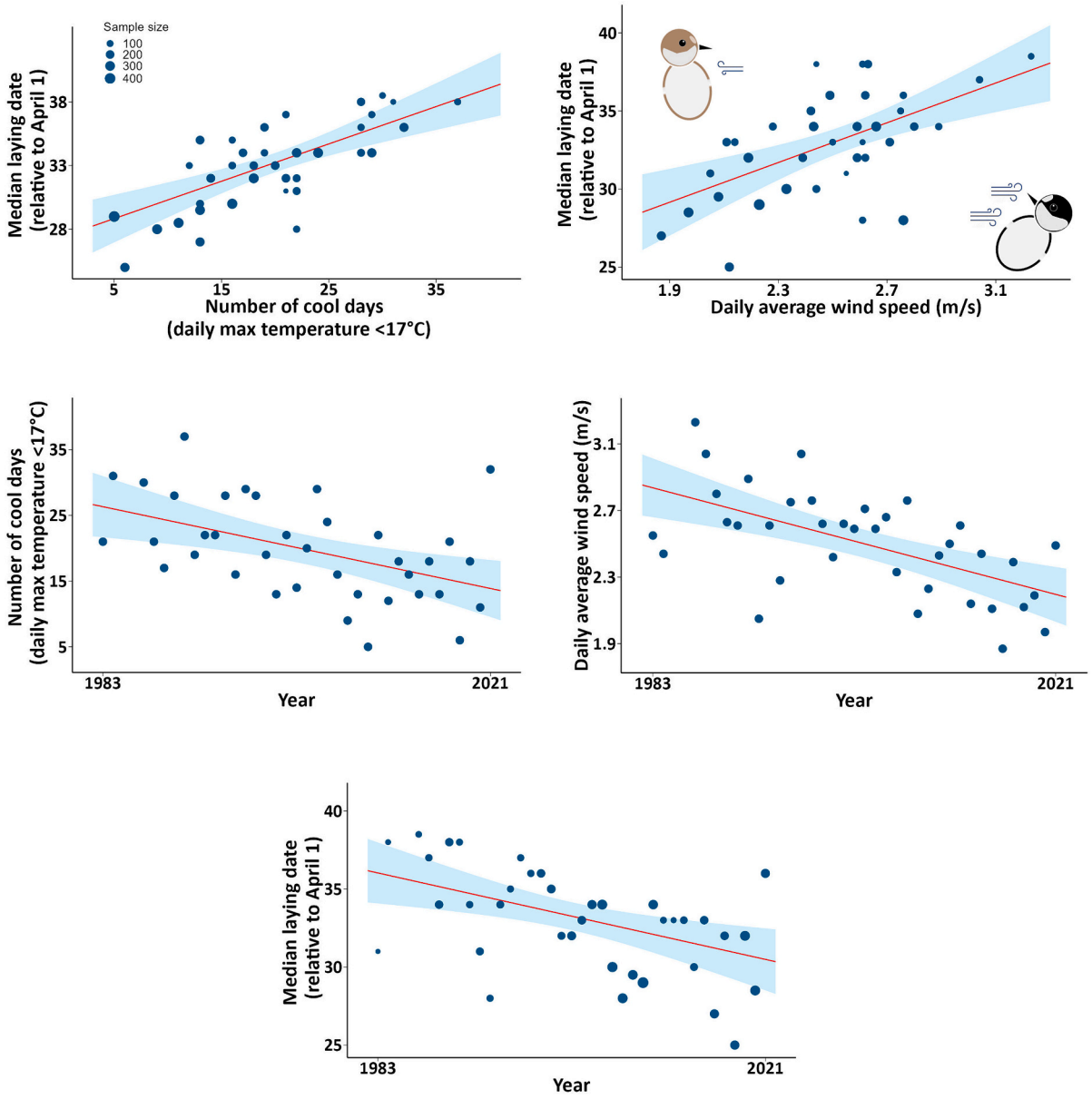


Fig. 1. Correlations between the collared flycatcher median laying date and local weather parameters, and their temporal changes. The number of cool days and the daily average wind speed were extracted from local weather data using sliding window approach. Dot size indicates the number of data points on which the annual value of the median laying date for a given year is based (N_{total} = 7286).

performed the analyses on data without taking into consideration the inverse of the variance as a weighting factor, we got the same associations between the breeding variables and the climatic signals (detailed results are shown in the supplementary data, Table S6).

3.4. Analyses of temporal trends and phenological mismatch

Analyses of temporal trends (detailed results are presented in Table 3) showed that the median laying date advanced linearly (Fig. 1E), and in parallel, the number of cool days and the mean wind speed within the respective time window decreased (Fig. 1C-D). The breeding season length correlated with the quadratic term of year (first contracted, then became more prolonged, Fig. 2E), similarly to the mean daily precipitation sum (Fig. 2D), and the related slope of temperature maximum showed exactly the opposite pattern (Fig. 2C). Through the study period, hatching deviation changed in both linear and quadratic ways, namely, it mostly decreased, but in the last few years it started rising again (Fig. 3E), and the number of cool days showed the same pattern of correlation with the quadratic term of year (Fig. 3C). Together with this, the number of rainy days (as a significant predictor of hatching deviation) was also correlated with the quadratic term of year (Fig. 3D). Surprisingly, clutch size showed a linear negative temporal trend (Fig. 4B), and the number of cool days as a predictor of clutch size also decreased linearly (Fig. 4C). The fledgling number showed no temporal changes. The relative hatching date (i.e. the measure of phenological mismatch) showed only a non-significant linear increase through the study period (Fig. 5A). If we performed the analyses without taking into consideration the inverse of the variance as a weighting factor, we got the same results, except that the temporal change of the relative hatching date became significant (detailed results are shown in the supplementary data, Table S7). Finally, the fledgling number correlated negatively with the relative hatching date ($F = 11.55$, $df = 1,16$, $p = 0.004$, effect size $r = -0.65$, 95 % CIs = −0.86 and − 0.24).

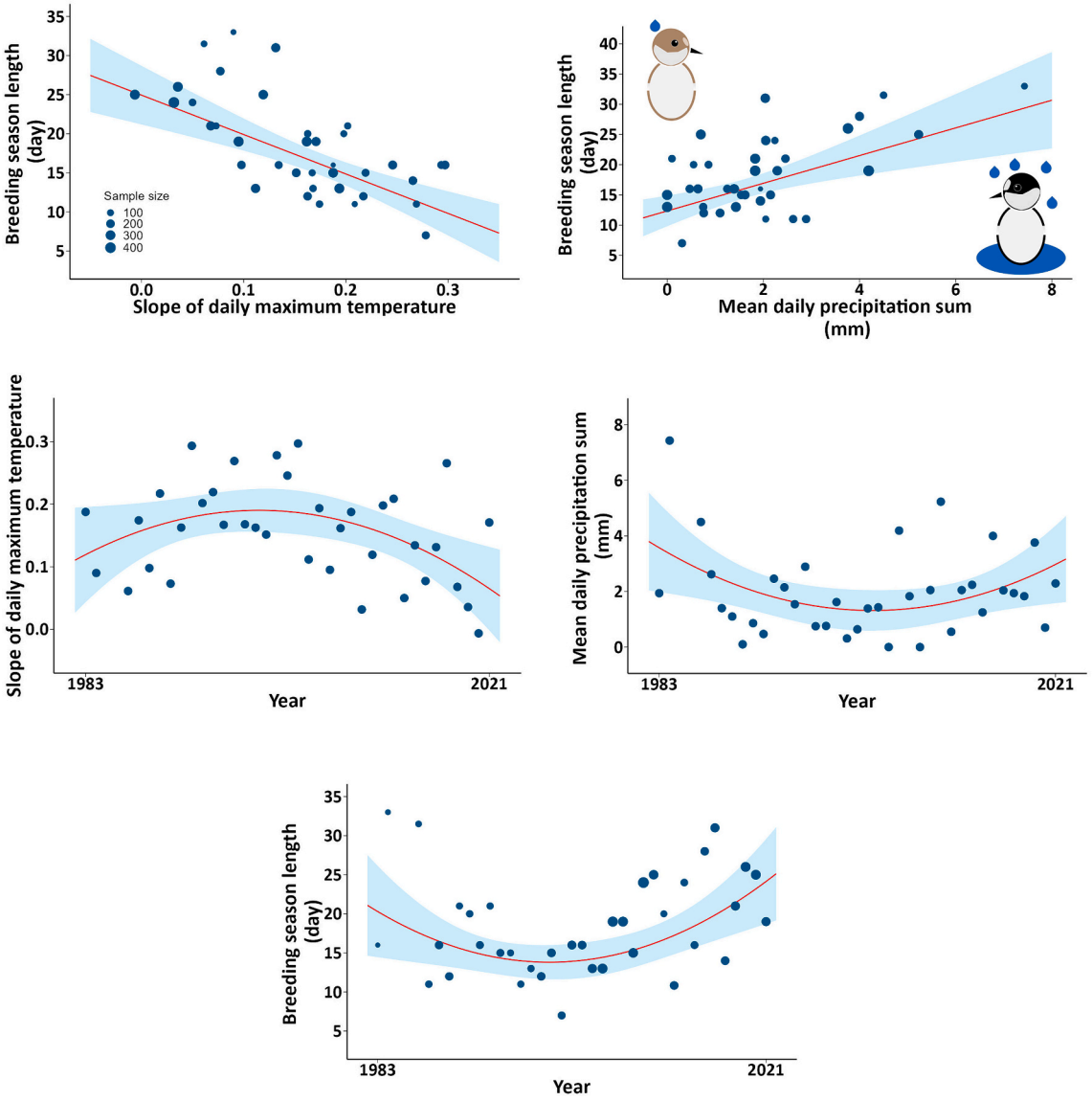


Fig. 2. Correlations between the collared flycatcher breeding season length and local weather parameters, and their temporal changes. The slope of daily maximum temperature and the mean daily precipitation sum were extracted from local weather data using sliding window approach. Dot size indicates the number of data points on which the annual value of the breeding season length for a given year is based (N_{total} = 7286).

