

# AVIAN BIOLOGY

## Article

### Teleconnections and local weather orchestrate the reproduction of tit species in the Carpathian Basin

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Variation in climatic conditions is an important driving force of ecological processes. Populations are under selection to respond to climatic changes with respect to phenology of the annual cycle (e.g. breeding, migration) and life-history. As teleconnections can reflect climate on a global scale, the responses of terrestrial animals are often investigated in relation to the El Niño–Southern Oscillation and North Atlantic Oscillation. However, investigation of other teleconnections and local climate is often neglected. In this study, we examined over a 33-year period the relationships between four teleconnections (El Niño–Southern Oscillation, North Atlantic Oscillation, Arctic Oscillation, East Atlantic Pattern), local weather parameters (temperature and precipitation) and reproduction in great tits *Parus major* and blue tits *Cyanistes caeruleus* in the Carpathian Basin, Hungary. Furthermore, we explored how annual variations in the timing of food availability were correlated with breeding performance. In both species, annual laying date was negatively associated with the Arctic Oscillation. The date of peak abundance of caterpillars was negatively associated with local temperatures in December–January, while laying date was negatively related to January–March temperature. We found that date of peak abundance of caterpillars and laying date of great tits advanced, while in blue tits clutch size decreased over the decades but laying date did not advance. The results suggest that weather conditions during the months that preceded the breeding season, as well as temporally more distant winter conditions, were connected to breeding date. Our results highlight that phenological synchronization to food availability was different between the two tit species, namely it was disrupted in blue tits only. Additionally, the results suggest that in order to find the climatic drivers of the phenological changes of organisms, we should analyze a broader range of global meteorological parameters.

Keywords: breeding phenology, *Cyanistes caeruleus*, *Parus major*, precipitation, teleconnection, temperature

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## Introduction

Systematic or cyclic variation of global or local weather conditions may influence migration and breeding phenology of birds (Ottersen et al. 2001, Møller et al. 2010). Because of this, shifting phenology through time might be an indicator of the response of ecosystem dynamics to global warming including advancing spring (Parmesan 2006, Møller et al. 2010).

Temporal changes in teleconnections (linkages between climate anomalies occurring in widely separated geographical regions) reflect climatic conditions over large areas (Stenseth et al. 2003, Latif and Keenlyside 2008). Teleconnections are therefore often considered to be more capable of predicting and explaining ecological changes than local-scale climatic indices, because they have reduced stochasticity and dimensionality than those (Stenseth et al. 2003, Hallett et al. 2004). Maybe the two most investigated teleconnections are the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). Both of these have effects on weather variability in Northern Europe. For example, strong El Niño phases are associated with drier and colder winters (Brönnimann 2007), and positive NAO index coincides with more precipitation and warmer winters in Northern Europe, while Southern Europe experiences the opposite (Hurrell 1995). These are also associated with ecological processes in different taxa (Waite et al. 2007, Park et al. 2011, Zhai et al. 2013, Li et al. 2015). Particularly in bird species, these climatic phenomena may correlate with annual survivorship (García-Pérez 2012), arrival date (MacMynowski et al. 2007), onset of breeding (Przybylo et al. 2000, Wilson and Arcese 2003), length of the breeding season (Weatherhead 2005), reproductive success (Both et al. 2006, Surman et al. 2012), and the phenology of migration (Hüppop and Hüppop 2003). In the Northern Hemisphere, the dynamics of the Arctic Oscillation (AO) and the East Atlantic Pattern (EA) are also important predictors of weather variability (AO: Thompson and Wallace 1998, Luterbacher et al. 2004, EA: Barnston and Livezey 1987, Bojariu and Reverdin 2002). In spite of this, our knowledge is scarce with respect to their ecological impacts (but see Aanes et al. 2002).

The relationships between teleconnections and local weather are often non-linear and non-stationary (Knippertz et al. 2003). Hence, teleconnections sometimes predict only a small part of local weather changes (Stenseth et al. 2003). However, it is demonstrated in birds that local weather parameters (e.g. rainfall, air temperature) may correlate with clutch size (Patten and Rotenberry 1999), nestling body condition (Rodríguez and Bustamante 2003), recruitment rates (Gullett et al. 2015) and advancement of reproduction (Cucco et al. 1992, Bourret et al. 2015, Simmonds et al. 2017). Unfortunately, only few studies have analysed teleconnections and local weather simultaneously (Rodríguez and Bustamante 2003, MacMynowski et al. 2007 on terrestrial birds; Álvarez and Pajuelo 2011, Pakanen 2018 on seabirds).

