


Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders

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Abstract

Many organisms adjust their reproductive phenology in response to climate change, but phenological sensitivity to temperature may vary between species. For example, resident and migratory birds have vastly different annual cycles, which can cause differential temperature sensitivity at the breeding grounds, and may affect competitive dynamics. Currently, however, adjustment to climate change in resident and migratory birds have been studied separately or at relatively small geographical scales with varying time series durations and methodologies. Here, we studied differential effects of temperature on resident and migratory birds using the mean egg laying initiation dates from 10 European nest box schemes between 1991 and 2015 that had data on at least one resident tit species and at least one migratory flycatcher species. We found that both tits and flycatchers advanced laying in response to spring warming, but resident tit populations advanced more strongly in relation to temperature increases than migratory flycatchers. These different temperature responses have already led to a divergence in laying dates between tits

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and flycatchers of on average 0.94 days per decade over the current study period. Interestingly, this divergence was stronger at lower latitudes where the interval between tit and flycatcher phenology is smaller and winter conditions can be considered more favorable for resident birds. This could indicate that phenological adjustment to climate change by flycatchers is increasingly hampered by competition with resident species. Indeed, we found that tit laying date had an additional effect on flycatcher laying date after controlling for temperature, and this effect was strongest in areas with the shortest interval between both species groups. Combined, our results suggest that the differential effect of climate change on species groups with overlapping breeding ecology affects the phenological interval between them, potentially affecting interspecific interactions.

KEYWORDS

adaptation, birds, climate change, competition, information use, laying date, nest boxes, timing

1 | INTRODUCTION

Climate warming causes the advancement of organismal phenology, but phenological sensitivity to climate warming often differs among trophic levels (Thackeray et al., 2010, 2016), which can cause mismatched reproductive timing between predator and prey (Parmesan & Yohe, 2003; Stenseth & Mysterud, 2002; Visser & Both, 2005). This may consequently lead to lowered offspring condition (Durant, Hjermmann, Ottersen, & Stenseth, 2007; García-Navas & Sanz, 2011; Reed, Jenouvrier, & Visser, 2013; Samplonius, Kappers, Brands, & Both, 2016). Residents and migrants have been hypothesized to differ in response to temperature trends in their breeding areas, with residents being more flexible to respond than (especially long-distance) migrants (Berthold, Fiedler, Schlenker, & Querner, 1998). Long distance migrants were recently shown to be the least responsive to climate warming on the migrant-resident continuum (Usui, Butchart, & Phillimore, 2017), and the consequences of climate change on population demography appear to be most negative for long-distance migratory bird species (Both, Bouwhuis, Lessells, & Visser, 2006; Both et al., 2010). This is especially true for those migratory species with the weakest phenological response to temperature changes (Møller, Rubolini, & Lehikoinen, 2008; Newson et al., 2016), supporting the role of trophic synchrony, although this likely depends on the specific ecology of each species (Dunn, Winkler, Whittingham, Hannon, & Robertson, 2011). The basic rationale underlying inflexible adjustment of migratory birds is that a flexible response of laying date to directional temperature changes is constrained by arrival date at the breeding grounds (Both & Visser, 2001), whereas resident species can more easily adjust the onset of breeding to local temperature changes.

Two recent long-term studies gave contrasting evidence to the hypothesis that migrants adjust their laying dates to a lesser extent to temperature than sympatric residents: in the UK, the migratory pied flycatcher, *Ficedula hypoleuca*, was less sensitive in its laying date response to spring temperature (-2.3 days/ $^{\circ}$ C) than resident

tits (-4.8 days/ $^{\circ}$ C) (Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016). In contrast, in Sweden, the difference in response between flycatchers and tits was mostly absent (pied flycatchers: mean: -1.62 days/ $^{\circ}$ C ($N = 3$ time series; $SE = 0.19$); blue tits, *Cyanistes caeruleus* and great tits, *Parus major*: mean: -1.90 days/ $^{\circ}$ C ($N = 6$ time series; $SE = 0.14$); time series from 1970/80s to 2010s, Källander et al., 2017). The causes of these contrasting patterns are unclear, but could in part be due to differential time series durations or differential methodologies. For example, Phillimore et al. (2016) used a sliding window approach to determine the temperature window that was best correlated with egg laying phenology, whereas Källander et al. (2017) used the 30-day temperatures before the mean egg laying phenology. Both methods are widely used, but it is possible that different methods impact estimates of phenological sensitivity (van de Pol et al., 2016), and so a comparison between these studies remains problematic. Such differences in methodologies and published phenological responses to temperature plead for a more general and standardized description on how migrants and resident species sharing the same environment respond to between year variations in temperatures, and how this may affect the interaction between these species.