4. Discussion

We simultaneously investigated the relationships between multiple weather parameters and multiple biological parameters in the collared flycatcher. We revealed that the median laying date was positively correlated with cool day number, and with average wind speed. It has already been confirmed that higher temperatures allow laying females to reach a physical condition that enables them to breed sooner (Slagsvold, 1976; García-Navas et al., 2008). But in addition to temperature, there are a number of other weather components, including wind speed, that can jointly influence when breeding activity may begin (Ricklefs, 1971). In adverse weather, aerial insect activity is reduced (Williams, 1961; Bryant, 1975; Peng et al., 1992), making it increasingly challenging to locate prey (Avery and Krebs, 1984), which is thought to reduce foraging efficiency (Cantar and Montgomerie, 1985). This may slow down the restoration of body condition after migration and increase foraging activity, which can result in reduced courtship activity and delayed territory establishment or nest building (Avery and Krebs, 1984; Strain and Mumme, 1988). Additionally, a higher air temperature can reduce daily energy expenditure (Tinbergen and Dietz, 1994), high wind speeds may increase thermoregulation costs (Wolf and Walsberg, 2000) and make aerial manoeuvring more difficult and costly (Shepard et al., 2019). It is important to highlight that changes in wind speed could be partly due to changes in temperatures, but changed wind conditions can themselves affect reproduction in the ways detailed above.

Shift in the median laying date may be affected not only due to weather-related food availability. Another explanation may be that the birds arrive earlier in the breeding area due to weather factors affecting migration (Marra et al., 2005; Saino et al., 2007; Tøttrup et al., 2010). In our population, however, the detection date of first arrivals remained similar over the years (1999–2021 (note that we had no data from 2008): $r = -0.06$, $p = 0.80$), but breeding onset advanced, suggesting that weather and not arrival date may be the main determinant of breeding onset.

We found that breeding season length extended with heavy rains and shortened with the magnitude of temperature increases. On one hand, this may suggest that the occurrence of rainy days may elevate the frequency of nest desertion (Wiggins et al., 1994; Enemar, 1995; Bordjan and Tome, 2014). This will result in an increase in the number of

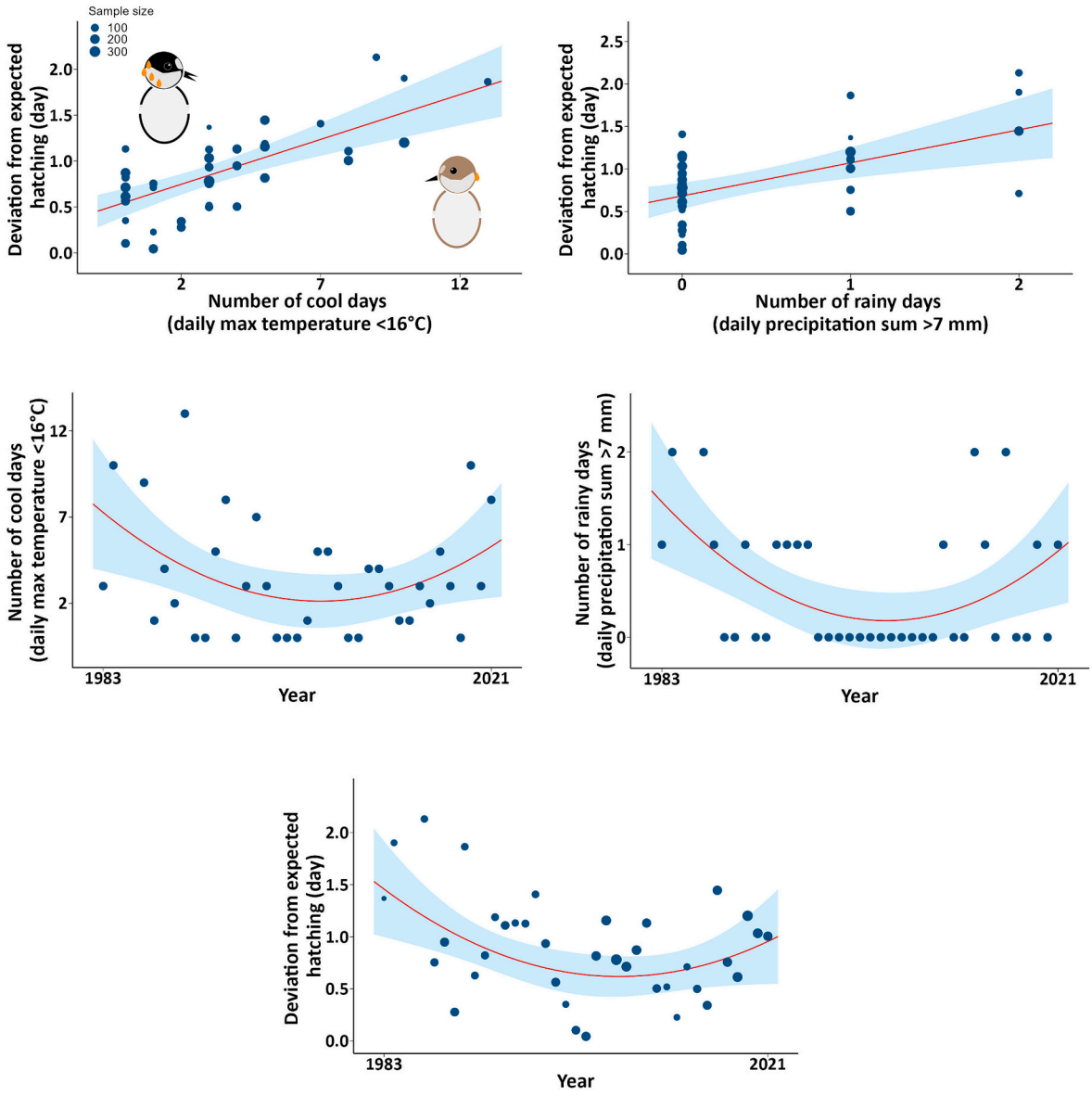


Fig. 3. Correlations between the deviation from the expected hatching date in the collared flycatcher and local weather parameters, and their temporal changes. The number of cool days and rainy days were extracted from local weather data using sliding window approach. Dot size indicates the number of data points on which the annual value of the expected hatching date for a given year is based (N_{total} = 5327).

subsequent replacement clutches, which could lead to the lengthening of the breeding season. During or after rainy time periods, the prey are less accessible due to their reduced availability and the reduced flight abilities of wet birds (Kennedy, 1970; Tinbergen and Dietz, 1994), both of these increasing off-nest time devoted to foraging, which risks the fatal cooling of the clutch, additionally, the insulation properties of the wet nest material (due to wet plumage) decrease (Hilton et al., 2004). It is important to note that the effect of precipitation conditions on breeding season length seems to be strong, even though we may underestimate season length according to our data selection criteria, as we excluded re-nesting events of the same female if its identity was known. However, nest desertion usually occurs before hatching (Wiggins et al., 1994; our field observations), which means that in the vast majority of abandoned nests, the identity of the females was not known, so if they were involved in re-nesting, these nests could not be excluded.

Interestingly, we found that the magnitude of the day-to-day increase in daily maximum spring temperature correlated negatively with the breeding season length. Other studies revealed that the variation of the season length related to the absolute temperature, which pattern was found in blackbirds (*Turdus merula*) (Jankowiak and Wysocki, 2016), blue tits and marsh tits (*Poecile palustris*) (Andreasson et al., 2023). It is possible that temperature increase itself also serves as an environmental cue based on which the birds assess when it is optimal to start egg-laying (Perrins and McCleery, 1989; Meijer et al., 1999; Schaper et al., 2012). Our results suggest that faster temperature rises trigger more birds at a time to start breeding in an aggregated manner, which can lead to a shortened season. One of the reasons for this relationship may be that egg production is costly because it significantly increases the protein requirements of females (Nager, 2006; Robbins, 1981), and meeting these requirements depends on food availability, which is closely related to temperature (see above). An ultimate explanation could be the fact that late breeders almost never produce recruiting young, so it is highly advantageous to start breeding as early as possible, given suitable conditions (Herényi et al., 2014).