In the literature, there are very few long-term dataseries of the breeding biology of different bird species from exactly the same study site (Samplonius et al. 2018). Such previous studies showed that the closely related great tits *Parus major* and blue tits *Cyanistes caeruleus* could show different temporal patterns through decades in their breeding phenology in sympatric populations (Goodenough et al. 2011, Vátka et al. 2014), despite the similarities in their behavioural features and ecological needs.

Here, we used data from a 33-year period to examine long-term trends in the breeding phenologies and clutch sizes of great tits and blue tits and timing of their maximum food availability in the Carpathian Basin, an area in Europe where such long-term studies are lacking in birds. We specifically looked for correlations with local weather patterns (temperature and precipitation) and large-scale climatic variation (ENSO, NAO, AO and EA). We predicted 1) that food availability of tits, folivorous caterpillars, is related to local temperature parameters (Salis et al. 2016). As spring temperatures have increased in this region (Beuer et al. 2017), we further predicted that 2) the timing of caterpillar food peak has advanced. Consequently, we predicted that 3) phenological advancement has occurred in both tit species in order to maintain a temporal match with the caterpillar food peak. Because the physiology, foraging and breeding behaviour of tits could be connected not exclusively to temperature but to a broader spectrum of meteorological parameters (Brotans 1997, Mainwaring and Hartley 2016), we 4) predicted that temporal changes in breeding biology of the two tit species in the Carpathian Basin is related not only to the local weather variables, but also teleconnections (Pongrácz et al. 2003, Zsilinszki et al. 2014, 2015).

## Material and methods

### Field data

This study was carried out between 1982 and 2015 in the Pilis-Visegrád Mountains, Duna-Ipoly National Park, Hungary (47°43'N 19°01'E). The study site is located at 300–550 m a.s.l. It is covered by deciduous woodland dominated by oaks and contains around 800 artificial nest-boxes placed out in a grid system that are used most abundantly by collared flycatchers *Ficedula albicollis*, great tits and blue tits. Collared flycatchers were excluded from this study as they start egg-laying two-three weeks later than tits. Furthermore, flycatchers migrate and thus they do not experience local weather in winter and early spring.

Great tits and blue tits are resident or partially vagrant (short-distance movement in an erratic fashion with no fixed direction or pattern). In our study site, females start laying eggs from the end of March. Great tits (blue tits) typically lay 6–13 (6–16) eggs, incubate for 12–15 (14) d and feed offspring for 20–22 (18–22) d. A small proportion of the great tit population produces a second nest with smaller clutch

size. The diet of the offspring of the two tit species mainly consists of foliage-eating caterpillars (Török 1985).

Nest-box plots were checked regularly (at least once a week) to determine laying date of the first egg and clutch size. We recorded the following breeding variables for each species in each year: 1) clutch size was the arithmetic mean of egg number within nests; 2) annual median laying date was used to investigate the effects of local weather and teleconnections; it was the median of the laying dates of the first egg in the nests, compared to 26 March (number of days from 26 March), which was, the earliest laying onset over the study period (we used median given that laying dates showed skewed distributions within years); 3) relative laying date was used to investigate phenological advancement; it was calculated as median of laying date deviations from the caterpillar peak date, as there were significant correlations between caterpillar peak (see below) and laying date (great tits:  $r=0.67$ ,  $p<0.001$ ,  $n=29$ ; blue tits:  $r=0.59$ ,  $p=0.001$ ,  $n=29$ ); 4) the difference in median laying date between the two tit species (great tit minus blue tit as the former starts breeding later) was calculated in order to capture divergence in phenology in the long term. Tit breeding density was calculated as breeding pairs  $\text{ha}^{-1}$ , pooled for the two species. According to the data selection criteria (see below), we used 1873 great tit and 877 blue tit breeding events in the analyses. Before determining the above variables, we excluded data from the first year of the newly established study plot because of potential density-dependent effects (Both and Visser 2005). We analyzed data only from those clutches that had started within 30 days of the earliest clutch initiation within each year (Van Noordwijk et al. 1995) and excluded all re-nesting events and secondary broods which could bias the breeding variables. We excluded predated broods and the few atypical broods with less than six eggs. We did not exclude from the analyses the among-year repeats of females, for multiple reasons. First, there is no possibility to gain any information of past reproduction events of unringed or newly ringed breeding birds, and removing the known second breeders would bias the dataset. In great tit females, 72.76% of birds were ringed, of which 12.41% bred in multiple years (only twice in 78.01% of these cases), ringed females bred 1.17 times on average. The values for blue tit females: 79.80, 8.94, 84.62, 1.11%, respectively. Second, within-individual laying date and clutch size between the first and second breeding of the females showed low correlations (great tits, laying date:  $r=0.01$ ,  $p=0.90$ ; clutch size:  $r=0.36$ ,  $p<0.001$ ; blue tits:  $r=0.01$ ,  $p=0.91$ ;  $r=0.24$ ,  $p=0.023$ ). Finally, and most importantly, here we investigated the breeding events of pairs and not individual females alone, and in our population returning tits nearly always chose new mates for their second breeding (among ringed birds, there were only six pairs in great tits and in blue tits too which bred together again).

