

# Advancement of spring arrival in a long-term study of a passerine bird: sex, age and environmental effects

Luis Cadahía<sup>1</sup> · Antonieta Labra<sup>1,2</sup> · Endre Knudsen<sup>1</sup> · Anna Nilsson<sup>1</sup> · Helene M. Lampe<sup>1</sup> · Tore Slagsvold<sup>1</sup> · Nils Chr. Stenseth<sup>1</sup>

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**Abstract** In migratory birds, mistimed arrival might have negative consequences for individual fitness, causing population declines. This may happen if arrival time is not synchronized with breeding time, especially when earlier springs favour earlier reproduction. We studied spring arrival time to the breeding areas in a pied flycatcher *Ficedula hypoleuca* population in southern Norway during a 30-year period (1985–2014). We investigated trends in arrival both for the entire population and for different population fractions (e.g. early vs. late arrivals). We also studied sex and age class differences, along with repeatability of arrival. Finally, we explored how arrival is influenced by environmental conditions at the areas birds use throughout the year, using mixed-effects models and quantile regressions with individual-based data. Spring arrival advanced over five days, at a similar rate through the entire population. Males and adult birds arrived earlier than females and yearlings. Arrival was significantly repeatable for males and females. Birds arrived earlier in years with high temperature and rainfall at the breeding grounds, and low NDVI both on the Iberian Peninsula and in central Europe. Later fractions

of the population showed a steeper response to these environmental variables. This intra-population heterogeneity in the responses to the environment probably stems from a combination between the different selection pressures individuals are subject to and their age-related experience. Our results highlight the importance of studying how migration phenology is affected by the environment not only on the breeding grounds but also on the other areas birds use throughout the year.

**Keywords** Mixed-effects models · NAO · NDVI · Phenology · Protandry · Quantile regression · Rainfall · Repeatability · Temperature

## Introduction

The timing of recurring life-history events, or phenology, has important consequences for natural populations (Knudsen et al. 2011; Gienapp and Bregnballe 2012). One key life-history event is the arrival at the breeding grounds after migration. In birds, early arrival facilitates selection of higher quality territories and mates, in addition to opportunities for replacement broods and extra matings (Newton 2008). However, arriving too early can be detrimental owing to poor weather conditions during the migratory journey and upon arrival (Newton 2007). Arrival time becomes particularly relevant in the case of long-distance migrants, because they often depart from a different climate zone (Newton 2008).

Migratory birds show a strong phenological response to climate change (Knudsen et al. 2011), which has been related to a general advancement in spring phenology (Menzel et al. 2006). This advancement has favoured an earlier peak of food availability for many species, and thereby also

