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**Phenological plasticity and
reproductive responses
under changing climate:
A long-term study in
Pied Flycatchers.**

By Fernando.

Director:
Co-Director:
Tutor Académico:
Lugar de realización:

David Canal
Enrique González Bernardo
M^a Carmen Hernández González
Museo Nacional de Ciencias Naturales (MNCN-CSIC)
Departamento Ecología Evolutiva

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Abstract

Synchronizing reproduction with optimal environmental conditions is essential for temperate-zone breeders, as phenological mismatches can reduce fitness. Phenological plasticity in timing and investment is crucial under rapid climate change. We investigated whether pied flycatchers (*Ficedula hypoleuca*) from a Mediterranean population adjust laying dates and clutch size in response to specific pre-laying conditions, buffering fitness under shifting spring environments. Analyzing 3,207 breeding records over 34 years, we (i) quantified long-term trends in spring temperature and precipitation; (ii) evaluated whether pre-laying conditions at individual level remained similar over time, suggesting active timing to optimal conditions; (iii) assessed laying date advances with year and spring warming; (iv) quantified clutch size plasticity in relation to laying date, laying synchrony and pre-laying conditions and (v) examined fledging success as a function of phenology and pre-laying conditions. Spring mean temperatures increased, and rainfall declined over time, with laying dates advanced accordingly. Despite climatic shifts, pre-laying conditions remained stable, supporting active adjustment of laying onset. Clutch size declined more steeply with delayed laying when pre-laying temperatures were high. Fledging success increased with earlier laying, regardless of pre-laying conditions. These results suggest that pied flycatchers maintain reproductive performance under changing spring conditions through plastic adjustments in laying date and clutch size.

Resumen

Sincronizar la reproducción con condiciones ambientales óptimas es crucial para los reproductores de zonas templadas, ya que desajustes fenológicos pueden reducir la aptitud biológica. Plasticidad fenológica en el momento e inversión es esencial ante un cambio climático acelerado. Hemos investigado si papamoscas cerrojillos (*Ficedula hypoleuca*) de una población mediterránea ajusten fechas y tamaños de puesta en respuesta a condiciones previas a la puesta específicas, mitigando la reducción de la aptitud biológica bajo cambios de condiciones primaverales. Analizando 3,207 registros de cría a lo largo de 34 años, hemos (i) cuantificado tendencias a largo plazo en temperatura y precipitación primaveral; (ii) evaluado si condiciones previas a la puesta a nivel individual permanecían similar sobre el tiempo, sugiriendo sincronización activa con condiciones óptimas; (iii) evaluado avances en fecha de puesta con el año y calentamiento en primavera; (iv) cuantificado plasticidad en tamaño de puesta en relación a la fecha de puesta, sincronización de fecha de puesta y condiciones previas a la puesta y (v) examinado éxito de vuelo en función de fenología y condiciones previas a la puesta. La temperatura media primaveral aumentó, y la precipitación bajó con el tiempo, con fechas de puesto avanzado proporcionalmente. A pesar de cambios climáticos, condiciones previas a la puesta permanecieron estables, apoyando un ajuste activo del comienzo de la puesta. El tamaño de puesto declinó con más pronunciadamente con la puesta tardía cuando las temperaturas previas a la puesta eran altas. El éxito de vuelo aumento con puestas tempranas, independientemente de condiciones previas a la puesta. En conclusión, estos resultados aluden a que los papamoscas cerrojillos mantienen su adecuación reproductiva ante los cambios en condiciones primaverales mediante ajustes plásticos en fecha y tamaño de puesta.

1. Introduction

Since the mid 20th century environmental changes are accelerating with ongoing human pressure, posing a major global threat to biospheres (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019; Steffen et al., 2015). Despite conservation efforts, the five major drivers of biodiversity decline—habitat loss, pollution, overexploitation, invasive species and climate change (in order of most to least impactful)—are continuing their devastation (Convention on Biological Diversity, 2020; Jaureguiberry et al., 2022). Above all, the rise in global temperatures is accelerating the fastest (Minière et al., 2023). Besides increasing threats synergistically, projections expect rising temperatures to advance in the ranking (Arneth et al., 2020; Wudu et al., 2023). Thus, conservation must consider all those changes, such as climatic factors as even lower-end projections of rising temperatures induce significant consequences for ecosystems and their inhabitants (Arneth et al., 2020). Regarding this certainty of quickly changing conditions, it is crucial to understand the variation in the ability of different individuals and species to cope with biotic and abiotic alterations, as this capacity will largely determine their likelihood to persist.

A primary defense is plasticity, enabling species to keep up with the fast pace of environmental change, while much slower evolution begins to work (Diamond & Martin, 2021). As most ecosystems and organisms function in cycles that are shaped by the rhythm of abiotic cues (e.g. light or climate), alterations in the latter have widespread effects among various taxa (Mougi, 2021). Especially spring is connected to major biological events such as flowering and leafing in plants or migration and breeding in animals, thus most phenological plasticity—adaptations in timing—can be observed here. Early seasonal onset—driven by increased temperature—is matched by advanced and prolonged greening, blossoming or seed germination, insect emergence, animal migration or start of the breeding season (Buitenwerf et al., 2015; Diamond & Martin, 2021; Ettinger et al., 2021; Nash et al., 2023; Parmesan, 2007; Parmesan & Yohe, 2003). These shifts are accompanied by phenotypic adjustments, including physiological modifications like number of offspring to account for resource availability, behavioural changes such as shifting the activity window towards favorable conditions and morphological traits such as increased thickness of leaves or nutrient concentration (Earhart et al., 2022; Stotz et al., 2021). This flexibility increases the ability to maintain fitness under changing environmental stressors. Phenological plasticity—in both timing and investment—is therefore crucial for coping with rapid climate change with minimal fitness consequences.