We collected caterpillar frass from 1987 to 2015 in each year, during the reproductive seasons, every five days on average. The date of caterpillar peak was defined as the date half-way between the date when the maximum frass mass was collected and the date of the previous collection

(Verboven et al. 2001). The 12–15 collectors (each  $0.25 \text{ m}^2$ ) were placed at standard locations. We weighed the frass samples to the nearest  $0.001 \text{ g}$  and controlled for collection intervals by dividing the measured mass value by the number of days elapsed between consecutive collections.

## Meteorological data and statistical methods

Local weather data were acquired from the E-OBS gridded dataset (Haylock et al. 2008, European Climate Assessment and Dataset, ECAD <<http://www.ecad.eu>>) by separating the time series for the gridcell representing the region  $47.50\text{--}47.75^\circ\text{N}$   $19\text{--}19.25^\circ\text{E}$ . We used the following variables: daily mean, maximum, minimum temperature and daily precipitation. Because we were primarily interested in overall trends, we calculated arithmetic means for months. Based on previous studies (Van Balen 1980, Wesolowski and Cholewa 2009), we assumed that weather conditions from December to April were relevant for tits' breeding performance. For large-scale climate parameters we used the multivariate ENSO index (MEI) and the indices of the following teleconnections: NAO, AO and EA. These indices in monthly resolution were obtained from the United States National Oceanic and Atmospheric Administration's Climate Prediction Center (<[www.cpc.ncep.noaa.gov/](http://www.cpc.ncep.noaa.gov/)>) and the Earth System Research Laboratory (<[www.esrl.noaa.gov/psd/data/correlation/mei.data](http://www.esrl.noaa.gov/psd/data/correlation/mei.data)>). We carried out principal components analysis (PCA), with orthogonal varimax rotation of the axes on all three (mean, min. and max.) of the five monthly local temperature measurements and separately on the five single monthly precipitation amounts. We also carried out PCAs with varimax rotations separately for the MEI, NAO, AO and EA indices. In the cases of the NAO, AO and EA, we used the monthly mean values from November to March because of the possible time-lag in the influence of these indices in the Carpathian Basin (Pongrácz 2003). In the case of the MEI, the time lag is longer (Knippertz et al. 2003, Bartholy and Pongrácz 2006), hence we used the monthly mean values from October to February. In the analyses, from each PCA we used only the first PC and the second if its eigenvalue was greater than one.

As a result of PCAs, we found robust and similar patterns in the composition of PC axes with regards to grouping of the monthly meteorological parameters. Temperature PC1 was loaded with temperatures of January, February and March and PC2 associated with temperatures of December and January (Supplementary material Appendix 1 Table A1). Precipitation PC1 represented the precipitation of January, February and March, while PC2 was loaded with the precipitation of December and January (Supplementary material Appendix 1 Table A2). The composition of PC axes resulting from PCAs conducted on the monthly teleconnection indices showed similar patterns to those of local variables, but in several cases with a time lag of one month, as expected (Supplementary material Appendix 1 Table A3). All MEIs loaded positively with the one PC axis (all loadings  $> 0.95$ , eigenvalue = 4.81, explained variance = 96%).