We found that the magnitude of hatching deviation increased with the number of cool days and heavily rainy days, similarly to eastern kingbirds (*Tyrannus tyrannus*) (Gillette et al., 2021), horned larks (*Eremophila alpestris*) (de Zwaan et al., 2019), and blue tits (Nord and

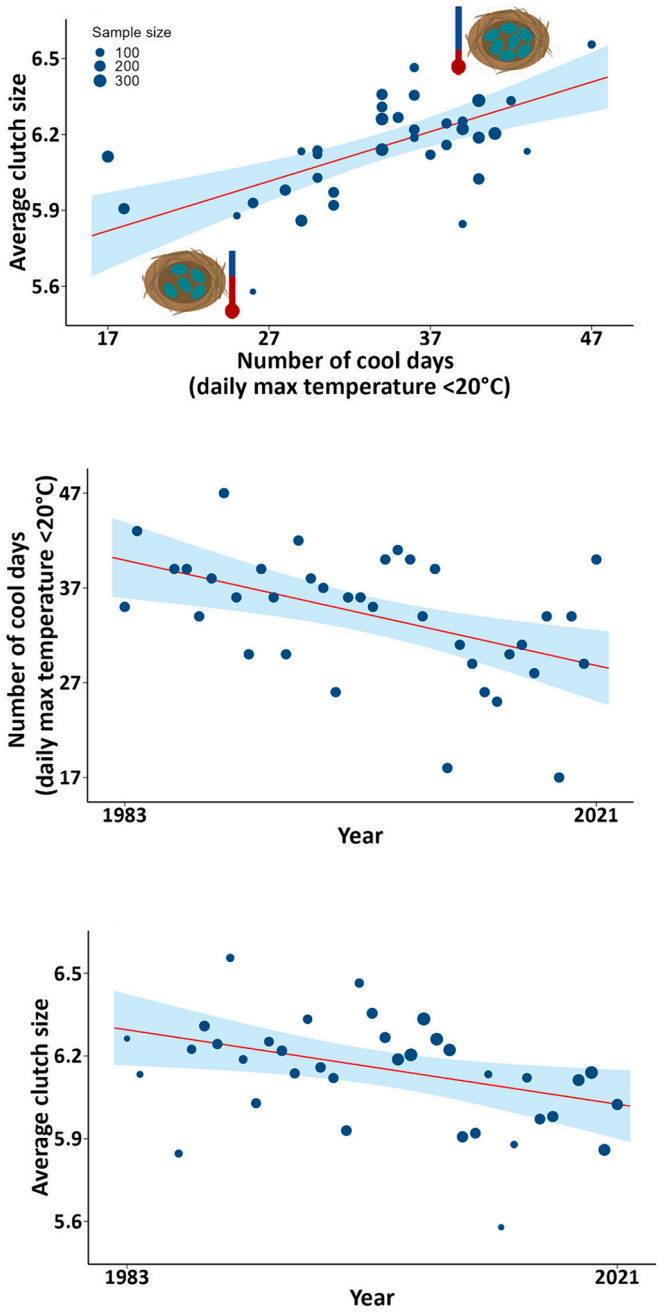


Fig. 4. Correlations between the collared flycatcher clutch size and local temperature conditions, and their temporal changes. The number of cool days was extracted from local weather data using sliding window approach. Sample size indicates the number of data points on which the annual value of the clutch size for a given year is based (N_{total} = 6225).

Nilsson, 2011). Low temperatures directly slow embryonic development (Olson et al., 2006), thereby prolonging the incubation period (Hepp et al., 2006; Martin et al., 2018). Under unfavourable weather conditions, eggs cool faster after the parent leaves the nest (Reid et al., 2000). Additionally, in the collared flycatcher, the female incubates the eggs alone, and this activity is in trade-off with self-maintenance (Deeming, 2002). Hence, if the male is less able to feed the female due to the adverse weather conditions, the female leaves the nest more often or for longer periods (Lyon and Montgomerie, 1985; Kötél et al., 2016), which can prolong the incubation period (Lyon and Montgomerie, 1985; Olson et al., 2006).

Considering the average clutch size, we found a decrease with

Table 3
Temporal changes of population-level breeding parameters and their related meteorological variables in the collared flycatcher. Note that the best climate windows differ among breeding parameters, and that is why the temporal trends of weather parameters may differ too.

Response variable	Predictor variable (function of year)	F(df1, df2)		Effect size R	95 % CI
Median laying date	Linear	10.26 (1,35)	**	−0.48	−0.69/ −0.18
	Quadratic	0.03 (1,34)		0.03	−0.30/ 0.35
	Cubic	3.40 (1,33)		0.31	−0.02/ 0.57
Mean wind speed	Linear	19.28 (1,35)	***	−0.60	−0.77/ −0.34
	Quadratic	1.22 (1,34)		−0.19	−0.48/ 0.15
	Cubic	0.64 (1,33)		0.14	−0.19/ 0.44
No. cool days (<17 °C)	Linear	10.48 (1,35)	**	−0.48	−0.70/ −0.18
	Quadratic	1.07 (1,34)		0.17	−0.16/ 0.47
	Cubic	3.62 (1,33)		0.31	−0.01/ 0.58
Breeding season length	Linear	2.12 (1,34)		0.24	−0.09/ 0.53
	Quadratic	8.50 (1,34)	**	0.45	0.14/ 0.67
	Cubic	0.39 (1,33)		−0.11	−0.42/ 0.22
Tmax slope	Linear	3.08 (1,34)		−0.29	−0.56/ 0.04
	Quadratic	6.21 (1,34)	*	−0.39	−0.64/ −0.08
	Cubic	1.60 (1,33)		−0.12	−0.43/ 0.21
Mean daily rain sum	Linear	0.07 (1,34)		−0.05	−0.37/ 0.28
	Quadratic	5.84 (1,34)	*	0.38	0.07/ 0.63
	Cubic	4.08 (1,33)		−0.33	−0.59/ −0.01
Hatching deviation	Linear	3.07 (1,34)		−0.29	−0.56/ 0.04
	Quadratic	5.89 (1,34)	*	0.38	0.07/ 0.63
	Cubic	0.02 (1,33)		0.03	−0.30/ 0.35
No. cool days (<16 °C)	Linear	0.43 (1,34)		−0.11	−0.42/ 0.22
	Quadratic	5.69 (1,34)	*	0.38	0.06/ 0.63
	Cubic	0.71 (1,33)		0.15	−0.19/ 0.45
No. rainy days (>7 mm)	Linear	0.91 (1,34)		−0.16	−0.46/ 0.17
	Quadratic	8.76 (1,34)	**	0.45	0.15/ 0.68
	Cubic	0.60 (1,33)		−0.13	−0.44/ 0.20
Clutch size	Linear	6.18 (1,35)	*	−0.39	−0.63/ −0.07
	Quadratic	0.63 (1,34)		−0.14	−0.44/ 0.20
	Cubic	1.10 (1,33)		0.18	−0.15/ 0.48
No. cool days (<20 °C)	Linear	11.24 (1,35)	***	−0.49	−0.70/ −0.20
	Quadratic	0.00 (1,34)		0.00	−0.32/ 0.32
	Cubic	1.50 (1,33)		0.21	−0.12/ 0.50
Fledgling number	Linear	2.34 (1,18)		−0.34	−0.68/ 0.12
	Quadratic	0.72 (1,17)		0.20	−0.26/ 0.59

(*continued on next page*)

Table 3 (*continued*)

Response variable	Predictor variable (function of year)	F(df1, df2)	Effect size R	95 % CI
	Cubic	0.00 (1,16)	−0.01	−0.45/ 0.43
Relative hatching date	Linear	1.37 (1,32)	0.20	−0.15/ 0.51
	Quadratic	0.18 (1,31)	0.08	−0.27/ 0.40
	Cubic	0.56 (1,30)	0.14	−0.21/ 0.45

*P < 0.05, **P < 0.01; CI refers to lower/upper boundaries of confidence interval.