Birds as many organisms have tight seasonal schedules for their breeding season. Especially migratory ones rely heavily on seasonal timing to coordinate to match optimal climatic conditions and food availability. With changing environments such as warmer spring temperatures, a general trend in earlier laying date has been observed (Bailey et al., 2022; Bates et al., 2023). This shows the strategy to shift timing of biological events with the shifts in environmental cues. In addition, birds may adapt their reproductive effort, namely clutch size based on prevailing environmental conditions.

Here, using a long term, individual-based dataset over 34 breeding seasons, we investigated whether pied flycatchers (*Ficedula hypoleuca*) from a Mediterranean population in central Spain adjust laying dates and clutch size in response to specific pre-laying conditions, buffering fitness under shifting spring environments. Our hypothesis is that (i) the breeding grounds of *Ficedula hypoleuca* are affected by changing climatic conditions in terms of temperature and precipitation (ii) the birds adapt to changing conditions tracking optimal climatic window before egg laying and adjusting egg laying dates accordingly and (iii) clutch size is adjusted to the pre-laying climatic conditions, laying date to reduce fitness cost under less favourable conditions.

2. Aim and objectives

This work analyses long-term data of a pied flycatcher population in central Spain to investigate temporal and life history trait changes in the breeding season caused by changing climatic conditions. The goal is to increase the knowledge about phenological plasticity and reproductive responses of the small, long-distance migrant, the pied flycatcher. Rapidly changing environmental conditions requires them to adopt their migration and breeding schedule as well as their reproductive phenotype in order to maintain their fitness and reproductive success.

We predicted that pied flycatchers track specific pre-laying environmental conditions, and that plastic adjustments in laying date and clutch size buffer fitness costs under shifting climate. To test this, we (i) quantified long-term trends in spring temperature and precipitation; (ii) evaluated whether pre-laying conditions at individual level have remained similar over the study period—implying active timing of laying date to specific conditions; (iii) assessed advances in laying dates over time and with warming; (iv) quantified clutch size plasticity as a function of

laying date, laying synchrony and pre-laying climatic conditions and (v) examined consequences of variation in pre-laying climatic conditions for fledging success.

3. Material and methods

3.1. Study species *Ficedula hypoleuca*

The short-lived (2-3 years) passeriform pied flycatcher (*Ficedula hypoleuca* Pallas, 1764) is a diminutive insectivorous member of the family Muscicapidae with a body mass of 12–13 g and a wingspan of 21.5–24 cm (Lundberg & Alatalo, 1992). It migrates over the Sahara to overwinter in tropical West Africa, returns in April to reproduce in the Western Palearctic until July and remains until October (Ouwehand et al., 2016). Reproduction is single brooded (Lundberg & Alatalo, 1992) and primarily socially monogamous, with some occurrence of facultative polygyny in polyterritorial males (Alatalo et al., 1984; Sternberg, 1989). The masculine sex is the first to arrive to increase chances of securing a high-quality territory and nest site to attract more females (Alatalo et al., 1984; Canal et al., 2012). While its African habitat is varied, in spring and summer it nests in cavities, especially tree holes, with preference for deciduous, but also coniferous and mixed woodlands (Lundberg & Alatalo, 1992). This passerine exhibits a prominent sexual dimorphism during breeding season (Cramp & Perrins, 1993).

Across the Iberian Peninsula, *F. hypoleuca* is irregularly distributed in agglomerations in the mountain ranges of the Central System, the Iberian System, the Cantabrian Mountains and the northern Pyrenees in a thermal range between -9,8 °C and 35,6 °C.

3.2. Study population and area

Data was collected from a breeding population of *F. hypoleuca* close to La Hiruela, Community of Madrid (41°04'N, 3°27'W, 1200–1400 m) and Colmenar de la Sierra, Castilla-La Mancha (40°40'N, 4°8'W, 1750 m) (González-Bernardo et al., 2024). They prefer inhabiting nest boxes over natural cavities (Lundberg & Alatalo, 1992). These artificial brood chambers are installed with a minimum distance of 100 meters in two montane forests (Porri & Montalvo, 1990). One is a 9.3 ha deciduous Spanish oakwood forest (*Quercus pyrenaica* Willd.) and the other a 4.8 ha mixed coniferous forest (mostly *Pinus sylvestris* L.). Both areas are separated by 1.1 km

wide zone lacking cavities for nesting (Camacho et al., 2013). There are 253 nest boxes divided into 172 boxes in the oakwood and 81 in the coniferous forest (Camacho et al., 2013). Both habitats differ not only in tree taxa but also in structure, as the oak forest is mature, structurally complex, and less anthropogenically disturbed, while the pine plantation is homogeneous and shows prominent human intervention (Camacho et al., 2013).

The long-term study began by observing the passerine in natural nest-cavities (Carrascal et al., 1987; Porri & Montalvo, 1990). Later in 1984, 172 nest boxes were installed in the oakwood forest and in 1989, 81 in the pine forest, both of which were maintained to date (Porri & Montalvo, 1990).

3.3. Field work and data collection

The data set analysed here is limited to 2022, as data from subsequent years were not yet added to the database. During the breeding season, starting with the first arrivals, nest boxes were regularly monitored (every 1-3 days) to document laying date, clutch size, date and number of eggs hatched as well as chick survival at day 13 after hatching (Camacho et al., 2016). Eight to ten days after the hatch date adult birds were caught in their nest transformed into a swing trap. The age of most captured adults (about 53 %) could be determined exactly, since hatchlings were ringed preceding fledging (Potti & Montalvo S, 1991), in combination with one of the highest natal philopatry rates for the species, averaging 13 % and reaching a maximum of 22 % (Canal et al., 2014; Potti et al., 2013; Potti & Montalvo S, 1991). For the remaining adults age was inferred as in their second calendar year or older according to moult pattern plus feather coloration (Potti & Montalvo, 1991; Svensson, 2023). Morphometric data registered were wing (± 0.5 mm) and torso length (± 0.01 mm) along with body mass (± 0.1 g) (González-Bernardo et al., 2025).