We investigated the effects of climatic conditions in the two tit species in separate analyses. We used general linear models (GLMs) with backward stepwise model simplification to reveal the associations between meteorological parameters with breeding variables and caterpillar peak. The different GLMs were conducted using annual median laying date, clutch size or caterpillar peak as single dependent variable and meteorological PCs were used as continuous predictors. In addition, the GLMs investigating clutch size included breeding density as an additional independent variable. Because of strong correlations between certain meteorological parameters, before the GLMs we corrected these to each other, i.e. using the regression residuals of NAO PC1 on AO PC1, NAO PC2 on AO PC2, precipitation PC1 on AO PC2 and temperature PC1 on AO PC2 as AO showed stronger correlations with local weather than NAO in this region (Zsilinszki et al. 2014, 2015). After this correction, we checked again for potential robust correlations and colinearities among these variables using Pearson's correlations and variation inflation factor (VIF) index, respectively.

Since neither climate system parameters nor biological responses of birds necessarily change in a linear way over time (Schlesinger and Ramankutty 1994, Charmantier et al. 2008), we conducted backward stepwise polynomial regressions to analyze the relationships between year (as independent variable, centered before analyses) and breeding variables, median laying date difference between species, relative laying date and caterpillar peak. Each initial model included the linear, quadratic and cubic terms of year. In each case, backward stepping was stopped when only significant ( $p < 0.05$ ) terms remained in the model.

All variables and residuals were normally distributed. Analyses were performed in Statistica ver. 7.0 (StatSoft, Inc.).

## Results

Correlation patterns among meteorological parameters were weak after the corrections mentioned in the methods, suggesting no need for further correction to each other (Supplementary material Appendix 1 Table A4).

In both species, laying date was negatively related to AO PC2 (i.e. February–March AO index) (Fig. 1, Table 1) and temperature PC1 (i.e. temperature in January–March) (Fig. 2, Table 1). Neither the weather or climatic variables, nor breeding density showed significant relationships with clutch size (Table 1). Caterpillar peak was negatively related to temperature PC2 (i.e. December–January temperature) (Table 1). All VIFs were below three, except for residuals of NAO PC2 in the models of laying dates ( $VIF = 3.35$ ).

In the long term, laying date in great tits was marginally negatively related to year (linear term (LT) hereafter):  $F_{1,31} = 3.94$ ,  $p = 0.056$ ; quadratic term (QT):  $F_{1,31} = 1.59$ ,  $p = 0.21$ ; cubic term (CT):  $F_{1,31} = 2.94$ ,  $p = 0.09$ ). Median laying date of blue tits did not advance (LT:  $F_{1,31} = 0.39$ ,  $p = 0.54$ ; QT:  $F_{1,31} = 2.34$ ,  $p = 0.13$ ; CT:  $F_{1,31} = 0.30$ ,  $p = 0.59$ ). The laying date difference between the two species decreased markedly (LT:  $F_{1,31} = 11.91$ ,

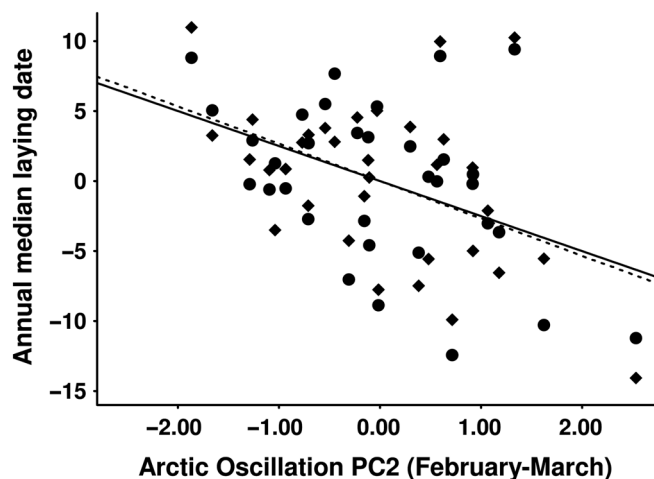


Figure 1. Relationship of great tit and blue tit laying date with the Arctic Oscillation in the study area. Annual median laying date values came from model residuals of GLM. Circles, continuous line: great tit; diamonds, dashed line: blue tit.