Responses in laying or hatching date are often interpreted in relation to the phenology of underlying trophic levels, but it is important to consider that also changes in interspecific competitor timing (Samplonius & Both, 2017) could act as selection pressures that determine the optimal timing response. European tits and flycatchers are ideal model species to study differential adjustment to climate change. Both resident tits and migratory flycatchers readily breed in nest boxes, which have been recorded across European locations for several decades. Blue and great tits are year round residents, although in Northern latitudes, they show irruptive migration, which highly depends on the annual conditions (Ulfstrand, 1962). Pied flycatchers and collared flycatchers *Ficedula albicollis* breed in Europe, but pied flycatchers migrate to Western Africa in the fall (Ouwehand et al., 2016) and collared flycatchers winter south of the

equator (Briedis et al., 2016). Tits and flycatchers fiercely compete for nesting sites during the breeding season (Ahola, Laaksonen, Eeva, & Lehtikoinen, 2007; Merilä & Wiggins, 1995; Slagsvold, 1976, 1978) and also partly capitalize on the same diet (Cholewa & Wesolowski, 2011; Török, 1986). Aside from being competitors, flycatchers may also benefit from social information gained from tits (Kivelä et al., 2014; Samplonius, Kromhout Van Der Meer, & Both, 2017; Seppänen & Forsman, 2007; Seppänen, Forsman, Mönkkönen, Krams, & Salmi, 2011; Slagsvold & Wiebe, 2017). Both information use and competition have phenological components: flycatcher mortality in tit nest boxes increased with more phenological overlap between tits and flycatchers (Ahola et al., 2007; Merilä & Wiggins, 1995), and an experimental study showed that flycatchers preferentially settled in forest patches with early breeding tits (Samplonius & Both, 2017). If climate warming has differential effects on the phenology of these (and other) resident and migratory species of the same guild, then phenological components of interspecific interactions may be affected.

In this study, we capitalize on 10 long-term nest box schemes from across Europe, which vary in the extent of spring warming. For each site, time series on laying date phenology of at least one species of resident tit and one species of migrant flycatcher was available (for details, please refer to Table S1). This study addresses three questions. First, does the degree of adjustment of mean laying date to temperature differ between resident tits and migratory flycatchers? We expect that resident tits are more flexible in their laying date response to temperature than migratory flycatchers. Second, does differential climate sensitivity between residents and migrants (if the first hypothesis is true) affect the phenological interval over time between these species groups? We expect that the phenological interval between resident and migratory birds diverges if residents respond more strongly to climate change. We also expect that this divergence over time differs across latitudes: in areas that are biogeographically more hospitable for resident species (Southern latitudes: Herrera, 1978), we expect stronger phenological divergence because resident tits may force flycatchers to adopt a later phenology due to increased competition. Related to this, our final hypothesis is that resident species may affect the timing response of migratory species. Our main expectation here is that the timing response of flycatchers may in part be adjusted to their timing in relation to resident tits (after controlling for the effect of temperature on laying date). This effect is expected to be stronger in populations where the phenological interval between tits and flycatchers is smaller.

2 | MATERIALS AND METHODS

2.1 | Data selection

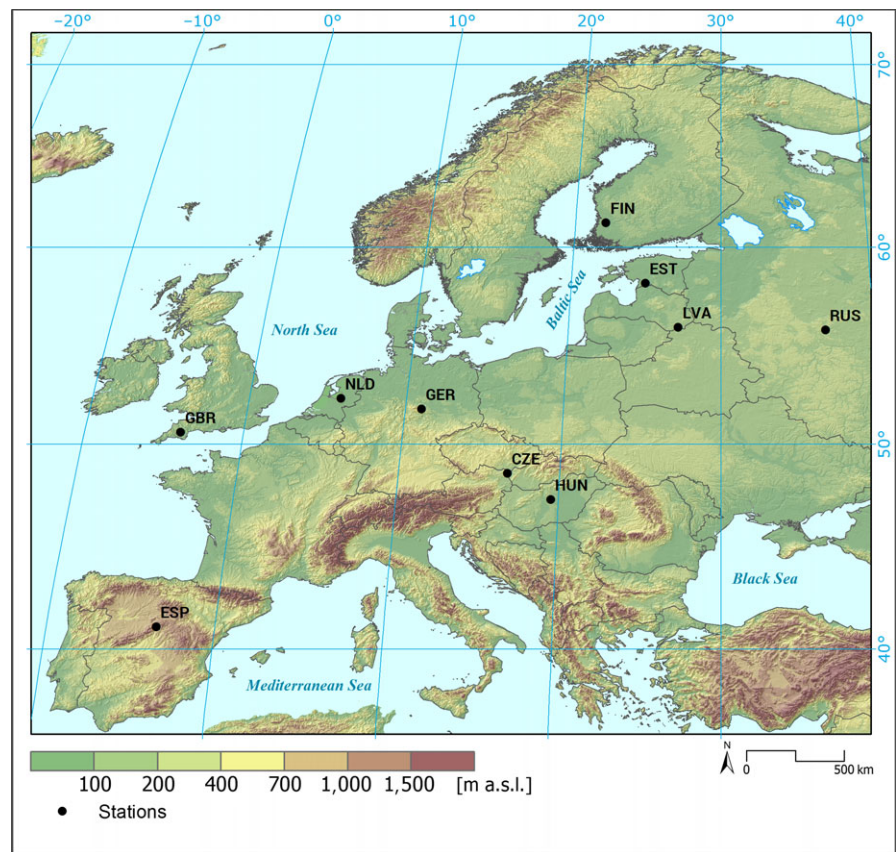
To standardize our approach and avoid reporting bias, we used all the data series of which at least 20 years of phenological data of both tits and flycatchers were available (Figure 1, Table S1). The species we used in this analysis were resident great and blue tits and migratory pied and collared flycatchers (Table S1). Although in