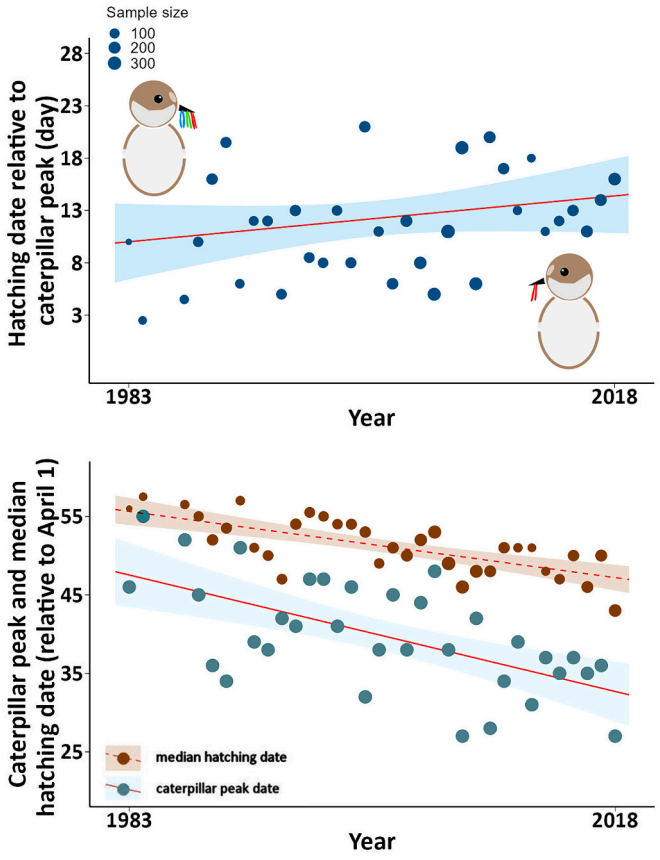


Fig. 5. Temporal changes of (a) phenological synchrony between hatching date and caterpillar peak date. Part (b) of the figure is for illustrative purposes only, to show that the hatching date and peak food availability are becoming more and more distant over the years. Sample size indicates the number of data points on which the value of the hatching date for a given year is based (N_{total} = 6025).

increasing number of warmer days. It is possible that changes in spring temperatures may be an indication of the food availability to birds (Visser et al., 1998; Matthysen et al., 2011). Thus, the warmer it is, the more they need to 'speed up' the brood completion, in order to be less off the food peak which can be both advanced and shortened by warm weather conditions (Burger et al., 2012). Additionally, the viability of eggs can decline more at higher ambient temperatures with off-bout duration (Arnold et al., 1987; Deeming and Ferguson, 1991), so it would be beneficial to start incubation earlier (Cooper et al., 2005). However, if incubation advances by more days before clutch completion, it elevates the hatching asynchrony (Veiga, 1992; Veiga and Viñuela, 1993). To avoid this potentially adverse scenario, it would be a reasonable compromise to lay fewer eggs, which would allow starting incubation earlier without increasing the chance of hatching asynchrony. Furthermore, at higher temperatures, the risk of hyperthermia could be higher for larger broods (Van Balen and Cavé, 1969). From another perspective, it is also possible that warmer conditions may make it more difficult to find nutrients for egg-forming, as the physiological functions, abundance, and seasonal activity of millipedes (Diplopoda) and woodlice (Isopoda), which are the main calcium sources for the collared flycatcher (Bureš and Weidinger, 2003), are negatively affected by higher temperatures (Bailey and Kovaliski, 1993; Cooper, 2022; Ďurajková et al., 2022).

All reproductive parameters (except the fledgling number) changed over the four-decade period, and these inter-annual variations were correlated with climate-change driven weather conditions. (We have to note that the lack of change over time in the number of fledglings may be the result of lower sample sizes, i.e. years with high predation and experimental broods had to be omitted from our analysis.) Climate change could pose an increasing threat even to those populations that currently appear stable. Additionally, a species may be more vulnerable if it is long-distance migratory (Both et al., 2010) and if the availability of its food highly varies seasonally (Foden et al., 2013), like in the collared flycatcher. Although we found that the breeding season advanced in our population, it is possible that this otherwise strong shift may not be enough in the future to maintain synchronization between caterpillar peak abundance and the nestling phase (see also Hegyi et al., 2013) as apparently the nestling hatching date has advanced less than the food peak (Fig. 5B). This is probably due to the fact that, as a migratory species, the collared flycatcher could advance breeding only to a lesser degree than residents (Samplonius et al., 2018). However, it should also be remembered that even long-distance migrants, such as the closely related pied flycatcher, have the potential for greater adaptation (see e.g. Helm et al., 2019). A higher degree of phenological mismatch is not necessarily a problem in itself, as late breeding is not necessarily a disadvantage in years when the amount of food is high, as it is described in wood warblers (*Phylloscpus sibilatrix*) (Maziarz and Wesołowski (2010).

A study has predicted in the pied flycatcher that increasing mistiming could result in population declines (Both et al., 2006). Although we found no clear evidence that fledgling numbers were correlated with weather (unlike in other species, see e.g. Vatka et al., 2014; Bowers et al., 2016) or varied with year (see also Halupka et al., 2023), we did reveal that the yearly mean fledgling number was strongly negatively correlated with the increasing phenological mismatch (see e.g. Reed et al., 2013). It has been assumed that if the divergence of phenologies exceeds a certain level, then this can lead to population extinction even in formerly stable populations (Simmonds et al., 2020). As the regional effects of global climate change are expected to manifest in the future in higher temperatures and drought with more frequent temperature extremes and precipitation extremes in the Carpathian Basin (Bartholy et al., 2007; Pongrácz et al., 2009), collared flycatchers may face an even greater phenological mismatch to food than at present, which may therefore increase the likelihood of a possible population decline. This effect may be exacerbated if the season is more stretched (which is the current trend in our population), as an increasing number of birds will fall into the extremely mismatched category. Interestingly, in contrast to our result, a study found breeding season shortening, but specifically in resident and short-distance migrant species in Finland over a 43-year period (Hällfors et al., 2020).

Although in the last 2–3 years, the number of cool days was higher in the relevant time window of hatching deviation, leading to a higher hatching deviation, it is very likely that this variable will ultimately follow the decreasing trend seen in the preceding period, like in the case of the time window correlated with the breeding onset. Certainly, incubation duration cannot be reduced unlimitedly (Ricklefs, 1993), because the earlier incubation starting increases the frequency of asynchronous hatchings, which may facilitate brood reduction by sibling competition (e.g. Amundsen and Slagsvold, 1998), and this is not

necessarily adaptive (Magrath, 1990; Szöllősi et al., 2007 for evidence from our population).

Surprisingly, contrary to other studies, we detected a slight decrease in clutch size through the decades. However, in many other species, studies found no inter-annual temporal change in average primary reproductive investment (Dunn and Møller, 2014), as described, for example, in boreal owl species (Lehikoinen et al., 2011), the tree-swallow (*Tachycineta bicolor*) (Stenseth and Mysterud, 2002), the pied flycatcher (Sanz et al., 2003), and an increase has been described only in a few species, like in the reed warbler (*Acrocephalus scirpaceus*) and great reed warbler (*Acrocephalus arundinaceus*) (Schaefer et al., 2006). However, if we look at the blue tit breeding in the same study area as the studied collared flycatchers, we can see a similar pattern to our result, namely decreasing clutch size with increasing phenological mismatch, which could be an adaptive response to the escalation of adverse conditions (Laczi et al., 2019).

In summary, our four-decade-long study highlights that multiple aspects of changing climate may have been associated with different components of reproduction at the population level in a Central European population of the long-distance migratory collared flycatcher. In detail, the breeding onset, the breeding season length, the incubation time, and the clutch size changed with certain weather conditions (e.g. temperatures, surface wind speed, number of rainfall extremities). We also found that these reproductive parameters showed similar temporal trends as the meteorological parameters with which they were associated. As global climate change shows spatial differences, forcing different populations to face different challenges, a comprehensive view of detailed responses in reproduction is necessary to explore and understand how and why populations within and among species differ in their responses to global climate change.

Ethical approval

The study was conducted under a long-term research agreement with the Pilis Park Forestry, and with research permits from the regional nature conservation authority (PE-06/KTF/920–7/2018). All applicable international, national, and institutional guidelines for the use of animals were followed.

Data statement

The primary data supporting the results of this study can be available from the Figshare digital repository (Laczi et al., 2023).

CRediT authorship contribution statement

Miklós Laczi: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Fanni Sarkadi:** Writing – review & editing, Visualization, Investigation, Formal analysis, Data curation. **Márton Herényi:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Gergely Nagy:** Data curation, Investigation, Writing – review & editing. **Gergely Hegyi:** Writing – review & editing, Investigation, Data curation. **Mónika Jablonszky:** Writing – review & editing, Investigation. **Réka Könczey:** Writing – review & editing, Investigation, Data curation. **Katalin Krenhardt:** Writing – review & editing, Investigation. **Gábor Markó:** Writing – review & editing, Investigation, Funding acquisition. **Balázs Rosivall:** Writing – review & editing, Investigation, Funding acquisition. **Eszter Szász:** Investigation, Writing – review & editing. **Eszter Szöllősi:** Writing – review & editing, Investigation. **László Tóth:** Writing – review & editing, Investigation. **Sándor Zsebők:** Writing – review & editing, Investigation, Funding acquisition. **János Török:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have shared the link to the data at the Attach File step

Acknowledgments

This research was funded by the Hungarian National Research, Development and Innovation Office (OTKA/NKFIH) grants (F68295, FK127917, K115970, K120249, K124443, K129215, K139992, K75618, PD115730, PD124043, PD121276, PD75481, T017058, T022014, T029753, T034880, T049650, T049678), János Bolyai Research Fellowships (BO/663/17, BO/00163/22) and ÚNKP Bolyai+ Fellowships (ÚNKP-18-4-ELTE-54, ÚNKP-19-4-ELTE-779, ÚNKP-22-5-ELTE-1151)), the Pilis Park Forestry, the Erdők a Közjóért Alapítvány and the Doctoral School of Biology, Eötvös Loránd University. We acknowledge the E-OBS dataset from the EU-FP6 project UERRA (http://www.uerra.eu) and the data providers in the ECA&D project (https://www.ecad.eu). We are grateful to many members of the Behavioural Ecology Group for their help during the past four decades, and Tímea Seregi for her long-term administrative work. This project has received funding from the HUN-REN Hungarian Research Network. ML thanks the special help in the field work to Emma Nóra Rosivall, Lilla Török and Pál Benedek Markó, and to Neil Young for his warning lines "*Look at Mother Nature on the run / In the twenty-first century*".