$p = 0.002$ , Fig. 3a; QT:  $F_{1,30} = 0.12$ ,  $p = 0.73$ ; CT:  $F_{1,30} = 0.30$ ,  $p = 0.59$ ). Great tit clutch exhibited very little change (LT:  $F_{1,31} = 0.08$ ,  $p = 0.79$ ; QT:  $F_{1,31} = 0.06$ ,  $p = 0.80$ ; CT:  $F_{1,31} = 0.14$ ,  $p = 0.71$ ), in contrast to blue tit clutch size, which showed a minimum in the middle of the study period (LT:  $F_{1,30} = 1.29$ ,  $p = 0.26$ ; QT:  $F_{1,31} = 4.50$ ,  $p = 0.04$ , Fig. 3b; CT:  $F_{1,30} = 1.70$ ,  $p = 0.20$ ). Laying date relative to caterpillar peak did not change in great tits (LT:  $F_{1,27} = 1.92$ ,  $p = 0.18$ ; QT:  $F_{1,27} = 1.26$ ,  $p = 0.27$ ; CT:  $F_{1,27} = 0.02$ ,  $p = 0.90$ ), while in blue tits it increased at the beginning and the end of the study period (LT:  $F_{1,26} = 0.07$ ,  $p = 0.78$ ; QT:  $F_{1,26} = 0.16$ ,  $p = 0.70$ ; CT:  $F_{1,27} = 4.87$ ,  $p = 0.03$ , Fig. 3c). Finally, the caterpillar peak markedly shifted towards earlier dates with year (LT:  $F_{1,27} = 13.77$ ,  $p = 0.0009$ , Fig. 3d; QT:  $F_{1,26} = 1.35$ ,  $p = 0.26$ ; CT:  $F_{1,26} = 0.19$ ,  $p = 0.66$ ).

## Discussion

### Phenology and teleconnections

We show here that the laying date of two sympatrically breeding passerine species breeding in the Carpathian region were negatively associated with the February–March AO index, while it was unrelated to NAO. These patterns remained the same if NAO was not corrected for the AO (results not shown here). Our result differs from several studies that revealed associations of biological phenomena in birds with the ENSO (Hüppop and Hüppop 2003, Both et al. 2006, Gordo 2007) and the NAO (MacMynowski et al. 2007, Garcia-Pérez 2012, Paxton et al. 2014 for NAO). The NAO correlates with the shifts of breeding phenology of tits in other European regions (Hinsley et al. 2016) and response in the shifts of our study species shows geographical differences across the western Palearctic (Sanz 2002).

The apparent lack of relationships between the biological parameters and the ENSO and NAO in our study can be due

Table 1. Summary of relationships of great tit and blue tit reproduction and caterpillar peak date to local temperature and precipitation, Arctic Oscillation (AO), North Atlantic Oscillation (NAO), Multivariate ENSO Index (MEI) and East Atlantic Pattern (EA), and breeding tit density, using general linear models (for detailed statistics see material and methods).

Response variable	Laying date			Clutch size			Caterpillar peak			
	Great tit		Blue tit	Great tit		Blue tit	Great tit		Caterpillar peak	
	F (df)	CI	F (df)	F (df)	CI	F (df)	CI	F (df)	CI	
Temperature PC1	9.63 (1,30)**	-0.72/-0.18	12.95 (1,30)**	-0.44/0.24	0.23 (1,31)	-0.42/0.26	0.02 (1,31)	-0.36/0.33	3.13 (1,26)	-0.62/0.04
Temperature PC2	1.06 (1,29)	-0.50/0.17	3.78 (1,29)	-0.66/-0.08	0.00 (1,31)	-0.34/0.34	0.58 (1,31)	-0.29/0.39	4.42 (1,27)*	-0.65/-0.01
Precipitation PC1	0.05 (1,29)	-0.38/0.31	0.00 (1,29)	-0.36/0.32	0.05 (1,31)	-0.31/0.38	0.33 (1,31)	-0.39/0.30	1.60 (1,26)	-0.56/0.14
Precipitation PC2	0.71 (1,29)	-0.20/0.47	1.04 (1,29)	0.17/0.71	0.94 (1,31)	-0.18/0.49	1.05 (1,31)	-0.40/0.28	0.35 (1,26)	-0.26/0.46
AO PC1	1.09 (1,29)	-0.50/0.16	0.57 (1,29)	-0.69/-0.12	1.27 (1,31)	-0.16/0.51	0.66 (1,31)	-0.29/-0.40	0.26 (1,26)	-0.45/0.28
AO PC2	6.99 (1,30)*	-0.68/-0.11	8.27 (1,30)**	-0.53/0.12	0.01 (1,31)	-0.36/0.33	0.17 (1,31)	-0.31/0.38	2.49 (1,26)	-0.60/0.08
NAO PC1	0.05 (1,29)	-0.30/0.38	0.01 (1,29)	-0.27/0.42	1.30 (1,31)	-0.15/0.51	0.54 (1,31)	-0.29/0.39	0.22 (1,26)	-0.28/0.44
NAO PC2	2.02 (1,29)	-0.10/0.55	1.26 (1,29)	0.18/0.72	0.06 (1,31)	-0.38/0.30	0.09 (1,31)	-0.37/0.32	0.00 (1,26)	-0.37/0.37
EA PC1	0.31 (1,29)	-0.43/0.25	0.64 (1,29)	-0.69/-0.13	0.39 (1,31)	-0.44/0.24	0.02 (1,31)	-0.36/0.33	0.33 (1,26)	-0.46/0.27
EA PC2	0.40 (1,29)	-0.24/0.44	1.67 (1,29)	0.18/0.72	0.13 (1,31)	-0.29/0.40	0.46 (1,31)	-0.29/0.39	0.45 (1,26)	-0.47/0.25
MEI PC	1.57 (1,29)	-0.13/0.53	0.46 (1,29)	0.10/0.67	0.17 (1,31)	-0.28/0.41	0.11 (1,31)	-0.31/0.37	2.92 (1,26)	-0.06/0.61
Tit density					1.47 (1,31)	-0.52/0.14	0.46 (1,31)	-0.39/0.29		