Cases of marginal ages (six or more) were grouped as to create a broader category with enough data points to improve statistical power and reliability, as well as to simplify the model and to decrease their weight in the model to reduce noise from outliers. After all, the data set confirmed the short-lived life span with most living to 3 years or younger (78.2 %) and some under good conditions reached until 5 years with few birds reaching age 10.

Field protocols for capturing, measuring, and recording data on *Ficedula hypoleuca* have been extensively described in earlier studies belonging to the same data collection project

3.4. Meteorological data

The climatic record used in this thesis stems from the second closest weather station (AEMET in Colmenar Viejo, Madrid , 40°39'N, 3°45'W, 879 m), as the most proximate station (AEMET in Buitrago de Lozoya, 41°00'N, 3°36'W) provides only incomplete documentation of the study period (Agencia Estatal de Meteorología, 2016). Even though, the data available strongly correlates in terms of average temperature and precipitation, thus proving the station in Colmenar Viejo adequate for weather analysis in this study, as also confirmed by Le Vaillant and collaborators (2021). The data of interest here stems from the reproductive season, spanning April to June.

3.5. Statistical analysis

For annual-based analyses I used dataset spanning 33 years throughout the study period (see Supplementary Table S1 in Appendix for descriptive statistics). For individual-based analyses I used a dataset including 3207 reproductive events (see Supplementary Table S2 in Appendix for descriptive statistics). For the clutch size plasticity analysis (see below), I used the 3207 events, while for the fledgling success analysis, I excluded nests with missing clutches/broods (e. g. predated) or those in which experiments that could alter reproductive success were conducted, remaining with 2,550 breeding events. The response variables, predictors, and models used in each phase of the analysis are detailed below.

3.5.1. Assessment of long-term trends in local spring climatic conditions

I quantified long-term trends in spring temperature and precipitation by fitting two separate linear model (lm's) to evaluate directional change in spring temperature and precipitation through the study period: (i) with annual mean spring temperature as the response and (ii) with mean annual spring cumulative precipitation as the response. In both models the main predictor was year (continuous).

3.5.2. Evaluation of temporal stability of pre-laying climatic conditions at the individual level

To evaluate if evaluated whether pre-laying conditions at individual level remained similar over time, I fitted two linear models (lm's) based on annual individual means: (i) with annual mean of pre-laying temperature (calculated as the mean of the individual mean temperatures of the 15 days prior to laying) as the response and (ii) annual mean of pre-laying cumulative precipitation (calculated as the mean of the individual cumulative precipitations of the 15 days prior to laying) as the response. This individual time window was selected to calculate climate variables in accordance with the one selected for the clutch size plasticity model (see subsection 3.6.4). In both cases year was included as the predictor to test whether individual-level pre-laying climatic conditions changed through time.

3.5.3. Analysis of advances in laying date with year and spring warming

I analysed shifts in laying phenology with time and with interannual variation in spring temperature by using two linear models (lm's) to model annual mean laying dates (calculated per year) as the response variable: (i) with year as predictor (to test temporal trend) and (ii) with annual mean spring temperature as predictor (to test association with spring warming).

3.6.4. Quantification of clutch-size plasticity in relation to phenology and pre-laying conditions

Determinants of clutch size plasticity were examined with a linear mixed-effects model (LMM) using clutch size as the response variable. Fixed effects included female age (both at its linear and quadratic terms), laying date, laying synchrony, female body mass, female tarsus length, pre-laying (15 days-window) mean temperature and cumulative precipitation (linear and quadratic terms, allowing the model to test for linear changes as well as for the presence of environmental optima), and the two-way interactions between laying date and each pre-laying variable (both linear and quadratic interaction terms). Breeding habitat (oak forest/pine plantation) and bird origin (locally born/immigrant) were included as categorical predictors, and random intercepts for Female ID, Male ID and Year accounted for repeated measures and among-year variation. Laying synchrony is a parameter that indicates the number of females in a population that are laying eggs at the same time as a given female on a given day and was calculated

following Kempnaers (1993). As a footnote, given that I did not initially know which time window in pre-laying climatic conditions affects the reproduction of pied flycatchers, in a preliminary step I calculated the average temperatures and accumulated precipitation for 5, 10, 15, 20, and 30 days prior to the laying date. I then adjusted different models with the same model structure described above, changing only the climatic variables calculated for different pre-laying time windows, and compared them by AIC, with the 15 days prior to the laying date proving to be the most informative.

3.6.5. Estimation of fledging success responses in relation to phenology and pre-laying conditions

Fledging success as a function of phenology and pre-laying conditions was modelled using a generalized linear mixed model (GLMM, binomial error structure and logit link function). Our response variable was a 2-column matrix that combined the number of chicks that fledged and the number of eggs that failed to produce fledglings (e.g. due to hatching failure or early chick loss, Grueber et al. 2011). Using this matrix as the response variable rather than the ratio of chicks fledged to eggs laid accounts for differences in the absolute number of chicks produced. That is, the breeding success of an individual producing, for example, 3 chicks from 6 eggs, is considered higher than that of a bird producing 2 chicks from 4 eggs, despite the chick-to-egg ratio being 50% in both cases (González-Bernardo et al. 2024). This model included the same fixed and random effects structure as in the LMM modelling the clutch size.