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171945.

References

Ahola, M.P., Laaksonen, T., Eeva, T., Lehikoinen, E., 2012. Selection on laying date is connected to breeding density in the pied flycatcher. Oecologia 168, 703–710. https://doi.org/10.1007/s00442-011-2135-5.

Amundsen, T., Slagsvold, T., 1998. Hatching asynchrony in great tits: a bet-hedging strategy? Ecology 79, 295–304. https://doi.org/10.1890/0012-9658(1998)079[0295:HAIGTA]2.0.CO;2.

Andreasson, F., Nord, A., Nilsson, J.Å., 2023. Variation in breeding phenology in response to climate change in two passerine species. Oecologia 201, 279–285. https://doi.org/10.1007/s00442-022-05306-5.

Arnold, T.W., Rohwer, F.C., Armstrong, T., 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. Am. Nat. 130, 643–653.

Avery, M.I., Krebs, J.R., 1984. Temperature and foraging success of Great Tits *Parus major* hunting for spiders. Ibis 126, 33–38. https://doi.org/10.1111/j.1474-919X.1984.tb03661.x.

Bailey, P.T., Kovaliski, J., 1993. Summer quiescent behaviour of the millipede *Ommatoiulus moreleti* (Julida: Julidae). J. Zool. 231, 523–532. https://doi.org/10.1111/j.1469-7998.1993.tb01935.x.

Bailey, L.D., van de Pol, M., 2016. Climwin: an R toolbox for climate window analysis. PloS One 11, e0167980. https://doi.org/10.1371/journal.pone.0167980.

Bartholy, J., Pongrácz, R., Gelybó, G.Y., 2007. Regional climate change expected in Hungary for 2071-2100. Appl. Ecol. Environ. Res. 5, 1–17. https://doi.org/10.15666/aeer/0501_001017.

Bathiany, S., Dakos, V., Scheffer, M., Lenton, T.M., 2018. Climate models predict increasing temperature variability in poor countries. Sci. Adv. 4, 1–11. https://doi.org/10.1126/sciadv.aar5809.

Bibby, C., Burgess, N., Hill, D., Mustoe, S., 2000. Bird Census Techniques. Academic Press.

Boersma, J., Enbody, E.D., Karubian, J., Watts, H.E., Schwabl, H., 2022. Drought disrupts year-round breeding readiness in a tropical songbird. Avian Conserv. Ecol. 17, 44. https://doi.org/10.5751/ACE-2343-170244.

Bordjan, D., Tome, D., 2014. Rain may have more influence than temperature on nest abandonment in the great tit *Parus major*. Ardea 102, 79–85. https://doi.org/10.5253/078.102.0107.

Both, C., Visser, M.E., 2005. The effect of climate change on the correlation between avian life-history traits. Glob. Chang. Biol. 11, 1606–1613. https://doi.org/10.1111/j.1365-2486.2005.01038.x.

Both, C., Tinbergen, J.M., Visser, M.E., 2000. Adaptive density dependence of avian clutch size. Ecology 81, 3391–3403. https://doi.org/10.1890/0012-9658(2000)081[3391:ADDOAC]2.0.CO;2.

Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E.V., Järvinen, A., Metcalfe, N.B., Nyholm, N.E.I., Potti, J., Ravussin, P.A., Sanz, J.J., Silverin, B., Slater, F.M., Sokolov, L.V., Török, J., Winkel, W., Wright, J., Zang, H., Visser, M.E., 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc. R. Soc. B Biol. Sci. 271, 1657–1662. https://doi.org/10.1098/rspb.2004.2770.

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

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J., Foppen, R.P. B., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc. R. Soc. B Biol. Sci. 277, 1259–1266. https://doi.org/10.1098/rspb.2009.1525.

Bowers, E.K., Grindstaff, J.L., Soukup, S.S., Drilling, N.E., Eckerle, K.P., Sakaluk, S.K., Thompson, C.F., 2016. Spring temperatures influence selection on breeding date and the potential for phenological mismatch in a migratory bird. Ecology 97, 2880–2891. https://doi.org/10.1002/ecy.1516.

Breuer, H., Ács, F., Skarbit, N., 2017. Climate change in Hungary during the twentieth century according to Feddema. Theor. Appl. Climatol. 127, 853–863. https://doi.org/10.1007/s00704-015-1670-0.

Briedis, M., Krist, M., Král, M., Voigt, C.C., Adamík, P., 2018. Linking events throughout the annual cycle in a migratory bird—non-breeding period buffers accumulation of carry-over effects. Behav. Ecol. Sociobiol. 72, 93. https://doi.org/10.1007/s00265-018-2509-3.

Bryant, D.M., 1975. Breeding biology of the house Martin Delichon urbica in relation to insect abundance. Ibis 117, 180–216. https://doi.org/10.1111/j.1474-919X.1975.tb04206.x.

Bureš, S., Weidinger, K., 2003. Sources and timing of calcium intake during reproduction in flycatchers. Oecologia 137, 634–641. https://doi.org/10.1007/s00442-003-1380-7.

Burger, C., Belskii, E., Eeva, T., Laaksonen, T., Mägi, M., Mänd, R., Qvarnström, A., Slagsvold, T., Veen, T., Visser, M.E., Wiebe, K.L., Wiley, C., Wright, J., Both, C., 2012. Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. J. Anim. Ecol. 81, 926–936. https://doi.org/10.1111/j.1365-2656.2012.01968.x.

Burnham, K.P., Anderson, D.R. (Eds.), 2004. Model Selection and Multimodel Inference. Springer New York, New York, NY. https://doi.org/10.1007/b97636.

Callaghan, C.T., Nakagawa, S., Cornwell, W.K., 2021. Global abundance estimates for 9,700 bird species. Proc. Natl. Acad. Sci. U. S. A. 118, e2023170118 https://doi.org/10.1073/pnas.2023170118.

Cantar, R.V., Montgomerie, R.D., 1985. The influence of weather on incubation scheduling of the white-Rumped sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour 95, 261–289. https://doi.org/10.1163/156853985X00154.

Capilla-Lasheras, P., Harrison, X., Wood, E.M., Wilson, A.J., Young, A.J., 2021. Altruistic bet-hedging and the evolution of cooperation in a Kalahari bird. Sci. Adv. 7, eabe8980 https://doi.org/10.1126/sciadv.abe8980.

Carey, C., 2009. The impacts of climate change on the annual cycles of birds. Philos. Trans. R. Soc. B Biol. Sci. 364, 3321–3330. https://doi.org/10.1098/rstb.2009.0182.

Chaplyhina, A.B., Yuzyk, D.I., Savynska, N.O., Hramma, V.M., 2022. Invertebrates in the diet of collared flycatcher (*Ficedula albicollis*) nestlings in transformed forest ecosystems of North-Eastern Ukraine. Balt. For. 28, 439 (10.46490/BF439).

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., Sheldon, B.C., 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320, 800–803. https://doi.org/10.1126/science.1157174.

Cooper, M.I., 2022. Abundance varies with minimum temperature in red millipedes Centrobolus cook 1897. Acta Entomol. Zool. 3, 8–11.

Cooper, C.B., Hochachka, W.M., Butcher, G., Dhondt, A.A., 2005. Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. Ecology 86, 2018–2031. https://doi.org/10.1890/03-8028.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An ensemble version of the E-OBS temperature and precipitation data sets. J. Geophys. Res. Atmos. 123, 9391–9409. https://doi.org/10.1029/2017JD028200.

Cramp, S., Perrins, C.M., 1993. The birds of the Western Palearctic. In: Flycatchers to Shrikes, Vol. VII. Oxford University Press.

Cresswell, W., McCleery, R., 2003. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. J. Anim. Ecol. 72, 356–366. https://doi.org/10.1046/j.1365-2656.2003.00701.x.

Crick, H.Q.P., Dudley, C., Glue, D.E., Thomson, D.L., 1997. UK birds laying eggs earlier. Nature 388, 526.

de Zwaan, D.R., Camfield, A.F., MacDonald, E.C., Martin, K., 2019. Variation in offspring development is driven more by weather and maternal condition than predation risk. Funct. Ecol. 33, 447–456. https://doi.org/10.1111/1365-2435.13273.

Deeming, D.C., 2002. Avian Incubation. Oxford University Press, Oxford.