NAO PC1 was corrected for AO PC1 and NAO PC2, while temperature PC1 and precipitation PC1 were corrected for AO PC2. CI, 95% confidence interval; \* p<0.05; \*\* p<0.01.

to the weak associations of these teleconnections and local weather in this region (Pongrácz et al. 2003). To the contrary, it has been described that AO usually correlates more strongly with local weather than NAO in the Carpathian Basin (Zsilinszki et al. 2014, 2015), which assigns greater biological relevance to this. Another possibility is that ENSO and NAO act jointly (Pongrácz and Bartholy 2000, Pongrácz 2003, Mares et al. 2003), making it difficult to detect associations of breeding phenology with these teleconnections, at least using our analytical approach.

However, caterpillar peak date showed no correlation with the AO. One scenario may be that the AO acts on the availability of other prey in the pre-breeding periods, which could determine the condition of tits and the timing of territory occupancy and pair bonding. In a population of great tits in Slovakia, the winter diet composition consisted not only of plants, but also of arthropods and these formed the dominant part of diet in November and in March (Veľký et al. 2011). The winter activity and the availability of prey may not only depend on a single weather parameter like temperature, but on a wide variety of conjugated parameters, the variation of which is captured effectively by the AO fluctuations.

Our findings highlight the importance of using 'uncommon' teleconnections, the biological importance of which is unexplored in terrestrial animals (Naef-Daenzer et al. 2012). In birds, until these days, correlations with the AO have been documented only in the Arctic and sub-Arctic regions (Dickey et al. 2008, Smith and Gaston 2012, Aubry et al. 2013, Doiron et al. 2015, Fossøy et al. 2015). Our results support that although the NAO and the AO are sometimes treated as the same phenomenon (Wallace 2000) and could show similar biological associations (Uboni et al. 2016, Weijers et al. 2017), these two indices may correlate with biological processes in a different way (Aanes et al. 2002, Smith and Gaston 2012).

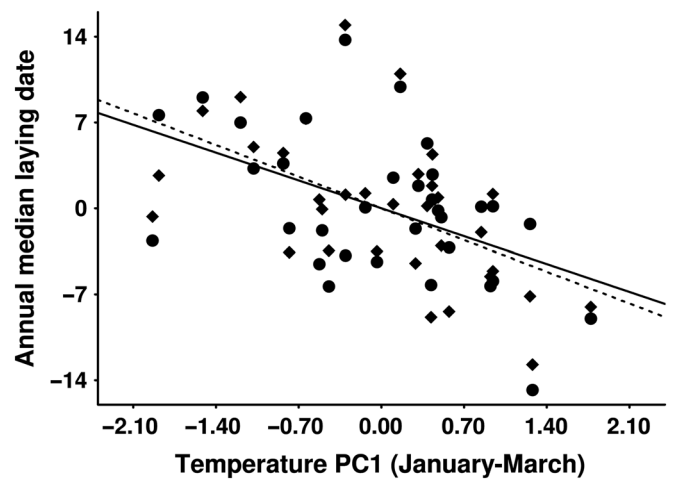


Figure 2. Relationship of great tit and blue tit laying date with temperature conditions between January and March in the study area. Annual median laying date values came from model residuals of GLM. Temperature PC1 was corrected for AO PC2. Circles, continuous line: great tit; diamonds, dashed line: blue tit.