Northern latitudes tits are irruptive migrants, there are data showing that populations have become more resident over the past decades (Smallegange, Fiedler, Köppen, Geiter, & Bairlein, 2010), but not in all populations (Meller et al., 2016; Nilsson, Lindström, Jonzén, Nilsson, & Karlsson, 2006). At most these populations are short distance migrants and arrive much earlier at the breeding grounds than long distance migratory flycatchers. We restricted the time series length to the period 1991–2015 because all populations had data for these years (except Czech Republic, which ran until 2012; Finland missed the year 2001; Spain missed the year 2003). Only datasets with an average sample size larger than 15 nests per species per year were used in the analyses (lowest in a single year: $n = 6$ in a Russian population of great tits). Nest boxes were checked at least weekly in most populations, and laying initiation dates (hereafter laying dates) were established under the assumption that these species lay one egg each day. For each population, we calculated the annual mean and standard deviation in laying date. Only first broods were included in this analysis, the range of which was defined as the mean laying date of the first five nests plus 30 days (per year, per population, per species). In one population (Germany), we only had hatch dates available, which were used for the analysis instead of laying dates, because the temperature slopes in relation to hatch dates closely match those in relation to laying dates ($R^2 = .93$, Table S3). Daily mean temperature data were taken from meteorological stations near (<100 km) each breeding site (Table S2). In some cases, temperature data from several stations had to be combined due to missing data in one of the stations. For example, in the case of Germany, we used the average temperature of three weather stations in the Harz Mountains at similar altitudes, because for some relevant days, the data from one or two of the stations were missing.

2.2 | Sliding window analyses

It is well known that most birds lay earlier during warm years, but it is unknown which cues are directly responsible for this response. Earlier analyses of responses of laying date to temperature have often used an arbitrary window (i.e., the 30 days prior to the overall or to the start of the time series population mean laying date: Both et al., 2004; Visser et al., 2003). When comparing responses for more populations, such a fixed time window length may not capture the local variation in ecology because habitats may differ in the speed of the phenological responses to temperature (Mägi et al., 2009). Therefore, we have selected for each area and species combination the best explaining time window, using a sliding window approach with the climwin package (Bailey & Van De Pol, 2016; van de Pol et al., 2016) in R 3.3.1 (R Development Core Team, 2016). The mean temperature during the period that was best correlated with the mean timing of laying across years will hereafter be referred to as the “climate window.” We restricted the possible time windows by letting the starting date vary from 15 to 60 days prior to the overall average annual laying date, the window being at least 15 days. In all cases, more than one climate window was within 2 AIC of the best climate window, and the window was calculated using a model average of the opening and closing of these best

FIGURE 1 Geographical locations of the breeding data used in the analysis with at least one tit and one flycatcher species. All time series ran from 1991–2015 (except Czech Republic 1991–2012). More details on the locations and species can be found in Table S1



climate windows. Climwin compares the model outputs of thousands of models, the AIC of which it plots graphically as when the temperature window opens (y-axis) and closes (x-axis) in relation to the reference date, which were set to the mean average laying date per population per species, rounded up to the next integer. For example, if a great tit population had a mean laying date of 20.1 April, climwin compared all temperature windows larger than 15 days ranging from 21 February to 21 April. An example output of climwin for the Dutch population of great tits can be found in the supplementary information (Figure S1). In all cases, the best explaining models fell in the same cluster of window openings and window closings, so using a model averaging approach was justified. Finally, bird laying dates were regressed against the mean temperature of the previously identified climate window. Slopes and intercepts of the top models were highly similar (Figure S1).

2.3 | Phenological sensitivity to temperature

To analyze whether resident tits and migratory flycatchers had similar or different laying date responses to temperature, we centered all data for each specific population and species climate window by subtracting the mean, and the same was done with laying date for each population and species. We centered for each population separately to avoid over- or underestimation of the overall slope due to spatial variation (de Keyser, Rafferty, Inouye, & Thomson, 2017). Next, statistical analyses on the relative temperature vs. relative laying date slopes were performed using linear mixed effect models

(LMER) in lme4 in R (Bates, Mächler, Bolker, & Walker, 2015), using sample size as a weight factor. We regressed “Laying date (centered per population and species group)” against “Species (blue tit, great tit, pied flycatcher, or collared flycatcher),” “Spring temperature (output from climwin, centered per population and species),” “Year (centered, continuous),” the interaction between “Species” and “Spring temperature” (as we wanted to test whether tit and flycatcher laying dates ~ temperature slopes differed), and “tit: temperature|population” and “flycatcher: temperature|population” as a random slopes (as we expected laying date ~ temperature slopes to vary between species and populations). “Year” was used as a continuous covariate to account for temporal patterns in laying date that were not attributable to temperature, and the interaction between “Year” and “Species” was included to test whether temporal patterns not governed by temperature differed between tits and flycatchers. Backwards elimination was implemented if interactions or covariates were non-significant. We also tested for multicollinearity between “Year” and “Spring temperature” and found a variance inflation factor of 1.062, which does not present a multicollinearity issue.