Statistical analyses were done using R-4.5.0 (R Core Team, 2025, <http://cran.r-project.org/>). For the mixed modelling, we used the package “lme4” (Bates et al., 2015). In the GLMM built to analyze the breeding success, the bivariate response variable was calculated using the “cbind” function in R software (R Core Team, 2025). Outliers and influential values were checked for both the response variables and the corresponding whole models using the “performance” package, and none were detected. We also graphically inspected the normality of residuals (Zuur et al. 2010) and discarded both correlation among quantitative predictors using the “stats” package (R Core Team 2022), and collinearity among predictors (all VIFs were below 5; James et al. 2013) using the package “performance”. We compared error distributions and random structures of the models described above by comparing Akaike’s information criterion (AIC; Akaike 1973; Zuur et al. 2009) estimated using the R library “MuMIn” (Barton, 2020). Numeric variables were standardized to mean = 0 and standard deviation = 1 to make

the estimates comparable (Schielzeth, 2010). We assessed the statistical significance of fixed effects, verifying that the 95% confidence intervals of the estimates did not contain 0 (computed using the “car” package; Fox and Weisberg 2011). For data visualization, we used the “ggplot2” package (Wickham, Chang and Wickham, 2016).

4. Results

4.1. Assessment of long-term trends in local spring climatic conditions

Mean spring temperature showed a clear increasing trend over the study period, whereas cumulative spring precipitation did not show a consistent directional change (Table 1; see Figure 1a-b)

Table 1. Results and parameters of the models built to quantify long-term trends in yearly spring (i) mean temperature and (ii) cumulative precipitation. For each fixed effect, the estimate (β), standard error (SE), t-statistic (t), and 95% confidence interval (CI) are indicated. Significant parameters are highlighted in bold.

<i>(i) Mean spring temperature (per year)</i>	Model coefficients and confidence intervals			
Fixed effects	β	SE	t	CI
Intercept	15.362	0.172	85.955	14.997 - 15.726
<i>Year</i>	0.451	0.182	2.484	0.081 - 0.821
<i>(ii) Mean spring cumulative precipitation (per year)</i>	Model coefficients and confidence intervals			
Fixed effects	β	SE	t	CI
Intercept	1354.8	114.36		1121.608 - 1588.089
<i>Year</i>	-	116.13	0	-268.112 - 205.601
	31.260	0	-0.269	

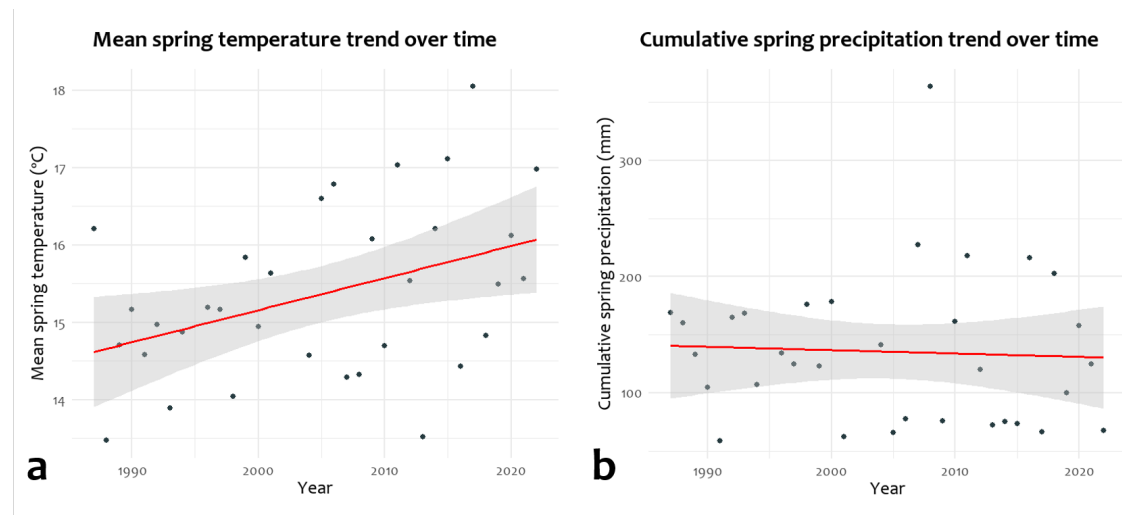


Figure 1. Variation over the study period of spring (a) mean temperatures and (b) cumulative precipitations. The shaded areas around the regression lines show the 95% confidence intervals.

4.2. Evaluation of temporal stability of pre-laying climatic conditions at the individual level

Neither annual mean pre-laying temperature nor annual mean pre-laying cumulative precipitation at the individual level showed significant trends over time (Table 2; see Figure 2a-b).

Table 2. Results and parameters of models built to evaluate whether annual means of pre-laying conditions-(i) mean temperature and (ii) cumulative precipitation of the 15 days prior to laying, calculated at individual level-remained similar over time. For each fixed effect, the estimate (β), standard error (SE), t-statistic (t), and 95% confidence interval (CI) are indicated. Significant parameters are highlighted in bold.

<i>(i) Annual mean of pre-laying temperature</i>	Model coefficients and confidence intervals			
Fixed effects	β	SE	t	CI
Intercept	14.695	0.2634	55.734	14.157 - 15.233
<i>Year</i>	0.010	0.268	0.036	-0.537 - 0.555
<i>(ii) Annual mean of pre-laying cumulative precipitation</i>	Model coefficients and confidence intervals			
Fixed effects	β	SE	t	CI

Intercept	245.24	181.182 -
	0	31.410 7.808 309.305
Year	-	-80.062 -
	15.010	31.900 -0.470 50.049