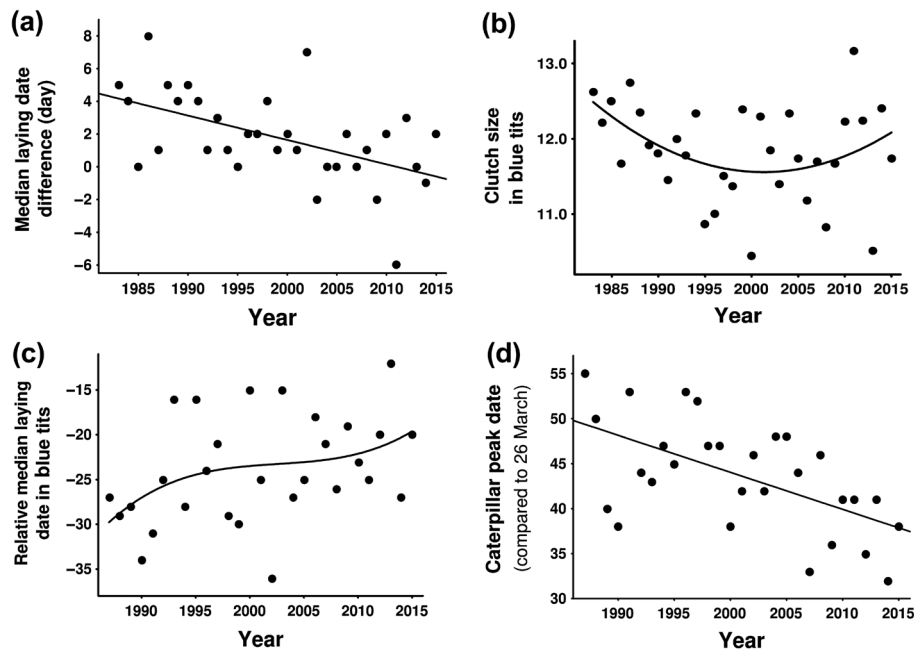


Figure 3. Yearly trends in the breeding variables of the great tit and the blue tit (a–c) and in the caterpillar peak date in the study area (d). Median laying date difference refers to annual laying date difference between species (great tit minus blue tit). Relative median laying date refers to median of laying date deviations from the caterpillar peak date.

### Phenology and local weather

We found that December–January and January–March temperatures were negatively associated with the peak availability of the main food supply of tits and their breeding phenology, respectively. Similarly to our results, several studies found associations between advancement of reproduction and temperature (Bourret et al. 2015, Simmonds et al. 2017), furthermore, it is well-known that winter and spring temperatures affect caterpillar peak date and biomass (Visser et al. 1998, Visser and Holleman 2001). Overwintering moth egg development and hatching dynamics are specifically related to local temperature patterns (Embree 1970, Kimberling and Miller 1988). Winter precipitation (e.g. duration of snow cover) and the frequency of extreme cold events (below  $-30^{\circ}\text{C}$ ), which are usually associated to AO index rather than to local temperature, have a limited effect on caterpillar egg survival (Andresen et al. 2001). Moreover, the lowest temperature registered in our study site was  $-21.3^{\circ}\text{C}$ , which may explain why we did not find any relationship between caterpillar phenology and precipitation or teleconnection indices.

Because there is a constraint on some insectivorous songbirds breeding in seasonal environments to synchronize their breeding with the main prey abundance (Blondel et al. 1993, Van Noordwijk et al. 1995), it is not surprising that interannual variation of winter temperature is indirectly correlated with laying date.

Temperature can affect the physiological state of the birds (see below). The developmental condition of testes in male tits shows a seasonal cycle and before breeding, they need

four to six weeks to reach their maximum size (Silverin and Viebke 1994). However, despite the photoperiodic trigger, lower ambient temperature slows down gonadal maturation (Silverin and Viebke 1994), which could lead to a delayed breeding. Moreover, global warming induces earlier but shorter gonadal cycles resulting in earlier breeding (Silverin et al. 2008). Additionally, temperature influences fat reserve levels in great tits (Gosler 2002), so a colder winter can cause worse condition, which may lead to later breeding onset.