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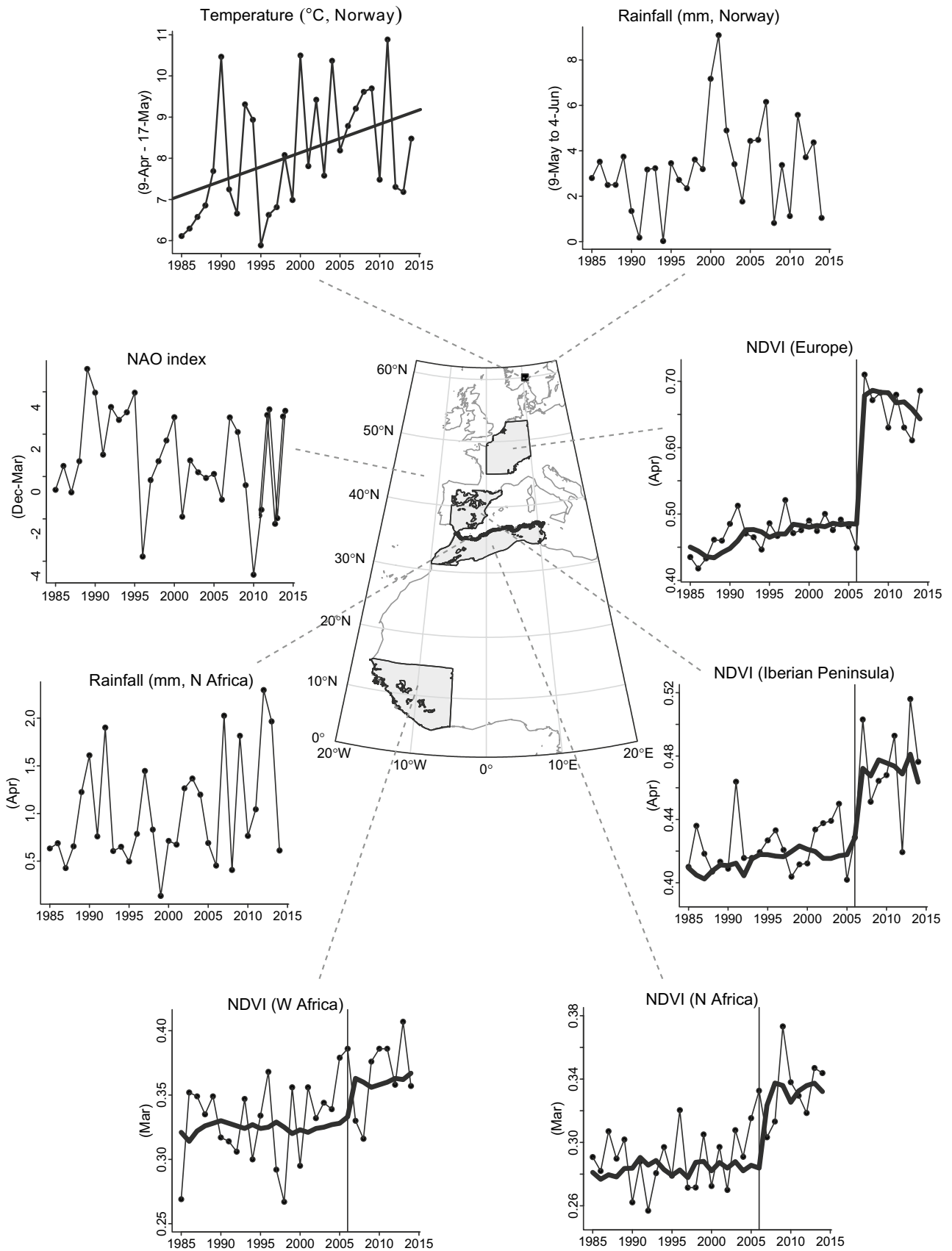
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✉ Luis Cadahía  
luis.cadahia@gmail.com; luis.cadahia-lorenzo@ibv.uio.no

<sup>1</sup> Department of Biosciences, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Blindern, 0316 Oslo, Norway

<sup>2</sup> Instituto de Ciencias Biomédicas, Facultad de Medicina, University of Chile, Santiago, Chile



**Fig. 1** Variables used to study the influence of environmental variation on spring arrival phenology of a pied flycatcher population in southern Norway (1985–2014). X-axes represent time in years; y-axes show the period for which each variable was used. The straight regression line represents a significant temporal trend. The NDVI time series were composites of AVHRR data before 2006 (vertical line) and MODIS data afterwards, and were smoothed with an ARIMA(0,1,1) model (thick lines). The black square shows the study area in Norway

advancements in their breeding times (Dunn and Winkler 2010). For migratory birds, earlier reproduction can be constrained by the timing of arrival to the breeding grounds in spring (Both and Visser 2001). If arrival is not adjusted, the resulting mistiming might have negative consequences for individual fitness and cause population declines in the long term (Both et al. 2006a; Møller et al. 2008; Saino et al. 2011).