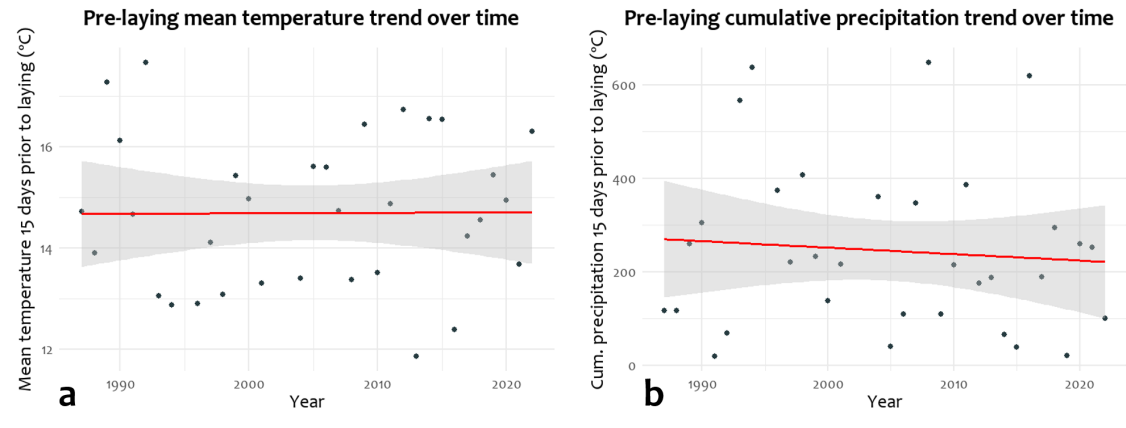


Figure 2. Variation over the study period of annual means of pre-laying conditions: (a) mean temperature and (b) cumulative precipitation of the 15 days prior to laying, calculated at individual level. The shaded areas around the regression lines show the 95% confidence intervals.

4.3. Analysis of advances in laying date with year and spring warming

Annual mean laying date advanced significantly over the study period and was negatively associated with per-year mean spring temperature, indicating earlier laying in warmer years (Table 3; see Figure 3a-b).

Table 3. Results and parameters of models built to assess laying date advances with (i) time and (ii) spring warming. For each fixed effect, the estimate (β), standard error (SE), t-statistic (t), and 95% confidence interval (CI) are shown, while for each random effect, (σ^2) and standard deviation (SD) are indicated. Significant parameters are highlighted in **bold**.

<i>(i) Mean laying date vs. year</i>	Model coefficients and confidence intervals
--------------------------------------	---

Fixed effects	β	SE	t	CI
Intercept	21.11 6	0.598	35.29 4	19.895 - 22.336
<i>Year</i>	-1.952	0.608	-3.213	-3.191 - (-0.713)

(ii) *Mean laying date vs. mean spring temperature*

Fixed effects	β	SE	t	CI
Intercept	21.11 6	0.475	44.41 4	20.146 - 22.085
<i>Mean spring temperature</i>	-2.833	0.483	-5.868	-3.818 - (-1.848)

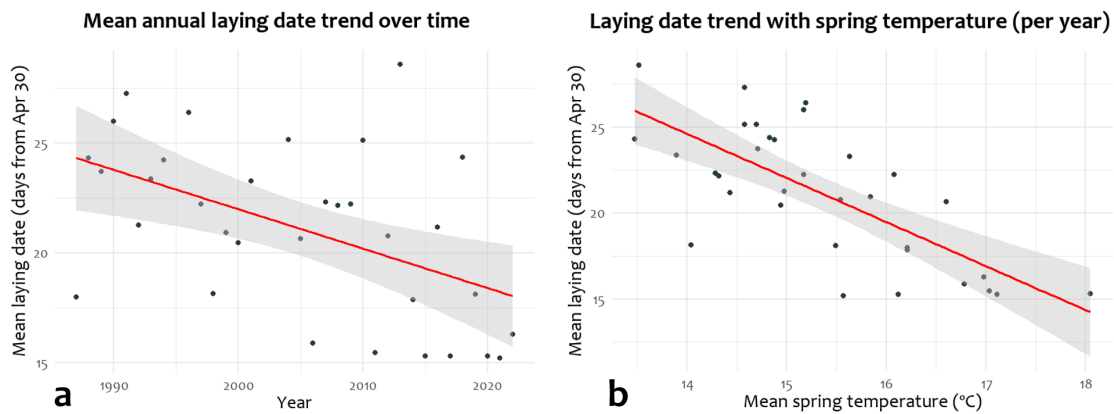


Figure 3. Variation in mean laying date (calculated per year) in relation to (a) years over the study period and (b) annual mean spring temperature. The shaded areas around the regression lines show the 95% confidence intervals.

4.4. Quantification of clutch-size plasticity in relation to phenology and pre-laying conditions

Clutch size exhibited a quadratic age effect, with medium-aged females showing greater clutch sizes (Table 4). Pre-laying mean temperature (15 days) was negatively and linearly associated with clutch size (Figure 5b), as well as with pre-laying mean temperature; however, it was the two-way interaction that led this significance, indicating that the effect of laying date on clutch size depends on pre-laying temperature (Table 4; Figure 4a-c). Specifically, the decrease in clutch size as the season progresses was more pronounced if the pre-laying temperatures were

higher. Finally, cumulative precipitation showed a slight but positive quadratic effect, meaning that the clutch size was slightly larger at intermediate levels of pre-laying rainfall (Table 4; Figure 4b).

Table 4. Results and parameters of the model built to evaluate clutch size plasticity in relation to laying date, synchrony and pre-laying conditions. For each fixed effect, the estimate (β), standard error (SE), t-statistic (t), and 95% confidence interval (CI) are shown, while for each random effect, variance (σ^2) and standard deviation (SD) are indicated. Baseline for factors *Habitat* and *Bird origin* are “oak forest” and “locally born”, respectively. Significant parameters are highlighted in **bold**.