Deeming, D.C., Ferguson, M.W.J., 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Egg Incubation. Cambridge University Press, pp. 147–172. https://doi.org/10.1017/CBO9780511585739.011.

Dunn, P.O., Møller, A.P., 2014. Changes in breeding phenology and population size of birds. J. Anim. Ecol. 83, 729–739. https://doi.org/10.1111/1365-2656.12162.

Dunn, P.O., Møller, A.P. (Eds.), 2019. Effects of Climate Change on Birds. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780198824268.001.0001.

Ďurajková, B., Hladký, R., Tuf, I.H., 2022. Higher temperature and substrate vibrations as stress factors for terrestrial isopods – model species matter. Zookeys 1101, 71–85. https://doi.org/10.3897/zookeys.1101.77549.

Easterling, D.R., Karl, T.R., Gallo, K.P., Robinson, D.A., Trenberth, K.E., Dai, A., 2000. Observed climate variability and change of relevance to the biosphere. J. Geophys. Res. Atmos. 105, 20101–20114. https://doi.org/10.1029/2000JD900166.

Enemar, A., 1995. Incubation, hatching, and clutch desertion of the Treecreeper *Certhia familiaris* in South-Western Sweden. Ornis Svecica 5, 111–124. https://doi.org/10.34080/os.v5.23000.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Şekercioğlu, Ç.H., Mace, G.M., 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS One 8, e65427. https://doi.org/10.1371/journal.pone.0065427.

Fox, J., Weisberg, S., 2018. An R Companion to Applied Regression, 3rd ed. Sage Publications, Thousand Oaks CA.

García-Navas, V., Arroyo, L., Sanz, J.J., Mario, D., 2008. Effect of nestbox type on occupancy and breeding biology of tree sparrows *Passer montanus* in Central Spain. Ibis 150, 356–364. https://doi.org/10.1111/j.1474-919X.2008.00799.x.

Gillette, S.M., Klehr, A.L., Murphy, M.T., 2021. Variation in incubation length and hatching asynchrony in eastern kingbirds: weather eclipses female effects. Ornithology 138, 1–15. https://doi.org/10.1093/ornithology/ukab031.

Goodenough, A.E., Hart, A.G., Elliot, S.L., 2011. What prevents phenological adjustment to climate change in migrant bird species? Evidence against the "arrival constraint" hypothesis. Int. J. Biometeorol. 55, 97–102. https://doi.org/10.1007/s00484-010-0312-6.

Gordo, O., Sanz, J.J., 2009. Long-term temporal changes of plant phenology in the Western Mediterranean. Glob. Chang. Biol. 15, 1930–1948. https://doi.org/10.1111/j.1365-2486.2009.01851.x.

Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., Grenfell, B.T., 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430, 71–75. https://doi.org/10.1038/nature02708.

Hällfors, M.H., Antaō, L.H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T., Saastamoinen, M., 2020. Shifts in timing and duration of breeding for 73 boreal bird species over four decades. Proc. Natl. Acad. Sci. U. S. A. 117, 18557–18565. https://doi.org/10.1073/pnas.1913579117.

Halupka, L., Halupka, K., 2017. The effect of climate change on the duration of avian breeding seasons: a meta-analysis. Proc. R. Soc. B Biol. Sci. 284, 20171710 https://doi.org/10.1098/rspb.2017.1710.

Halupka, L., Czyż, B., Macias Dominguez, C.M., 2020. The effect of climate change on laying dates, clutch size and productivity of Eurasian coots *Fulica atra*. Int. J. Biometeorol. 64, 1857–1863. https://doi.org/10.1007/s00484-020-01972-3.

Halupka, L., Borowiec, M., Neubauer, G., Halupka, K., 2021. Fitness consequences of longer breeding seasons of a migratory passerine under changing climatic conditions. J. Anim. Ecol. 90, 1655–1665. https://doi.org/10.1111/1365-2656.13481.

Halupka, L., Arlt, D., Tolvanen, J., Millon, A., Bize, P., Adamík, P., Albert, P., Arendt, W. J., Artemyev, A.V., Baglione, V., Bańbura, J., Bańbura, M., Barba, E., Barrett, R.T., Becker, P.H., Belskii, E., Bolton, M., Bowers, E.K., Bried, J., Brouwer, L., Bukacińska, M., Bukaciński, D., Bulluck, L., Carstens, K.F., Catry, I., Charter, M., Chernomorets, A., Covas, R., Czuchra, M., Dearborn, D.C., de Lope, F., Di Giacomo, A.S., Dombrovski, V.C., Drummond, H., Dunn, M.J., Eeva, T., Emmerson, L.M., Espmark, Y., Fargallo, J.A., Gashkov, S.I., Golubova, E.Y., Griesser, M., Harris, M.P., Hoover, J.P., Jagiełło, Z., Karell, P., Kloskowski, J., Koenig, W.D., Kolunen, H., Korczak-Abshire, M., Korpimäki, E., Krams, I., Krist, M., Krüger, S.C., Kuranov, B.D., Lambin, X., Lombardo, M.P., Lyakhov, A., Marzal, A., Møller, A.P., Neves, V.C., Nielsen, J.T., Numerov, A., Orłowska, B., Oro, D., Öst, M., Phillips, R.A., Pietiäinen, H., Polo, V., Porkert, J., Potti, J., Pöysä, H., Printemps, T., Prop, J., Quillfeldt, P., Ramos, J.A., Ravussin, P.-A., Rosenfield, R.N., Roulin, A., Rubenstein, D.R., Samusenko, I.E., Saunders, D.A., Schaub, M., Senar, J.C., Sergio, F., Solonen, T., Solovyeva, D.V., Stępniewski, J., Thompson, P.M., Tobolka, M., Török, J., van de Pol, M., Vernooij, L., Visser, M.E., Westneat, D.F., Wheelwright, N.T., Wiącek, J., Wiebe, K.L., Wood, A.G., Wuczyński, A., Wysocki, D., Zárybnická, M., Margalida, A., Halupka, K., 2023. The effect of climate change on avian offspring production: a global meta-analysis. Proc. Natl. Acad. Sci. 120, e2208389120 https://doi.org/10.1073/pnas.2208389120.

Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D., New, M., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. J. Geophys. Res. Atmos. 113, D20119 https://doi.org/10.1029/2008JD010201.

Hegyi, G., Laczi, M., 2015. Using full models, stepwise regression and model selection in ecological data sets: Monte Carlo simulations. Ann. Zool. Fenn. 52, 257–279.

Hegyi, G., Nagy, G., Török, J., 2013. Reduced compensatory growth capacity in mistimed broods of a migratory passerine. Oecologia 172, 279–291. https://doi.org/10.1007/s00442-012-2487-5.

Helm, B., Van Doren, B.M., Hoffmann, D., Hoffmann, U., 2019. Evolutionary response to climate change in migratory pied flycatchers. Curr. Biol. 29, 3714–3719. https://doi.org/10.1016/j.cub.2019.08.072.

Hepp, G.R., Kennamer, R.A., Johnson, M.H., 2006. Maternal effects in Wood ducks: incubation temperature influences incubation period and neonate phenotype. Funct. Ecol. 20, 308–314. https://doi.org/10.1111/j.1365-2435.2006.01108.x.

Herényi, M., Garamszegi, L.Z., Hargitai, R., Hegyi, G., Rosivall, B., Szöllősi, E., Török, J., 2014. Laying date and polygyny as determinants of annual reproductive success in