Birds cover vast distances between their wintering and breeding grounds (Newton 2008), and the rate, direction and variability of climatic and other environmental changes in these regions may differ considerably (IPCC 2013). This may disrupt the links between the successive stages of migratory birds' annual cycle, uncoupling the timing of arrival and the availability of food, territories or mates (Knudsen et al. 2011). Some studies show that European short-distance migrants advance their phenology more than long-distance species that cross the Sahara Desert (e.g. Møller et al. 2008; Saino et al. 2011), suggesting that at short distances it may be possible to better track the conditions at the breeding areas. However, other studies report the reverse situation (e.g. Jonzén et al. 2006). Long-distance migrants have evolved endogenous mechanisms to time their migration following cues related to photoperiod (Gwinner and Helm 2003). Some evidence suggests that these mechanisms can be fine-tuned by environmental cues (Studds and Marra 2011), but it is disputed whether these will be sufficient to induce birds to initiate migration in time to reach the peak of resource availability on their breeding grounds (Both and Visser 2001; Both et al. 2006a).

Here, we investigate the response to environmental variation of a Norwegian population of the pied flycatcher *Ficedula hypoleuca*, an insectivorous, long-distance migrant that breeds in temperate forests across large parts of Europe and Western Asia and winters in sub-Saharan, tropical West Africa (Lundberg and Alatalo 1992). Previous studies found that the timing of breeding has advanced over the last decades in many, but not all populations across Western Europe (Both et al. 2004). The timing of spring migration has also advanced in some populations, but not in others (Both 2010). Here, we use individual-based phenological data to provide a comprehensive analysis of (1) the entire arrival distribution of the population over a period of 30 years, (2) differences between different fractions of the population (e.g. early vs.

late arrivals), particularly with regard to sex and age, (3) how consistent individuals are in arriving early or late, i.e. the repeatability of arrival, and (4) how the environment in the areas where the birds range throughout the year influences arrival date. In this study, 'environment' refers to climatic parameters (e.g. temperature, rainfall) and indices reflecting ecological conditions, especially those related to food abundance (e.g. NDVI). We investigated the relationships between spring arrival and the environmental conditions on the African wintering quarters, along the migratory route, and on the Norwegian breeding grounds. Because of its relevance for breeding, we expected the environment on the breeding grounds to be most important for arrival.

## Materials and methods

### Pied flycatcher data

Our study area (Sinober in Sørkedalen; 59°59'N, 10°38'E) is located near Oslo, in SE Norway. Wooden nest boxes have been available in the area since 1985 and this study covers the period 1985–2014 (see Supplement S1 for details on the study area and ringing procedures). The area was visited daily from late April (normally around a week before the first arrivals) to early July. For males, arrival date was defined as the first day a male was observed in the area. Males occupy a nest site and the immediate surroundings and start singing soon after arrival, to attract a female. If not previously ringed, the identity of a male can be judged from which nest box he is singing at, his dorsal plumage colour and the size of his white forehead patch (Lundberg and Alatalo 1992). During this stage, males are readily attracted to nest boxes and trapped using song playback. Instances of male pied flycatchers helping with nest building have been reported (Martínez-de la Puente et al. 2009), but most nest construction is undertaken by females shortly after their arrival (Dale et al. 1992; Both et al. 2016). Thus, the start of nest construction was used to define female arrival dates (see Supplement S1 for a detailed explanation). Arrival data for females were not available or were of low quality for five years (1989, 2001, 2002, 2004 and 2005). Age (yearling or adult) was estimated according to Svensson (1992). All dates were transformed into Julian days (January 1st = 1) and, after taking leap years into account, used in subsequent analyses.

### Climate and NDVI data

To explore how between-year variability in environmental conditions influenced migration phenology, we considered eight variables representative of the wintering and breeding grounds, and along the migratory route (Fig. 1). For the

wintering areas and the migration route, we used the Normalized Difference Vegetation Index (NDVI; Pettorelli et al. 2005), which has been used as a proxy for insect abundance in a number of bird migration studies (e.g. Both et al. 2006b; Gordo and Sanz 2008). To obtain a NDVI time series covering the whole period, we needed to combine data from the NOAA AVHRR-based data from the GIMMS dataset before 2006, and MODIS data afterwards. To define the areas and periods relevant for flycatcher migration, we used averaged NDVI data and exploratory correlations with arrival dates (see Supplement S2 for details). Flycatchers breeding in Norway are not likely to depart from Africa before early April, and little is known on when they start preparing for migration (Ouwehand and Both 2016; Ouwehand et al. 2016). Therefore, March NDVI values for West Africa and along the migratory route in North Africa, and April values for the Iberian Peninsula and central Europe were considered in our models.