Clutch size was not affected by any of the meteorological parameters. Even if there was any connection, this could be masked by the conjugate effects of other factors. One of the major determinants of clutch size is food abundance (Hussell and Quinney 1987), so it may be possible that clutch size in our population is more sensitive to the fluctuations of food abundance than to food phenology as food limitation proximately affects reproductive decisions (Martin 1987). In accordance with this, we experienced folivorous caterpillar gradations (with sevenfold increase in the estimated abundance) with approximately decadal periodicity and the mean clutch size of great tits in the years after these events was larger (our unpublished data) suggesting a delayed effect of food supply.

### Long-term changes in phenology and fecundity

We found that the caterpillar peak advanced in our study site (by 0.59 day per year, Fig. 3d), similarly to other regions (Van Asch and Visser 2007), potentially because of the

warming temperature, which is supported by findings that climate change causes a general increase in temperature in the Carpathian Basin (Bartholy and Pongrácz 2007). As caterpillar availability is crucial for tit nestlings, it has a major role in the timing of breeding (Visser et al. 1998, Charmantier et al. 2008). There are areas where different tit species showed similar responses in breeding phenology to the climate change (Winkel and Hudde 1997, Wesolowski and Cholewa 2009, Gładalski et al. 2014), but it is also possible that tit species in the same location react differently due to different constraints. The latter pattern was found in great tits and willow tits *Poecile montanus* in the same location in Finland, where synchrony to the caterpillar peak was important with regards to timing of breeding only in great tits (Pakanen et al. 2016). In the same area, blue tits did not advance their breeding phenology over the decades (Vatka et al. 2014). In Germany, it was found that blue tits but not great tits adjusted their laying date to food peak (Smallegange et al. 2010), and in a British population, the phenology of blue tits but not great tits changed over time (Goodenough et al. 2011).

In our study, phenological advancement was different between the great tits and blue tits, and because of this, their median laying dates were converging to each other and in the last decade these became similar (Fig. 3a). Breeding of great tits slightly shifted towards earlier dates (by  $0.33 \text{ d yr}^{-1}$ ), thus the timing of breeding probably remained synchronized with the caterpillar peak. On the other hand, in the blue tit breeding time has not advanced, thus caterpillar peak date moved about 10 d closer to blue tit annual median laying date during the study period. Considering the duration of egg-laying, incubation and nestling feeding periods (see Material and methods), the optimal start of breeding would be around four weeks before caterpillar peak. In this case, the timing of food abundance peak and the maximum need of nestlings (which is between ca 6 and 16 d, see Royama 1966) would match. In blue tits, clutch size reduction appeared during the first half of the study period, which can be an adaptive response, as it shortens the egg-laying and incubation periods and makes it possible to provide enough food for the brood even if they miss the caterpillar peak. This inability to breed earlier may also explain why the blue tit does not increase its clutch size even after extreme caterpillar gradations (our unpublished data). In contrast to this, clutch size in great tits did not change over the decades, similarly to another population in England (Cresswell and McCleery 2003), which might be because of the optimal advancement of timing. The onset of breeding in blue tits may not be able to advance due to some unknown constraint. A photoperiod trigger on the physiological cycle of birds could be an obstacle to earlier breeding beyond a certain point, regardless of rising temperature, as the photoperiod does not change over a few decades, and as it has been demonstrated in blue tits, photoperiod could be very important in controlling reproductive behaviour (Lambrechts and Perret 2000). If warming cannot override the absence of this trigger in earlier dates with shorter daylight periods, it may preclude breeding shift in blue tits if they have already reached this border.

## Conclusions

Our results in part contradict the general hypothesis that teleconnection indices explain the long-term trends in biological processes better than local weather (Hallett et al. 2004). In our system, the AO and local temperature associated with phenology of tits and caterpillars. Across the 33-year period, laying date advanced more strongly in great tits, while clutch size showed a negative tendency in blue tits. These results indicate that using alone the most commonly analysed global climatic indices (i.e. the ENSO, the NAO) could be misleading when one interprets the climate change induced biological processes. Furthermore, as climatic fluctuations are spatially different, the responses of animal populations could also vary geographically, so it is essential to explore these processes in underinvestigated European regions like the Carpathian Basin.

## Data availability statement

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.zw3r2284n>> (Laczi et al. 2019).

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*Conflict of interest* – None.

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Supplementary material (available online as Appendix jav-02179 at <[www.avianbiology.org/appendix/jav-02179](http://www.avianbiology.org/appendix/jav-02179)>). Appendix 1.