male collared flycatchers (*Ficedula albicollis*): a long-term study. Naturwissenschaften 101, 305–312. https://doi.org/10.1007/s00114-014-1157-3.
Hidalgo Aranzamendi, N., Hall, M.L., Kingma, S.A., van de Pol, M., Peters, A., 2019. Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. J. Anim. Ecol. 88, 1799–1811. https://doi.org/10.1111/1365-2656.13068.
Hilton, G.M., Hansell, M.H., Ruxton, G.D., Reid, J.M., Monaghan, P., 2004. Using artificial nests to test importance of nesting material and nest shelter for incubation energetics. Auk 121, 777–787. https://doi.org/10.1093/auk/121.3.777.
Houghton, J., 2009. Global Warming. Cambridge University Press. https://doi.org/10.1017/CBO9780511841590.
Izsák, B., Szentimrey, T., 2020. To what extent does the detection of climate change in Hungary depend on the choice of statistical methods? GEM - Int. J. Geomathematics 11, 1–23. https://doi.org/10.1007/s13137-020-00154-y.
Jankowiak, L., Wysocki, D., 2016. Do individual breeding experience and parental effort affect breeding season length in blackbirds? Behav. Ecol. 27, 829–834. https://doi.org/10.1093/beheco/arv227.
Jankowiak, Ł., Pietruszewska, H., Wysocki, D., 2014. Weather conditions and breeding season length in blackbird (*Turdus merula*). Folia Zool. 63, 245–250. https://doi.org/10.25225/fozo.v63.i4.a3.2014.
Kennedy, R.J., 1970. Direct effects of rain on birds: a review. Br. Birds 63, 401–414.
Khan, N., Shahid, S., Ismail, T. bin, Wang, X.J., 2019. Spatial distribution of unidirectional trends in temperature and temperature extremes in Pakistan. Theor. Appl. Climatol. 136, 899–913. https://doi.org/10.1007/s00704-018-2520-7.
Knape, J., de Valpine, P., 2011. Effects of weather and climate on the dynamics of animal population time series. Proc. R. Soc. B Biol. Sci. 278, 985–992. https://doi.org/10.1098/rspb.2010.1333.
Kötél, D., Laczi, M., Török, J., Hegyi, G., 2016. Mutual ornamentation and the parental behaviour of male and female collared flycatchers *Ficedula albicollis* during incubation. Ibis 158, 796–807. https://doi.org/10.1111/ibi.12389.
Kwon, E., English, W.B., Weiser, E.L., Franks, S.E., Hodkinson, D.J., Lank, D.B., Sandercock, B.K., 2018. Delayed egg-laying and shortened incubation duration of Arctic-breeding shorebirds coincide with climate cooling. Ecol. Evol. 8, 1339–1351. https://doi.org/10.1002/ece3.3733.
Laczi, M., Garamszegi, L.Z., Hegyi, G., Herényi, M., Ilyés, G., Könczey, R., Nagy, G., Pongrácz, R., Rosivall, B., Szöllősi, E., Tóth, L., Török, J., 2019. Teleconnections and local weather orchestrate the reproduction of tit species in the Carpathian Basin. J. Avian Biol. 50, 1–10. https://doi.org/10.1111/jav.02179.
Laczi, M., Sarkadi, F., Herényi, M., Nagy, G., Hegyi, G., Jablonszky, M., Könczey, R., Krenhardt, K., Markó, G., Rosivall, B., Szász, E., Szöllősi, E., Tóth, L., Zsebők, S., Török, J., 2023. Data From: Responses in the Breeding Parameters of the Collared Flycatcher to the Changing Climate. https://doi.org/10.6084/m9.figshare.24564373.
Lehikoinen, A., Ranta, E., Pietiäinen, H., Byholm, P., Saurola, P., Valkama, J., Huitu, O., Henttonen, H., Korpimäki, E., 2011. The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. Oecologia 165, 349–355. https://doi.org/10.1007/s00442-010-1730-1.
Lorenz, R., Stalhandske, Z., Fischer, E.M., 2019. Detection of a climate change signal in extreme heat, heat stress, and cold in Europe from observations. Geophys. Res. Lett. 46, 8363–8374. https://doi.org/10.1029/2019GL082062.
Lv, L., Liu, Y., Osmond, H.L., Cockburn, A., Kruuk, L.E.B., 2020. When to start and when to stop: effects of climate on breeding in a multi-brooded songbird. Glob. Chang. Biol. 26, 443–457. https://doi.org/10.1111/gcb.14831.
Lyon, B.E., Montgomerie, R.D., 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? Behav. Ecol. Sociobiol. 17, 279–284. https://doi.org/10.1007/BF00300147.
Magrath, R.D., 1990. Hatching asynchrony in altricial birds. Biol. Rev. 65, 587–622. https://doi.org/10.1111/j.1469-185X.1990.tb01239.x.
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, 307–315. https://doi.org/10.1007/s00442-004-1725-x.
Martin, T.E., Mouton, J.C., 2020. Longer-lived tropical songbirds reduce breeding activity as they buffer impacts of drought. Nat. Clim. Chang. 10, 953–958. https://doi.org/10.1038/s41558-020-0864-3.
Martin, T.E., Ton, R., Oteyza, J.C., 2018. Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines. Auk 135, 101–113. https://doi.org/10.1642/AUK-17-124.1.
Matthysen, E., Adriaensen, F., Dhondt, A.A., 2011. Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). Glob. Chang. Biol. 17, 1–16. https://doi.org/10.1111/j.1365-2486.2010.02213.x.
Maziarz, M., Wesołowski, T., 2010. Timing of breeding and nestling diet of Wood warbler *Phylloscopus sibilatrix* in relation to changing food supply. Bird Study 57, 540–552. https://doi.org/10.1080/00063657.2010.512954.
McDermott, M.E., DeGroote, L.W., 2016. Long-term climate impacts on breeding bird phenology in Pennsylvania, USA. Glob. Chang. Biol. 22, 3304–3319. https://doi.org/10.1111/gcb.13363.
Meijer, T., Nienaber, U., Langer, U., Trillmich, F., 1999. Temperature and timing of egg-laying of European starlings. Condor 101, 124–132. https://doi.org/10.2307/1370453.
Mingozzi, T., Storino, P., Venuto, G., Massolo, A., Tavecchia, G., 2022. Climate warming induced a stretch of the breeding season and an increase of second clutches in a passerine breeding at its altitudinal limits. Curr. Zool. 68, 9–17. https://doi.org/10.1093/cz/zoab029.
Møller, A.P., 2013a. Biological consequences of global change for birds. Integr. Zool. 8, 136–144. https://doi.org/10.1111/1749-4877.12006.
Møller, A.P., 2013b. Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird. Ecosphere 4, 1–11. https://doi.org/10.1890/ES12-00310.1.
Murphy, M.T., Redmond, L.J., Dolan, A.C., Cooper, N.W., Shepherdson, K., Chutter, C. M., Cancellieri, S., 2022. Weather and climate change drive annual variation of reproduction by an aerial insectivore. Avian Conserv. Ecol. 17, 21. https://doi.org/10.5751/ACE-02203-170221.
Nager, R.G., 2006. The challenges of making eggs. Ardea 94, 323–346.
Nakazawa, T., Doi, H., 2012. A perspective on match/mismatch of phenology in community contexts. Oikos 121, 489–495. https://doi.org/10.1111/j.1600-0706.2011.20171.x.
Nord, A., Nilsson, J.Å., 2011. Incubation temperature affects growth and energy metabolism in blue tit nestlings. Am. Nat. 178, 639–651. https://doi.org/10.1086/662172.
Olson, C.R., Vleck, C.M., Vleck, D., 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. Physiol. Biochem. Zool. 79, 927–936. https://doi.org/10.1086/506003.
Peng, R.K., Fletcher, C.R., Sutton, S.L., 1992. The effect of microclimate on flying dipterans. Int. J. Biometeorol. 36, 69–76. https://doi.org/10.1007/BF01208916.
Perrins, C.M., McCleery, R.H., 1989. Laying dates and clutch size in the great tit. Wilson Bull. 101, 236–253.
Pierce, D., 2021. ncdf4: Interface to Unidata netCDF (Version 4: or Earlier) Format Data Files. R Package Version 1.19.
Pomeroy, D., Platz, E., Platz, K., Lack, P., Gottschalk, T.K., 2018. The problems of recording bird numbers in the breeding season as pairs. Ornithol. Sci. 17, 69–78. https://doi.org/10.2326/osj.17.69.
Pongrácz, R., Bartholy, J., Szabó, P., Gelybó, G., 2009. A comparison of the observed trends and simulated changes in extreme climate indices in the Carpathian Basin by the end of this century. Int. J. Glob. Warm. 1, 336–355. https://doi.org/10.1504/IJGW.2009.027097.
R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Reed, T.E., Jenouvrier, S., Visser, M.E., 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J. Anim. Ecol. 82, 131–144. https://doi.org/10.1111/j.1365-2656.2012.02020.x.
Reid, J.M., Monaghan, P., Ruxton, G.D., 2000. The consequences of clutch size for incubation conditions and hatching success in starlings. Funct. Ecol. 14, 560–565. https://doi.org/10.1046/j.1365-2435.2000.t01-1-00446.x.
Richardson, A.D., Hufkens, K., Milliman, T., Aubrecht, D.M., Furze, M.E., Seyednasrollah, B., Krassovski, M.B., Latimer, J.M., Nettles, W.R., Heiderman, R.R., Warren, J.M., Hanson, P.J., 2018. Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. Nature 560, 368–371. https://doi.org/10.1038/s41586-018-0399-1.
Ricklefs, R.E., 1971. Foraging behavior of mangrove swallows at Barro Colorado Island. Auk 88, 635–651.
Ricklefs, R.E., 1993. Sibling competition, hatching asynchrony, incubation period, and lifespan in Altricial birds. In: Current Ornithology. Springer US, Boston, MA, pp. 199–276. https://doi.org/10.1007/978-1-4757-9912-5_5.
Robbins, C.T., 1981. Estimation of the relative protein cost of reproduction in birds. Condor 83, 177–179. https://doi.org/10.2307/1367424.
Rosivall, B., Szöllősi, E., Török, J., 2005. Maternal compensation for hatching asynchrony in the collared flycatcher *Ficedula albicollis*. J. Avian Biol. 36, 531–537. https://doi.org/10.1111/j.0908-8857.2005.03458.x.
Rubolini, D., Ambrosini, R., Caffi, M., Brichetti, P., Armiraglio, S., Saino, N., 2007. Long-term trends in first arrival and first egg laying dates of some migrant and resident bird species in northern Italy. Int. J. Biometeorol. 51, 553–563. https://doi.org/10.1007/s00484-007-0094-7.
Saino, N., Rubolini, D., Jonzén, N., Ergon, T., Montemaggiori, A., Stenseth, N.C., Spina, F., 2007. Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. Climate Res. 35, 123–134. https://doi.org/10.3354/cr00719.
Samplonius, J.M., Bartošová, L., Burgess, M.D., Bushuev, A.V., Eeva, T., Ivankina, E.V., Kerimov, A.B., Krams, I., Laaksonen, T., Mägi, M., Mänd, R., Potti, J., Török, J., Trnka, M., Visser, M.E., Zang, H., Both, C., 2018. Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. Glob. Chang. Biol. 24, 3780–3790. https://doi.org/10.1111/gcb.14160.
Sanz, J.J., Potti, J., Moreno, J., Merino, S., Frías, O., 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. Glob. Chang. Biol. 9, 461–472. https://doi.org/10.1046/j.1365-2486.2003.00575.x.
Schaefer, T., Ledebur, G., Beier, J., Leisler, B., 2006. Reproductive responses of two related coexisting songbird species to environmental changes: global warming, competition, and population sizes. J. Ornithol. 147, 47–56. https://doi.org/10.1007/s10336-005-0011-y.
Schaper, S.V., Dawson, A., Sharp, P.J., Gienapp, P., Caro, S.P., Visser, M.E., 2012. Increasing temperature, not mean temperature, is a cue for avian timing of reproduction. Am. Nat. 179, E55–E69. https://doi.org/10.1086/663675.
Senapathi, D., Nicoll, M.A.C., Teplitsky, C., Jones, C.G., Norris, K., 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. Proc. R. Soc. B Biol. Sci. 278, 3184–3190. https://doi.org/10.1098/rspb.2011.0212.
Shepard, E., Cole, E.-L., Neate, A., Lempidakis, E., Ross, A., 2019. Wind prevents cliff-breeding birds from accessing nests through loss of flight control. Elife 8, e43842. https://doi.org/10.7554/eLife.43842.
Simmonds, E.G., Cole, E.F., Sheldon, B.C., Coulson, T., 2020. Phenological asynchrony: a ticking time-bomb for seemingly stable populations? Ecol. Lett. 23, 1766–1775. https://doi.org/10.1111/ele.13603.