We studied the influence of weather conditions when crossing from Africa to Europe by using average rainfall along the northern African coast (April), roughly covering the coasts of Morocco, Algeria and Tunisia (Taylor and Christie 2015). Rainfall was aggregated from daily gridded weather data from the NCEP-DOE Reanalysis 2 (Kanamitsu et al. 2002). Data were provided by the Physical Sciences Division, NOAA Earth System Research Laboratory, and downloaded via ftp (<http://cdc.noaa.gov/>). We also used the North Atlantic Oscillation (NAO; December–March) index (Hurrell 1995), as a general proxy for conditions along the migratory route (Supplement S3).

We used data from the Norwegian Meteorological Institute, Blindern, Oslo station ([eklima.met.no](http://eklima.met.no)) to quantify temperature and rainfall at the breeding grounds. To determine the period most relevant for arrival, we calculated correlations between annual median arrival dates and imbricate 3-week periods (moving in 3-day steps from 1-March until 30-June) for mean temperature and rainfall (Ahola et al. 2004). As a result, the time windows selected were 9-April–17-May (5.4 weeks) for temperature and 9-May–4-June (3.9 weeks) for rainfall (Supplement S3).

### Statistical analyses

Analyses were carried out using the statistical programming environment R, version 3.2.2 (R Core Team 2015). In general, we performed regression analyses with linear mixed-effects models (LMM) with Gaussian error structures to study both the change in spring arrival and the factors affecting it. All models included a random intercept effect for individual identity, to account for the fact that the same birds were caught in subsequent years, and a random intercept for year, to account for the year-specific environmental conditions that all individuals experienced. LMM were run

with the R package ‘lme4’ (Bates et al. 2013). To describe the proportion of variance explained by the models, we used  $R^2$  as implemented on the R package ‘MuMIn’ (Bartoń 2015), based on Nakagawa and Schielzeth (2013) and Johnson (2014). In LMM,  $R^2$  is categorized into marginal  $R^2$  (variance explained by fixed effects only), and conditional  $R^2$  (variance explained by both fixed and random effects, i.e. the entire model). Our analyses were based on 2485 arrivals registered for 1722 individuals.

### Temporal changes in arrival dates

No evidence of temporal autocorrelation was found in any time series of arrival dates. We also tested for and found no influence of a few late-arriving birds on our results (Supplement S4). The presence of a temporal trend in migration phenology was tested by regressing arrival date on year and comparing this model with another model fitted with the intercept only (null model), using a likelihood ratio test. In addition, trends in arrival of different fractions of the population were analysed by quantile regression (Cade and Noon 2003; Gordo et al. 2013), with year as explanatory variable, using the ‘quantreg’ package in R (Koenker 2015). We calculated rates of change (slopes) at 5%-interval percentiles. We also analysed temporal trends in the width of the distribution of arrival dates by regressing the annual standard deviation of arrivals against year (Gordo et al. 2013).

We calculated the difference between the mean annual arrival date in males and females and explored its temporal trend with linear regression to investigate changes in the degree of protandry (i.e. the earlier arrival of males relative to females). The same procedure was used to examine differences in mean annual arrival between adults and yearlings. Further, we evaluated the influence of sex and age on migration phenology by including these variables together with year in models fitted using maximum likelihood and ranked according to the Akaike’s Information Criterion (AIC).