2.4 | Laying date over time vs. temperature change over time

We wanted to test whether birds in areas that experience more warming also advance their laying date the most over the years (Both et al., 2004). Therefore, for each population and species group separately, we calculated the slope of laying date against year and

temperature against year and regressed those against each other. We then used a linear model (LM) with “laying date ~ year slope” as a response variable, and “Temperature ~ year slope” and “species group” and the interaction between them as predictors (as we expected, the response of tits and flycatchers to temperature may differ). The expectation was that in areas that have experienced more warming, birds have also adjusted their breeding phenology more. The Czech Republic population was not included for this analysis, as it did not include the years 2013–2015, which may affect temporal trends. Moreover, two tit populations from Hungary were included (both blue and great tit).

2.5 | Latitudinal variation timing interval tits and flycatchers

Next, we analyzed whether the phenological interval between mean tit and flycatcher laying dates within areas and years is affected by temperature, as this may affect competitive and facilitative interactions between species. Additionally, species-specific climate windows may experience different degrees of warming, so it is vital to study how this in turn affects phenological overlap between them (Ahola et al., 2007). To address this question, we calculated the differences per year in phenology between tits and flycatchers for each population by subtracting the mean tit laying date from the mean flycatcher laying date. This variable was regressed against the “Temperature difference” in species-specific climate window. This variable was calculated by subtracting the temperature of the tit climate window from the temperature of the flycatcher climate window (Ahola et al., 2007). Using LMER, covariates used were “Year” and “Latitude” and the interaction between them, as we expected, the degree of phenological divergence between residents and migrants to be more extreme at lower latitudes. The rationale for including the interaction between “Year” and “Latitude” comes from the biogeographical pattern that Northern latitudes are less hospitable to resident species (Herrera, 1978) and have a larger interval between tit and flycatcher phenology. Therefore, competition between tits and flycatchers may be more severe in more Southern areas, subsequently leading to a higher degree of phenological divergence between them. Thus, we hypothesized the temporal divergence between tit and flycatcher phenology to be higher in lower latitudes. All variables were centered per species per population except “Latitude” (which was centered by subtracting the mean latitude of 52.01376). We added a random slopes structure of “Temperature difference|Population,” as we expected, slopes to vary among populations. Backwards elimination was implemented if covariates were nonsignificant. We also tested for multicollinearity between “Year” and “Temperature difference” and found a variance inflation factor of 1.0067, which does not present a multicollinearity issue.

2.6 | Does tit timing predict flycatcher timing?

Finally, we were interested in whether the degree of phenological overlap with tits affected the response of flycatchers. To study this

question, we regressed flycatcher mean laying dates against “Temperature (centered for each population)” with “relative tit phenology (centered for each population)” and “mean population tit-flycatcher interval (centered across all populations)” as covariates and the interaction between the latter two using LMER. We expected that tit phenology would affect flycatcher phenology to a larger extent in populations with a smaller interval between tit and flycatcher phenology. In this analysis, we implemented “Temperature|population” as a random slope, as we expected, temperature slopes to differ between populations.

3 | RESULTS

3.1 | Sliding window analysis

Tit and flycatcher annual mean laying dates were negatively correlated with spring temperature, but responses were to species- and area-specific climate windows, with tits on average responding to earlier (paired *t* test: mean of differences -21 days, $t = -6.77$, $p < .001$), but not to longer (paired *t* test: mean of differences 6.11 days, $t = 1.09$, $p = .31$) climate windows (Figure 2, Table S3). The mean climate window across all populations was from 13 March to 24 April for tits, whereas for flycatchers, it spanned from 7 April to 12 May. Interestingly, the climate window (median value of the entire window) to which tits responded became significantly later toward Northern latitudes (1.04 days/latitude, R^2 (adj) = .425, $t = 2.765$, $p < .03$), but this was not the case for flycatchers (0.356 days/latitude, R^2 (adj) = $-.096$, $t = 0.543$, $p = .60$). Window length did not correlate with latitude for either species group (tits: $p = .267$, flycatchers: $p = .463$).

3.2 | Phenological sensitivity to temperature

Tits were on average twice as sensitive in their phenological response to temperature than flycatchers in the same regions

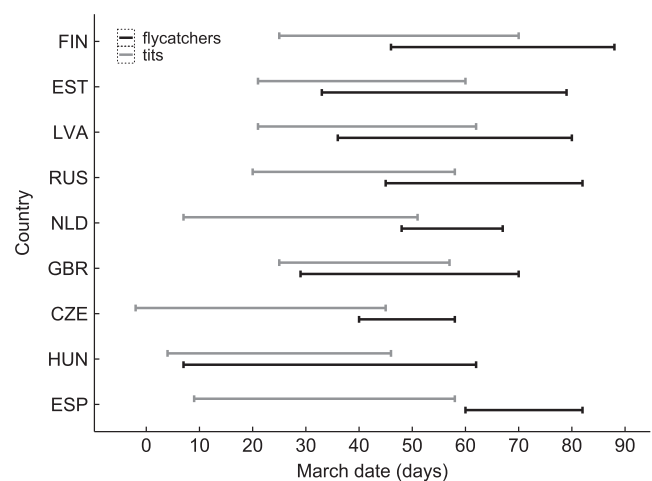


FIGURE 2 Best-fit climate windows as calculated by a sliding window approach in climwin. Temperatures in these windows were used for further analysis. Countries are ordered by latitude