<i>Clutch size plasticity, N = 3207</i>	Model coefficients and confidence intervals			
	β	SE	t	CI
Fixed effects				
Intercept	5.539	0.038	146.9 17	5.466 - 5.613
<i>Female age (linear)</i>	0.059	0.013	4.660	0.034 - 0.084
<i>Female age (quadratic)</i>	- 0.073	0.012	- 6.166	-0.097 - (-0.050)
<i>Laying date</i>	- 0.295	0.018	- 16.15 0	-0.331 - (-0.259)
<i>Laying synchrony</i>	- 0.029	0.031	0.924	-0.032 - 0.090
<i>Female body mass</i>	- 0.053	0.013	- 3.923	-0.079 - (-0.026)
<i>Female tarsus length</i>	0.024	0.013	1.782	-0.002 - 0.050
<i>Pre-laying (15 days) mean temperature (linear)</i>	- 0.125	0.022	- 5.553	-0.169 - (-0.081)
<i>Pre-laying (15 days) mean temperature (quadratic)</i>	- 0.021	0.019	- 1.110	-0.058 - 0.016
<i>Pre-laying (15 days) cumulative precipitation (linear)</i>	0.012	0.021	0.577	-0.029 - 0.054
<i>Pre-laying (15 days) cumulative precipitation (quadratic)</i>	0.047	0.018	2.604	0.012 - 0.083
<i>Laying date*pre-laying mean temperature (linear)</i>	- 0.079	0.017	- 4.631	-0.112 - (-0.046)
<i>Laying date*pre-laying mean temperature (quadratic)</i>	0.019	0.010	1.892	-0.001 - 0.039

<i>Laying date*pre-laying cumulative precipitation (linear)</i>	-	0.017	-	-0.062 - 0.003
	0.029		1.781	
<i>Laying date*pre-laying cumulative precipitation (quadratic)</i>	-	0.015	-	-0.032 - 0.025
	0.003		0.227	
<i>Habitat (pine plantation)</i>	-	0.030	-	-0.107 - 0.009
	0.049		1.651	
<i>Female origin (immigrant)</i>	-	0.028	-	-0.013 - 0.096
	0.041		1.490	
Random effects		σ^2		SD
<i>Female ID</i>		0.095		0.309
<i>Male ID</i>		0.012		0.111
<i>Year</i>		0.024		0.155

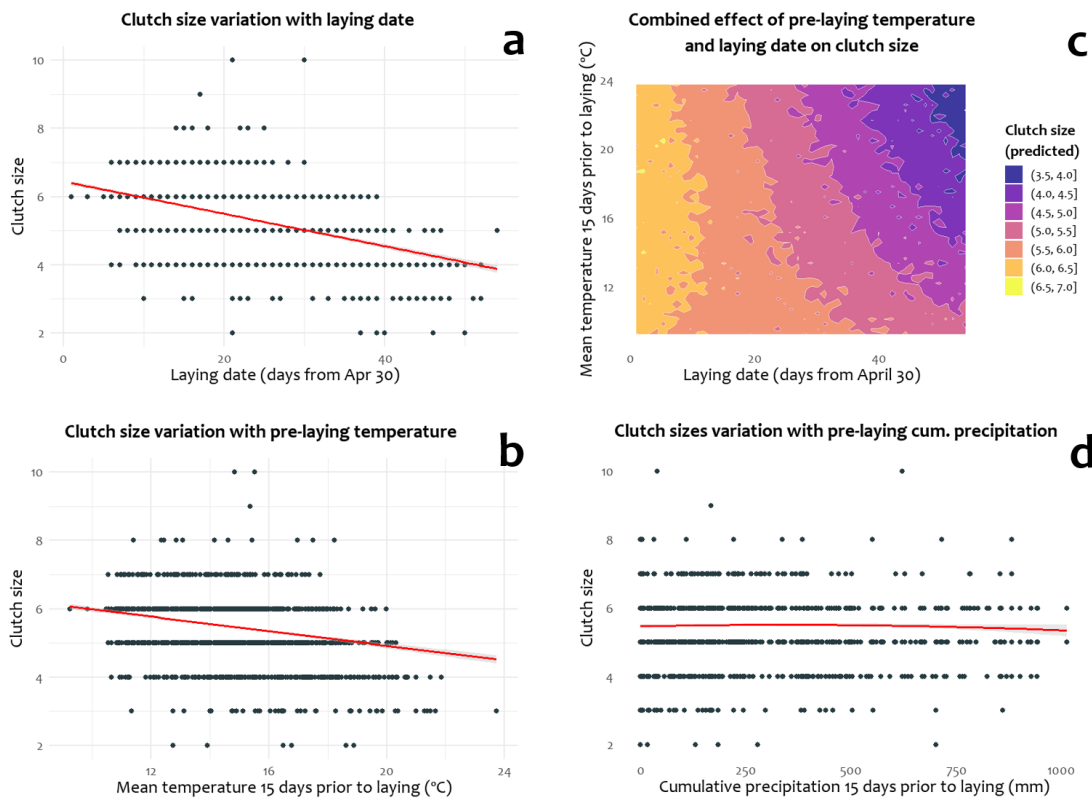


Figure 4. Variation in clutch size with (a) laying date, (b) mean temperature of the 15 days prior to laying, (c) the interaction between these two variables (showed as a contour plot with model-predicted values), and (d) cumulative precipitation of the 15 days prior to laying. The shaded areas around the regression lines show the 95% confidence intervals.

4.5. Estimation of fledging success responses in relation to phenology and pre-laying conditions

Fledging success declined with later laying date and was negatively associated with body mass in the reported model; pre-laying temperature and precipitation terms were not significant, nor the interactions between laying date and pre-laying conditions (Table 5; see Figure 5a–c).

Table 5. Results and parameters of the model built to quantify fledging success responses in relation to laying date, synchrony and pre-laying conditions. For each fixed effect, the estimate (β), standard error (SE), z-statistic (z), and 95% confidence interval (CI) are shown, while for each random effect, variance (σ^2) and standard deviation (SD) are indicated. Baseline for factors *Habitat* and *Bird origin* are “oak forest” and “locally born”, respectively. Significant parameters are highlighted in **bold**.