We estimated repeatability using a LMM approach implemented in the ‘rtpR’ package in R (Nakagawa and Schielzeth 2010), using restricted maximum likelihood (REML). Repeatability describes the relative partitioning of phenotypic variance into within-individual and between-individual sources, and it describes, in this case, how consistent individuals were in their arrival phenology throughout time. Therefore, for this analysis, we considered only the individuals for which we had multiple observations ( $n = 480$ ). We built models with arrival date as the dependent variable and individual identity as the random effect. We also included a fixed effect for age to account for differences between age classes. We analysed repeatability for absolute arrival dates and for arrival dates relative to the annual mean (i.e. standardized). Analyses were first run with all the individuals and then separated by sex. To evaluate the uncertainty of the

repeatability estimates, we used a bootstrapping approach as implemented in ‘rptR’.

### Climate and NDVI influence on arrival dates

All the NDVI variables presented high between-year autocorrelation. To solve this problem and capture their year-to-year dynamics, NDVI data were modelled using time series analysis with autoregressive integrated moving average (ARIMA) models. The model that best fit the data was an ARIMA(0,1,1) with an intervention variable coded as ‘0’ prior to the (northern hemisphere) winter 2006–2007 and ‘1’ thereafter. This was necessary to correct for the incomplete alignment between the AVHRR (1985–2006) and the MODIS (after 2006) data series (Supplement S2). The ARIMA models were fitted using the ‘arimax’ function in the R package ‘TSA’ (Chan and Ripley 2012). The residuals of the ARIMA (0,1,1) models were used as predictors in the subsequent analyses.

There was a temporal trend in temperature at the breeding grounds (Fig. 1). To avoid spurious significant relationships with arrival date, which also showed a temporal trend (see “Results”), we detrended temperature by regressing it on year and used the residuals as predictors in further analyses. Both temperature and the remaining environmental variables were standardized to mean = 0 and SD = 1 before use in subsequent analyses.

To test for multicollinearity, we calculated variance inflation factors for our predictors, using the ‘vif’ function in the R package ‘car’ (Fox and Weisberg 2011). Values of these were in all cases <5, which is commonly interpreted as the absence of multicollinearity. For model selection, we started with a model that included all the climatic and NDVI variables, along with year, sex and age, and ran all possible candidate models that could be built (2560), using the ‘MuMIn’ package in R (Bartoń 2015). Models were fitted using maximum likelihood and ranked according to both the Akaike’s (AIC) and the Bayesian Information Criteria (BIC). AIC favours models with a higher number of parameters, whereas BIC is more restrictive because it penalizes model complexity more heavily (Burnham and Anderson 2002). By referring to both, we aimed at getting a clearer picture of which environmental variables were most important to explain variability in arrival phenology. Top models were selected based on  $\Delta AIC < 2$  and  $\Delta BIC < 2$ , and the proportion of variance explained by each one of them ( $R^2$ ) computed. We calculated Akaike weights for each candidate model. We also calculated the relative importance (RI) for each predictor variable included in the set of top models as the sum of the Akaike weights for all models in which the variable appeared (Burnham and Anderson 2002).

We built partial regression plots to visualize the effects of the environmental variables retained in the set of top models

(hereafter these variables are denoted ‘top predictors’) on arrival date, using the function ‘avPlots’ from the ‘car’ package (Fox and Weisberg 2011). Partial regression plots show the effect of the predictor variable of interest on the response variable, while removing the effect of all the other predictor variables in the model. First, the residuals of regressing the response variable on all the predictors except the one of interest are computed; then, the residuals of regressing the predictor variable of interest on the remaining predictors are computed; finally, the residuals from the first regression are plotted against the residuals of the second regression, obtaining a relationship between the two after having removed the effects of the other predictor variables on both. The models used to build these graphs were LMM combining all the effects described, both regarding sex and age, along with the environmental effects given by the top predictors.

We built LMM to investigate possible interactions between the top predictors and sex and age, respectively, using the ‘MuMIn’ package in R (Bartoń 2015). Finally, we tested for within-population differences in the relationship between these top predictors and arrival date using the above-mentioned quantile regression method.