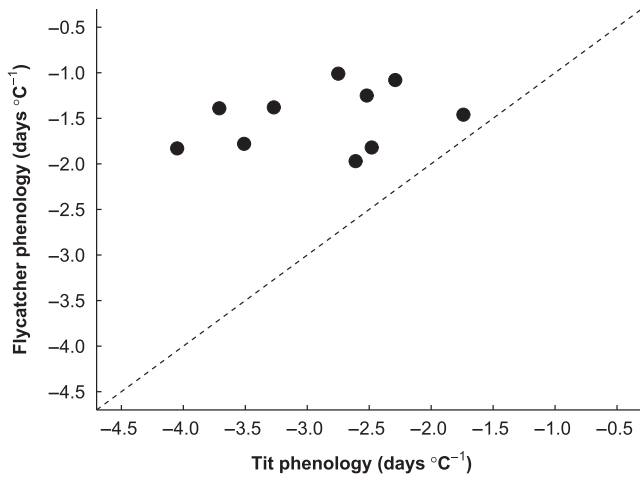


FIGURE 3 Comparison of phenological responses of tits and flycatchers to temperature within the same breeding locations. Each point compares two population specific laying date ~ temperature slopes. Tits clearly show a higher degree of phenological sensitivity to temperature than flycatchers (all points are above $x = y$ line). Tit and flycatcher responses within sites were not correlated

TABLE 1 LMER output of relative annual mean laying dates (LD) in relation to local spring temperature across 10 European sites. Laying dates and mean temperature were centered for each species and population so only differences in slopes remained. Random slopes were fitted for each species group and area. Blue tits were the baseline in the model. Great (GT) and blue tits (BT) did not differ in their response to temperature, but they responded more strongly to temperature than pied (PF) and collared (CF) flycatchers. Additional year effects did not differ between species (see also Figure 3)

Laying date (LD) ^a	Estimate (SE)	$t_{503,11}$	Pr(> t)
Temperature BT (°C)	-3.37 (0.36)	-9.07	<0.0001
Year	-0.0983 (0.014)	-6.85	<0.0001
Temperature × GT	0.53 (0.39)	1.36	0.181
Temperature × PF	1.85 (0.38)	4.89	<0.0001
Temperature × CF	1.83 (0.43)	4.29	<0.001

^aRandom effect variance ± SD 'flycatcher :temperature|area' = 0.0282 ± 0.168; 'tit : temperature|area' = 0.166 ± 0.407.

(Figure 3, Table 1). Tits on average advanced their phenology by -3.37 (blue tits) and -2.84 (great tits) days per °C, whereas the advancement was significantly less for pied and collared flycatchers with -1.52 and -1.54 days per °C, respectively (Table 1). Moreover, compared to flycatcher populations (-1.97 to -1.01 days/°C), the temperature slopes of tits (-4.05 to -1.74 days/°C) among populations was significantly more variable (Bartlett's $K^2 = 5.24$, $p = .022$). Interestingly, the temperature slopes of tit and flycatcher laying dates in the same populations were not significantly correlated (Figure 3, R^2 (adj) = -.034, $N = 10$, $p = .426$) even though the temperature cues for tits and flycatchers within years were positively correlated (R^2 (adj) = .178, $p < .0001$). We further found that independent of the temperature response, all species advanced their

TABLE 2 Model output of the annual mean laying dates slopes (LD/year) among populations in relation to the population-specific degree of warming (°C/year) across 10 European study sites. In areas that warmed more, tits advanced their laying date more, but flycatchers did so to a lesser degree (see also Figure 4)

LD/year slope	Estimate (SE)	$T_{15,3}$	Pr(> t)
(Intercept)	-0.122 (0.038)	-3.219	0.0054
°C/year slope	-3.014 (0.796)	-3.785	<0.0016
Species group flycatcher	0.130 (0.045)	2.913	0.010

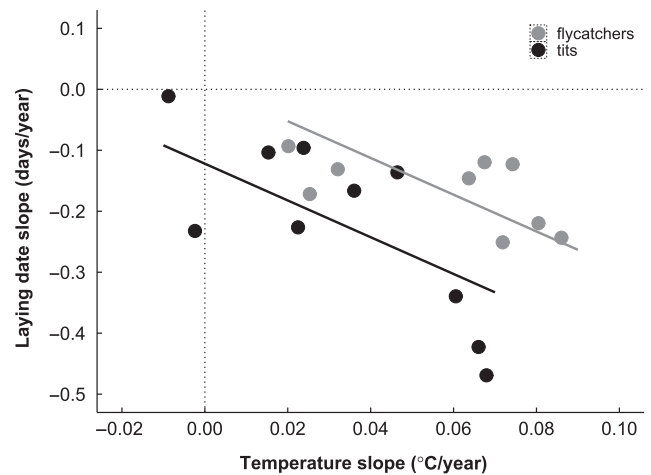


FIGURE 4 Comparison of the temporal laying date slope with the temporal temperature slope. Both tits and flycatchers adjusted their phenology more in areas with more warming between 1991 and 2015, but flycatchers did so to a lesser extent

laying dates by an estimated -0.10 days per decade, but this effect did not significantly differ between species (Table 1).

3.3 | Laying date over time vs. temperature change over time

The between-population variation in temporal laying date trends could be explained by the local trends in temperatures (as in Both et al., 2004), but to a lesser degree for flycatchers. Areas with more local spring warming over the past decades showed greater temporal phenological advancement of both tits and flycatchers ($p < .002$, Table 2, Figure 4), but less so in flycatchers for the same degree of warming compared to tits.