<i>Fledging success responses, N = 2550</i>	Model coefficients and confidence intervals			
	β	SE	z	CI
Fixed effects				
Intercept	1.759	0.125	14.068	1.515 - 2.005
<i>Female age (linear)</i>	0.003	0.035	0.086	-0.067 - 0.073
<i>Female age (quadratic)</i>	-	0.032	-	-0.125 - 0.001
Laying date	0.210	0.052	4.010	-0.313 - (-0.108)
<i>Laying synchrony</i>	0.183	0.108	1.687	-0.030 - 0.395
Female body mass	0.137	0.037	3.649	-0.210 - (-0.063)
<i>Female tarsus length</i>	0.027	0.0380	0.712	-0.047 - 0.101
<i>Pre-laying (15 days) mean temperature (linear)</i>	-	0.063	-	-0.188 - 0.061
<i>Pre-laying (15 days) mean temperature (quadratic)</i>	0.048	0.053	0.898	-0.057 - 0.152
<i>Pre-laying (15 days) cumulative precipitation (linear)</i>	-	0.060	-	-0.165 - 0.06
<i>Pre-laying (15 days) cumulative precipitation (quadratic)</i>	0.042	0.051	0.842	-0.057 - 0.143

<i>Laying date*pre-laying mean temperature (linear)</i>	-	0.047	-	-0.124
	0.031		0.665	0.061
<i>Laying date*pre-laying mean temperature (quadratic)</i>	-	0.030	-	-0.080
	0.022		0.731	0.037
<i>Laying date*pre-laying cumulative precipitation (linear)</i>	-	0.046	-	-0.140
	0.050		1.095	0.040
<i>Laying date*pre-laying cumulative precipitation (quadratic)</i>	-	0.041	-	-0.081
	0.001		0.027	0.079
<i>Habitat (pine plantation)</i>	0.092	0.132	1.433	-0.048
				0.312
<i>Female origin (immigrant)</i>	-	0.081	-	-0.173
	0.014		0.178	0.144
Random effects		σ^2		SD
<i>Female ID</i>		0.944		0.972
<i>Male ID</i>		0.759		0.871
<i>Year</i>		0.286		0.535

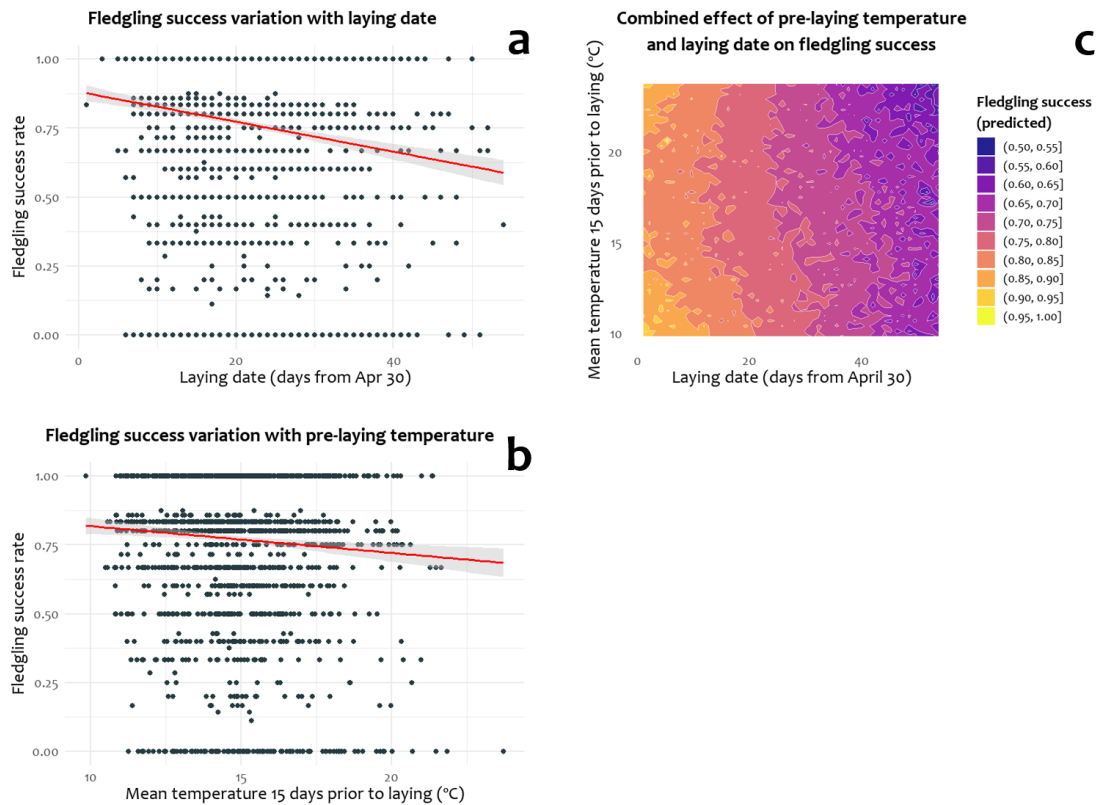


Figure 5. Variation in fledgling success with (a) laying date, (b) mean temperature of the 15 days prior to laying, and (c) the interaction between these two variables (showed as a contour plot with model-predicted values). The shaded areas around the regression lines show the 95% confidence intervals.

5. Discussion

5.1. Long-term trends in local spring climatic conditions

The rise in the mean spring temperature aligns with general trends of climatic changes in central Spain, whereas the shift in rainfall is less predictable. Thus, temperature seems like the driving environmental cue for phenological plasticity.

5.2. Temporal stability of pre-laying climatic conditions at the individual level

The consistent annual mean pre-laying conditions at the individual level, despite the above observed warming trend, alludes towards active adaptation to optimal conditions. A possible explanation is that the earlier laying dates shifted the pre-laying phase proportional to environmental change thus buffering the population from experiencing those changes during crucial breeding events.