## Results

### Temporal changes in arrival

Flycatchers arrived on average on 16-May (SD: 9.06 days; range: 24-April to 19-June;  $n = 2485$  arrivals). Spring migration phenology advanced over the study period (likelihood ratio test:  $\chi^2 = 5.42$ ,  $df = 1$ ,  $P = 0.02$ ) and birds arrived on average  $0.18 \pm 0.07$  (SE) days year<sup>-1</sup> earlier, resulting in an advancement of 5.4 days over the study period. For the model with the trend, the marginal  $R^2$  was 0.026 and the conditional  $R^2$  was 0.426, i.e. the amount of variation explained by year was 2.6% and by the entire model (including the random effects) was 42.6%. When analysing arrivals with quantile regression, all the fractions of the population showed a similar significant trend towards arriving earlier. The width of the arrival distribution did not present any temporal trend ( $F_{1,28} = 0.007$ ,  $P = 0.93$ ).

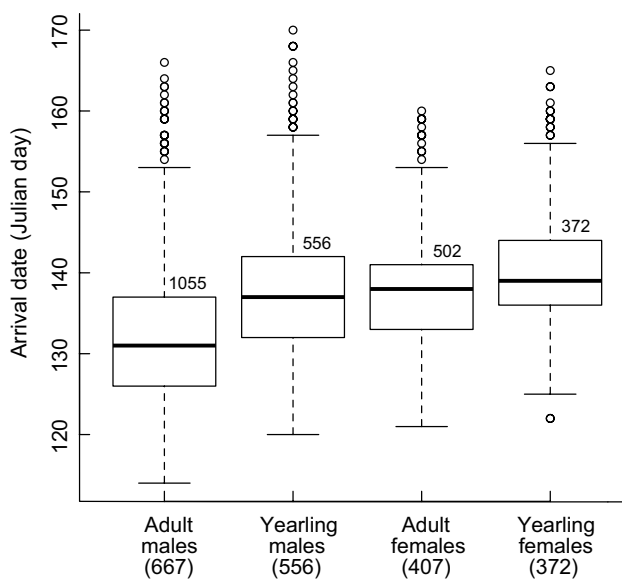
Males arrived on average on 14-May (SD: 9.33 days;  $n = 1611$  arrivals), and females on 19-May (SD: 7.67 days;  $n = 874$  arrivals). Adults arrived on average on 14-May (SD: 8.72 days;  $n = 1557$  arrivals), and yearlings on 19-May (SD: 8.46 days;  $n = 928$  arrivals). Thus, both the degree of pro-tandry and the difference in arrival between age classes were on average five days. This average difference did not change throughout the study period, neither with regards to sex ( $F_{1,23} = 0.134$ ,  $P = 0.71$ ) nor age ( $F_{1,28} = 1.291$ ,  $P = 0.27$ ). Across the years, mean values for male and female arrival were closely correlated (Pearson’s  $r = 0.56$ ,  $P = 0.003$ ), as



were those for adult and yearling arrival (Pearson's  $r = 0.73$ ,  $P < 0.001$ ).

Sex and age contributed to explain variation in arrival date, since both were included in the set of top models ( $n = 4$ ). The interactions between year, and sex and age, respectively, were not significant, indicating that the advancement in arrival was similar for sex and age classes. However, a significant interaction between sex and age was retained in the set of top models. The different sex and age classes arrived at significantly different times ( $F_{3,2485} = 120.7$ ,  $P < 0.001$ ; Fig. 2 and Supplement S5). Yearling males ( $n = 556$  arrivals) and adult females ( $n = 502$  arrivals) arrived, on average, at a similar time (17-May,  $t = -0.377$ ,  $P = 0.71$ ), whereas adult males ( $n = 1055$  arrivals) arrived significantly earlier (11-May,  $t = -12.64$ ,  $P < 0.001$ ), and yearling females ( $n = 372$  arrivals) significantly later (19-May,  $t = 4.021$ ,  $P < 0.001$ ).