3.4 | Latitudinal variation timing interval tits and flycatchers

The interval in laying dates between flycatchers and tits varied from about 30 days to only 5 days, and this interval was smaller when flycatcher-specific temperatures were high relative to the tit-specific temperatures from the same year (Figure 5, Table 3). The interval declined by 1.76 day per degree centigrade difference in species-specific climate window temperature (Figure 5, Table 3, $p = .002$),

showing that species-specific climate windows may be differentially affected by climate change. The mean interval between tits and flycatchers increased by 0.94 days per decade (Table 3, $p = .0015$), an effect that was larger at lower latitudes (Figure 6, Table 3, $p = .015$), showing that the divergence in laying dates between tits and flycatchers was mostly observed south of 50°N.

3.5 | Does tit timing predict flycatcher timing?

In the final analysis, we were interested in whether tit phenology explained additional variation in flycatcher phenology in addition to the temperature slope. Interestingly, we found that flycatchers were apparently affected by the phenology of tits in their laying date. In addition to the effect of temperature and year, residual flycatcher mean laying date was delayed by 0.077 days for each day that tits were relatively late ($p = .0067$, Table 4), and this effect was larger in populations where the mean interval between tit and flycatcher

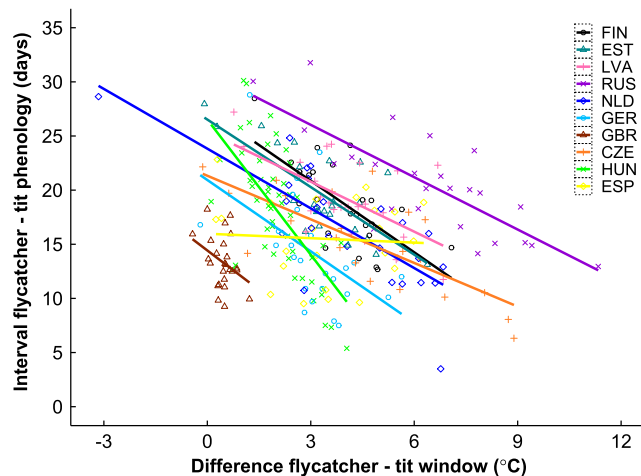


FIGURE 5 Comparison of the phenological interval between tits and flycatchers in relation to the difference in species-specific temperature windows. The interval between tits and flycatchers decreases when the tit climate window is relatively cold and the flycatcher climate window is relatively warm

TABLE 3 Determinants of the interval between tit and flycatcher mean laying dates include year (as continuous variable), the difference in species specific prelaying temperatures (see also Figure 5), latitude, and the interaction between year and latitude. Predictors were centered for each population and species

Flycatcher–tit LD interval ^a	Estimate (SE)	$t_{266,3}$	Pr(> t)
(Intercept)	5.978 (0.972)	6.149	<0.0001
Flycatcher–tit °C difference	-1.759 (0.347)	-5.062	0.0020
Year	0.0942 (0.0293)	3.216	0.0015
Latitude	0.215 (0.124)	1.742	0.151
Year × Latitude	-0.0131 (0.0053)	-2.454	0.0148

^aRandom effect variance ± SD '1 | area' = 6.68 ± 2.58; 'temperature difference|area' = 0.956 ± 0.978.

breeding was smaller (interaction "tit laying date" × "mean population tit flycatcher interval": 0.0286 day increase in effect size for each day that the laying date interval between tits and flycatchers decreases, Table 4). The overall mean interval between tits and flycatchers across all populations was 17.0 days, ranging from 13.3 (−3.7 centered) days in Dartmoor (GBR) to 20.6 (+3.6 centered) days in Zvenigorod (RUS). To illustrate the effect of the interaction term in this model (Table 4), the estimated effect of tit phenology on flycatcher phenology at these endpoints in the distribution ranged from (−0.0286 × −3.7 + 0.077) 0.183 flycatcher days/tit day to −0.026 flycatcher days/tit day. In other words, flycatchers adjusted their laying dates more in response to tit laying dates in populations where the mean timing interval between them was smaller. "Latitude" was not retained in the final model.

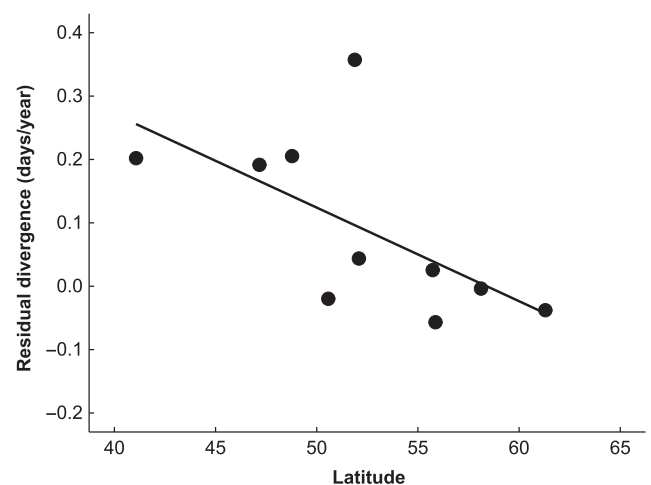


FIGURE 6 Model output of the temporal divergence trend (1991–2015) between tit and flycatcher phenology across latitudes after accounting for species-specific climate windows. Divergence between tits and flycatchers was larger at lower latitudes ($p = .015$, Table 3)