Slagsvold, T., 1976. Annual and geographical variation in the time of breeding of the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. Ornis Scand. 7, 127–145.
Smart, Z.F., Smith, M.G., Riehl, C., 2021. The El Niño–Southern Oscillation dramatically influences the probability of reproduction and reproductive rate of a tropical forest bird. J. Avian Biol. 52, e02799 https://doi.org/10.1111/jav.02799.
Smith, K.W., Smith, L., Charman, E., Briggs, K., Burgess, M., Dennis, C., Harding, M., Isherwood, C., Isherwood, I., Mallord, J., 2011. Large-scale variation in the temporal patterns of the frass fall of defoliating caterpillars in oak woodlands in Britain: implications for nesting woodland birds. Bird Study 58, 506–511. https://doi.org/10.1080/00063657.2011.616186.
Solís, I., Álvarez, E., Barba, E., 2023. Global warming modifies the seasonal distribution of clutches on a Mediterranean great tit population. Int. J. Biometeorol. 67, 367–376. https://doi.org/10.1007/s00484-022-02415-x.
Stenseth, N.C., Mysterud, A., 2002. Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. Proc. Natl. Acad. Sci. 99, 13379–13381. https://doi.org/10.1073/pnas.212519399.
Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol. Evol. 8, 1639–1644. https://doi.org/10.1111/2041-210X.12797.
Stott, P., 2016. How climate change affects extreme weather events. Science 352, 1517–1518. https://doi.org/10.1126/science.aaf7271.
Strain, J.G., Mumme, R.L., 1988. Effects of food supplementation, song playback, and temperature on vocal territorial behavior of Carolina wrens. Auk 105, 11–16. https://doi.org/10.1093/auk/105.1.11.
Szabó, S., Szopos, N.M., Bertalan-Balázs, B., László, E., Milošević, D.D., Conoscenti, C., Lázár, I., 2019. Geospatial analysis of drought tendencies in the carpathians as reflected in a 50-year time series. Hungarian. Geogr. Bull. 68, 269–282. https://doi.org/10.15201/hungeobull.68.3.5.
Szép, T., Gibbons, D., 2000. Monitoring of common breeding birds in Hungary using a randomised sampling design. Ring 22, 45–55.
Szép, T., Nagy, K., Nagy, Z., Halmos, G., 2012. Population trends of common breeding and wintering birds in Hungary, decline of longdistance migrant and farmland birds during 1999-2012. Orn. Hun. 20, 13–63. https://doi.org/10.2478/orhu-2013-0007.
Szép, T., Csörgő, T., Halmos, G., Lovászi, P., Nagy, K., Schmidt, A. (Eds.), 2022. Magyarország madáratlasza. Bird Atlas of Hungary, 2th ed. Agrárminisztérium, Magyar Madártani és Természetvédelmi Egyesület, Budapest.
Szöllősi, E., Rosivall, B., Török, J., 2007. Is hatching asynchrony beneficial for the brood? Behav. Ecol. 18, 420–426. https://doi.org/10.1093/beheco/arl100.
Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I. J., Wanless, S., 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob. Chang. Biol. 16, 3304–3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x.
Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M., Roeckner, E., 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398, 694–697. https://doi.org/10.1038/19505.
Tinbergen, J.M., Dietz, M.W., 1994. Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. Funct. Ecol. 8, 563–572. https://doi.org/10.2307/2389916.
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. Integr. Comp. Biol. 293–304. https://doi.org/10.1093/icb/icq028.
Trenberth, K.E., 2011. Changes in precipitation with climate change. Climate Res. 47, 123–138. https://doi.org/10.3354/cr00953.
Van Balen, J.H., Cavé, A.J., 1969. Survival and weight loss of nestling great tits, *Parus major*, in relation to brood-size and air temperature. Netherlands J. Zool. 20, 464–474. https://doi.org/10.1163/002829670X00231.
van de Pol, M., Bailey, L.D., McLean, N., Rijsdijk, L., Lawson, C.R., Brouwer, L., 2016. Identifying the best climatic predictors in ecology and evolution. Methods Ecol. Evol. 7, 1246–1257. https://doi.org/10.1111/2041-210X.12590.
Vatka, E., Rytkönen, S., Orell, M., 2014. Does the temporal mismatch hypothesis match in boreal populations? Oecologia 176, 595–605. https://doi.org/10.1007/s00442-014-3022-7.
Veen, T., Sheldon, B.C., Weissing, F.J., Visser, M.E., Qvarnström, A., Sætre, G.P., 2010. Temporal differences in food abundance promote coexistence between two congeneric passerines. Oecologia 162, 873–884. https://doi.org/10.1007/s00442-009-1544-1.
Veiga, J.P., 1992. Hatching asynchrony in the house sparrow: a test of the egg-viability hypothesis. Am. Nat. 139, 669–675. https://doi.org/10.1086/285351.
Veiga, J.P., Viñuela, J., 1993. Hatching asynchrony and hatching success in the house sparrow: evidence for the egg viability hypothesis. Ornis Scand. 24, 237–242. https://doi.org/10.2307/3676739.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Fourth edition. Springer, New York. https://www.stats.ox.ac.uk/pub/MASS4/.
Verboven, N., Tinbergen, J.M., Verhulst, S., 2001. Food, reproductive success and multiple breeding in the great tit *Parus major*. Ardea 89, 387–406.
Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M., Lessells, C.M., 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc. R. Soc. London. Ser. B Biol. Sci. 265, 1867–1870. https://doi.org/10.1098/rspb.1998.0514.
Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395. https://doi.org/10.1038/416389a.
Wiggins, D.A., Part, T., Gustafsson, L., 1994. Correlates of clutch desertion by female collared flycatchers *Ficedula albicollis*. J. Avian Biol. 25, 93. https://doi.org/10.2307/3677025.
Williams, C.B., 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. Philos. Trans. R. Soc. Lond. B Biol. Sci. 244, 331–378. https://doi.org/10.1098/rstb.1961.0011.
Wolf, B.O., Walsberg, G.E., 2000. The role of the plumage in heat transfer processes of birds. Am. Zool. 40, 575–584. https://doi.org/10.1093/icb/40.4.575.
Wu, J., Zha, J., Zhao, D., Yang, Q., 2018. Changes in terrestrial near-surface wind speed and their possible causes: an overview. Climate Dynam. 51, 2039–2078. https://doi.org/10.1007/s00382-017-3997-y.
Zha, J., Shen, C., Li, Z., Wu, J., Zhao, D., Fan, W., Sun, M., Azorin-Molina, C., Deng, K., 2021. Projected changes in global terrestrial near-surface wind speed in 1.5 °C–4.0 °C global warming levels. Environ. Res. Lett. 16, 114016 https://doi.org/10.1088/1748-9326/ac2fdd.