Spring arrival dates were significantly repeatable. Repeatability in arrivals relative to the annual mean was slightly higher ( $R = 0.234$ , CI = 0.175–0.306;  $n = 1243$  arrivals in 480 individuals) than in absolute arrival dates ( $R = 0.212$ , CI = 0.145–0.277), but the highly overlapping confidence intervals indicate that the estimates are not different. The same applies when studying repeatabilities separated by sex. In males, repeatability in relative arrivals was  $R = 0.195$  (CI = 0.119–0.265;  $n = 975$  arrivals in 364 males), and in absolute arrivals it was  $R = 0.167$  (CI = 0.095–0.239). For females, only the repeatability estimate for relative arrival



**Fig. 2** Sex- and age-related distribution of arrival dates to the breeding grounds in a Norwegian pied flycatcher population during the period 1985–2014. Numbers above the boxes indicate number of arrivals in each category. Numbers in brackets on the x-axis correspond to the unique individuals in each category. Note that individuals were caught several times as adults

dates was significantly different from zero ( $R = 0.173$ , CI = 0.032–0.309; absolute arrival dates  $R = 0.078$ , CI = 0.000–0.216;  $n = 268$  arrivals in 116 females).

### Climate and NDVI influence on arrival dates

All eight environmental variables contributed to explain variability in arrival dates when considering the set of models with  $\Delta\text{AIC} < 2$  ( $n = 14$ ; Table 1). However, only three were present in all the models (RI = 1.00): temperature and rainfall at the breeding grounds, and the NDVI in central Europe. The same three variables were retained on the set of top models when considering  $\Delta\text{BIC} < 2$  ( $n = 4$ ; Table 1), along with the NDVI at the Iberian Peninsula. The relative importance (RI) of the NDVI in central Europe was higher than on the Iberian Peninsula when considering AIC (1.00 vs. 0.70), but lower when considering BIC (0.15 vs. 0.59). Because of this, we considered both NDVI variables, along with temperature and rainfall at the breeding grounds, to be the top environmental predictors. Figure 3 shows the relationships between these variables and arrival date. Birds arrived earlier in warmer and rainier springs, and later in years with high NDVI both at the Iberian Peninsula and in central Europe. Year was not included in any of the models with  $\Delta\text{BIC} < 2$ , and in many but not all the models with  $\Delta\text{AIC} < 2$  (RI = 0.95), probably because its effect was captured by the environmental variables.

All the interactions between the four top predictors and sex and age were included in the set of top models with  $\Delta\text{AIC} < 2$  ( $n = 24$ ), but none of them were present in all of the models (RI < 1.00). In addition, no interactions were retained when considering  $\Delta\text{BIC} < 2$  ( $n = 1$ ). Because of this, we did not consider these interactions further.

When analysing the relationship between arrival and each of the four top predictors using quantile regression, we found a consistent pattern in almost all cases. The negative relationship between arrival and temperature got progressively more pronounced towards the end of the arrival distribution, implying that the later fraction of birds responded stronger to temperature (Fig. 4a). A similar pattern was observed with rainfall at the breeding grounds (Fig. 4b). The positive relationship between arrival date and NDVI was more pronounced towards the end of the arrival distribution (Fig. 4c), suggesting that late individuals arrived even later in years with high NDVI at the Iberian Peninsula. However, with the NDVI in central Europe no clear pattern could be recognized (Fig. 4d).

To integrate the results above, we built a model incorporating the main effects described, fitted it with restricted maximum likelihood (REML) and calculated its  $R^2$  (Table 2). Its marginal  $R^2$  was 0.231 and its conditional  $R^2$  was 0.452, i.e. the fixed effects explained around 23% of