TABLE 4 Effect of tit laying dates and other factors on flycatcher laying dates in the same population, across 10 European sites. The positive effect of tit laying date on flycatcher laying date was especially strong in populations where tits and flycatchers overlap more in seasonal timing. For this analysis, flycatcher phenology was regressed against spring temperature, year, population-specific relative tit phenology, mean population-specific interval between tits and flycatchers, and the interaction between this interval and relative tit phenology. All predictors were centered

Flycatcher LD ^a	Estimate (SE)	$t_{264,5}$	Pr(> t)
(Intercept)	-0.009 (0.120)	-0.073	0.941
Spring temperature	-1.205 (0.096)	-12.60	<0.0001
Year	-0.075 (0.018)	-4.189	<0.0001
Relative tit phenology	0.0765 (0.028)	2.752	<0.007
Mean tit–flycatcher interval	0.0034 (0.053)	0.063	0.950
Mean interval × tit phenology	-0.0286 (0.012)	-2.39	0.0183

^aRandom effect variance ± SD '1 | area' = 0.000 ± 0.006; 'temperature|area' = 0.005 ± 0.071.

4 | DISCUSSION

Here, we presented a Europe-wide assessment of phenological advancement of tits and flycatchers in response to climate change and show three important differences in the response of these resident and migratory nest box breeders. First, resident tits advanced their phenology on average twice as much in response to between year temperature variation than migratory flycatchers, and within site phenological sensitivity to temperature of tits and flycatchers were uncorrelated, even though the temperature cues of tits and flycatchers were highly correlated. Second, tit populations in areas that warmed more also advanced their laying date more, but the same was not true for flycatchers (in contrast to Both et al., 2004). Overall, the mean laying date interval between tits and flycatchers has diverged over the past 25 years by about 0.94 days per decade, an effect that was stronger at lower latitudes. Finally, in addition to temperature, flycatchers appeared to adjust their laying date partly in the same direction as the laying date of tits, an effect that was stronger in populations that had a smaller phenological interval between tits and flycatchers. Climate change may, therefore, affect the phenological interval between competing species with knock-on effects on species interactions including competition and information use.

Our results clearly demonstrate that resident tit populations are generally more flexible in adjusting to variation in temperatures than migratory flycatcher populations from the same breeding areas. The large geographical scale at which our analysis was performed allows us to draw more general conclusions about this pattern than previous studies, one of which corroborated our findings (Phillimore et al., 2016), while another did not (Källander et al., 2017). We further found that, in contrast to a previous study (Both et al., 2004), flycatchers in areas that warmed more did not also advance their laying dates more over time, but we found that pattern to hold for tits. A possible explanation of this is that the trends observed by Both et al. (2004) in both temperature and flycatcher laying dates included more extremes, probably because their time series started in the 1980s and lasted until 2002, a period with apparently more local spring warming than the period reported here, and more advancement of flycatcher laying dates. It must be noted that differences found between tits and flycatchers (interpreted as differences between residents and migrants) in this study may alternatively be explained by phylogeny. Interestingly, a recent meta-analysis found that phylogeny could explain some variation in phenological responses to temperature, but a larger degree of variation in responses between species was explained by them being along the resident migrant continuum (Usui et al., 2017). Long distance migrants had lower degrees of response to temperature changes than residents and short distance migrants (Usui et al., 2017), corroborating what we found in this study.

As climate warming continues, resident species are expected to cope better with such changes, as they are potentially better able to track phenological optima through plasticity (Phillimore et al., 2016; Vedder, Bouwhuis, & Sheldon, 2013). Our analyses show that

migratory bird populations may be particularly vulnerable to climate warming, as their capacity to respond flexibly to changes at the breeding grounds are more limited than resident species, although we have not analyzed phenotypic plasticity at the individual level in this study. This is also in line with a study that showed the most rapidly declining passerine populations are those of migratory birds breeding in seasonal habitats (Both et al., 2010). Alternatively, flycatchers may not need to adjust as much to temperature changes as tits because they have a more generalist diet than tits. Nevertheless, pied flycatchers in a Dutch population preferred caterpillar prey and their nestlings performed better when well matched with the caterpillar peak (Samplonius et al., 2016), and local population declines were strongly correlated with the date of the caterpillar peak (Both et al., 2006).

Plasticity is likely the most important mechanism through which individuals adjust to climate warming (Charmantier & Gienapp, 2013; Charmantier et al., 2008; Phillimore et al., 2016), but we also reported on an additional advancement over time by 0.98 days per decade in both tits and flycatchers (Table 1), potentially explained by other mechanisms. There is still the potential for phenotypic plasticity to operate through other (unknown) cues here, but alternatively, this pattern could reflect a microevolutionary response of laying date with selection favoring early reproduction in years where offspring return under warm spring conditions (Visser et al., 2015). However, this explanation cannot be tested here as we cannot discern individual from population responses in our data. In addition, being born early might entrain the circannual clock to an earlier schedule through ontogenetic effects, potentially leading to being earlier the following year (Both, 2010; Ouweland, Burger, & Both, 2017). Discerning between genetic and nongenetic effects in adjusting to climate change is critical in directing future decisions on species conservation. For example, directional selection on timing genes may reduce genetic variation in a population, whereas ontogenetic effects would not.