5.3. Advances in laying date with year and spring warming

The data shows a clear advancement of the mean laying date with a strong negative relation to spring temperature. The advancement of multiple days during the study period shows the long-term adoption, while the strong negative relation to the mean temperature indicates the latter as the driving factor for this change. The results show that rising temperatures have a significant impact on reproductive timing, and that temperature more than rainfall is the mayor driver of this change.

5.4. clutch-size plasticity in relation to phenology and pre-laying conditions

Clutch size was influenced both by intrinsic and extrinsic factors and showed a quadratic age effect. As was hypothesized medium-aged females producing the largest clutches, as they optimize both experience over younger females and physical state over older ones. Among the extrinsic effects the most pronounced were pre-laying conditions, showing a negative relation between clutch size and temperature. This suggests that higher temperatures increase the cost of later laying dates. This can be explained both by increased physical stress due to heat and decreased food availability as higher temperatures reduce the insect abundance. However, rainfall only showed weak effects on clutch size. The positive quadratic effect, even though weak suggests an optimum in intermediate rainfall with both excessive and lack of precipitation being suboptimal. This supports again that the dominant driver of phenological plasticity is temperature, while also acknowledging a multifaceted influence. This plasticity of clutch size might maintain reproductive success but shows also a low reproductive rate under more extreme conditions.

5.5. fledging success responses in relation to phenology and pre-laying conditions

Fledging success declined with later laying dates, shows the advantage of phenological plasticity to adapt to changing conditions and shift laying dates according to climatic shifts. The lowered success later on could be based on higher exertion after the shortened stay in wintering grounds, increased competition for optimal nesting site and reduced food availability due to earlier depredation pressure by the earlier laying birds. In conclusion, advancing laying dates seems to prove a valuable adoptive strategy.

The negative association with body mass is surprising as body mass is positively associated with fitness and health, which in turn is positively associated with clutch size. As our results have already shown that temperature has a strong effect on clutch size an increased body mass with a higher volume to surface ratio lowers cooling and thus leads to more exhaustion and overheating impacting health negatively.

As pre-laying climatic conditions show no significant effect on fledging success, it seems that populational reproductive outcome is mostly determined by the timing of the reproductive season than by climatic factors prior to laying dates. This supports again that earlier laying is essential for individuals to mitigate climatic shifts.

6. Conclusion and outlook

With the ongoing environmental changes, resulting in decreasing biodiversity and number of species across many taxa including a decrease in reproductive output of migratory birds, studies on their adoptive ability are crucial.

Pied flycatchers demonstrate behavioral and reproductive flexibility in response to changing spring conditions. By advancing laying dates and plastically adjusting clutch size, they are able to maintain reproductive performance, highlighting the role of phenotypic plasticity in buffering fitness under rapidly changing environmental conditions. This great flexibility might explain that they are among the lesser effected bird species of environmental change, still flourishing, categorized by ICUN as a species with the least concern of extinction. Still their adaptations to changing conditions are important to ensure well planned conservation strategies to ensure their protected, especially if environmental change outpaces their limits of plastic responses. The next step is to investigate further adoptive strategies, like genetic evolution of the species that complement the initial plastic response. Also, it is interesting to see how the here reported plasticity changes over time as those individuals with more flexibility have a fitness advantage.

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Anexo

Supplementary Table S1. List of variables included in the annual-based models built in this study (see 3.6 subsection). Means, standard deviations (SD) and minimum (min) and maximum (max) values are provided for numerical variables.

<i>Annual-based database (N = 33)</i>				
Numerical variables	mean	SD	min	max
<i>Spring (apr-jun) temperature (°C)</i>	15.36	1.11	13.47	18.04
<i>Spring (apr-jun) cumulative precipitation (mm)</i>	135.48	64.74	58.60	363.30
<i>Laying date (Julian days from 30 apr)</i>	21.12	3.91	15.19	28.58
<i>Individual pre-laying (15 days) mean temperature (°C)</i>	14.69	1.49	11.86	17.66
<i>Individual pre-laying (15 days) cumulative precipitation (mm)</i>	24.52	17.82	1.90	64.72

Supplementary Table S2. List of variables included in the individual-based models built in this study (see 3.6 subsection). Means, standard deviations (SD) and minimum (min) and maximum (max) values are provided for numerical variables, while level counts (n) and proportions (%) are provided for non-numerical variables. Variables marked with an asterisk were calculated on the subset of 2,550 breeding events used for the analysis of fledgling success (see Methods section).

Individual-based database (N = 3207)

Numerical variables	mean	SD	min	max
<i>Clutch size (number of laid eggs)</i>	5.49	0.80	2	10
<i>Number of fledglings (day 13 after hatching)*</i>	4.23	1.67	0	8
<i>Number of dead fledglings (day 13 after hatching)*</i>	1.24	1.55	0	8
<i>Female age (years)</i>	2.61	1.33	1	6
<i>Female body mass (g)</i>	12.5	0.64	10.31	15.30
<i>Female tarsus length (mm)</i>	19.54	0.58	17.26	22.34
<i>Laying date (Julian days from 30 apr)</i>	20.16	7.79	1	54
<i>Laying synchrony (number of females)</i>	34.33	7.89	19.68	58.49
<i>Pre-laying (15 days) mean temperature (°C)</i>	14.68	1.99	9.27	23.73
<i>Pre-laying (15 days) cumulative precipitation (mm)</i>	23.90	23.12	0	101.40
Non-numerical variables	Levels		N (% total)	
<i>Habitat</i>	Oakwood		2122 (66.17)	
	Pine plantation		1085 (33.83)	
<i>Female origin</i>	Locally born		1383 (43.12)	
	Immigrant		1824 (56.88)	