Our finding that the degree of phenological divergence over time between tits and flycatchers is higher in more Southern latitudes can be explained in different ways. First, Southern latitudes have milder winters, causing relatively more resident birds to survive and occupy more suitable breeding space (Berthold et al., 1998), which may push the timing of migratory birds to become relatively later through interspecific competition. This is partly supported by our observation that flycatchers are more affected by tit phenology in areas with more overlap between their phenologies (Table 4). However, this could also be a third variable effect as previously discussed. Second, it is possible that, especially in Southern latitudes, migratory birds are constrained by arrival date, as spring starts the earliest there. In our case, this is not true, because the most Southern population lays considerably later because it is mountainous. Finally, latitude could be a proxy for photoperiod, which may be used as a birth date cue during early life, the effect of which differs between Northern and Southern Europe. In Southern Europe, photoperiod increases for later born young, whereas Northern birds hatching after the solstice experience decreasing day lengths, which may have caused their

recovery dates during spring migration to advance with progression of the season (Both, 2010). The effect of photoperiod on flycatcher laying date may thus differ between North and South, causing differences across latitudes in phenological divergence between tits and flycatchers. Photoperiodic conditions during hatching before and after the solstice could then be an alternative explanation for why there is more phenological divergence in Southern populations than in Northern populations. However, experimental evidence so far shows that hatching date (photoperiodic conditions) probably does not provide birds with an ontogenetic route to adjust to climate change (Ouwehand et al., 2017).

Our finding that flycatcher phenology is positively affected by tit phenology in addition to temperature, especially in areas where the mean laying date interval between them is smaller, begs the question whether flycatchers adjust their laying date in response to the timing of resident tits. This could reflect social information use, a competition driven constraint, or an externally driven adjustment that has affected both species (third variable effect). In support of the information use hypothesis, an experimental study manipulating tit densities found that flycatchers bred the earliest in plots with intermediate densities of great tits (Forsman, Hjernerquist, Taipale, & Gustafsson, 2008), and it was also found that that flycatchers can use timing information of tits for their settlement decisions (Samplonius & Both, 2017). Evidence for competition-driven constraints comes from a study in which flycatchers had more fatal interactions when overlapping more in time with tits (Ahola et al., 2007). Alternatively, a third variable may have affected the response of tits and flycatchers in similar directions. In other words, tit phenology may have been affected by a range of variables aside from temperature, which also may have affected the response of flycatchers. The sum of environmental variables affecting phenology may, therefore, have been captured better by the phenology of the tits than solely by temperature, leading to a stronger association between (residual) tit phenology and flycatcher phenology. This would also explain why this effect was stronger in areas with a higher degree of average overlap between tits and flycatchers. However, the temperature response of tits and flycatchers within populations was not significantly correlated (Figure 3, $p > .4$), suggesting that temperature-driven effects may not be able to account for these patterns in phenological divergence. Nevertheless, we did not experimentally manipulate our birds, so further experimental studies are required to pinpoint whether flycatchers adjust their timing to the laying date of tits. Finally, it could be argued that in populations with higher incidence of second broods might have affected the timing of flycatchers. However, we do not deem this likely, as the timing of a second brood of tits is roughly 6 weeks after the first egg of the first brood is laid (1 week laying, 2 weeks incubation, 3 weeks chick rearing). The mean laying initiation date of flycatchers is 2–3 weeks after the mean laying dates of the first broods of tits, meaning that second broods could not be used as a cue by flycatchers to initiate laying.

The effect of climate change on species interactions has in the past mostly been studied among trophic levels. We here highlight that resident and migrant species of cavity nesting passerines differ

in their degree of adjustment to climate change, which may have knock on effects on species interactions. Nevertheless, both species groups are still generally advancing slower than the phenology of their food resources (Both, van Asch, Bijlsma, van den Burg, & Visser, 2009; Visser & Both, 2005). Such faster advancement of food resources may in turn exacerbate interspecific competition. As species increasingly initiate breeding on the declining slope of food resources, species must compete for fewer resources or change to different habitats with broader food peaks (Burger et al., 2012). In addition, climate warming may decrease adverse conditions in winter leading to increased survival of resident species (Robinson, Baillie, & Crick, 2007). More broadly, Northern latitudes generally contain more migratory than resident species (Herrera, 1978), and if climate warming and subsequent range shifts continue (Gillings, Balmer, & Fuller, 2015), the community composition in warming areas may change toward more resident species. In addition, selective pressures may depend on phenological distributions, in which the optimal response of early individuals may differ from that of late individuals (Miles et al., 2017), a factor that is rarely considered. The result of climate warming on species interactions may, therefore, be multifaceted and unpredictable. Our results indicate that species groups with varying annual cycles differentially respond to temperature changes and potentially affect each other's response to climate warming depending on their phenological interval. Understanding why resident and migratory bird populations differ in their phenological response to climate warming by uncovering the potential role of genetic and ontogenetic adaptation provide interesting avenues of future research. For understanding how this alters competitive interactions and thereby food web dynamics, a better knowledge is required about the ecological interactions between these species, especially in relation to shared and unshared diet components.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

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SUPPORTING INFORMATION

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