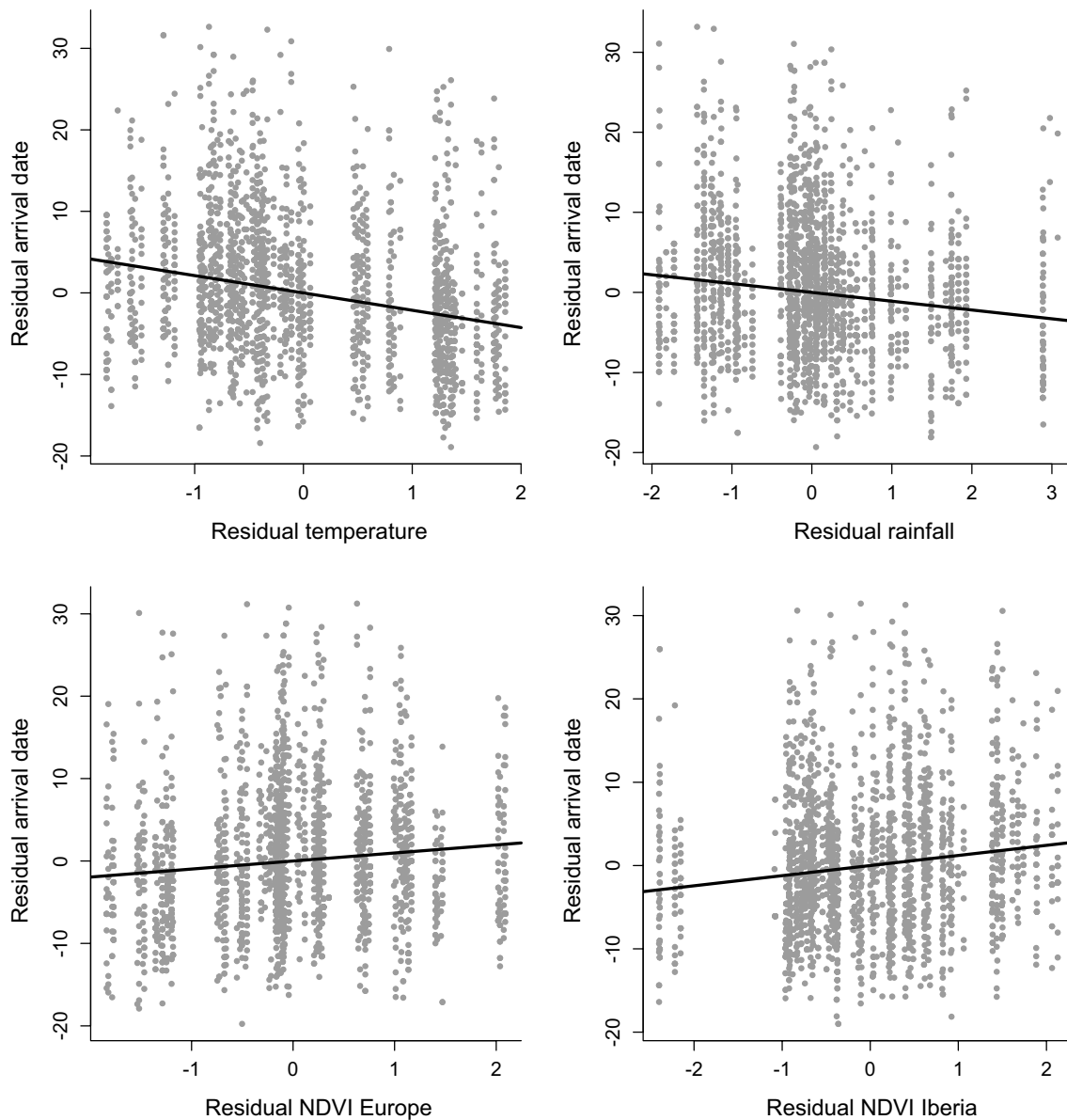
**Table 1** Top models ( $\Delta AIC < 2$  and  $\Delta BIC < 2$ ) relating age, sex and environmental conditions to spring arrival date in a pied flycatcher population in Norway during 1985–2014

| Id. | Model (AIC)   | $K$          | $\Delta AIC$ | Weights | Marginal $R^2$ | Conditional $R^2$ |
|-----|---|--------------|--------------|---------|----------------|-------------------|
| 1   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP                             | 13           | 0.00         | 0.13    | 0.248          | 0.447             |
| 2   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF                        | 14           | 0.64         | 0.10    | 0.249          | 0.447             |
| 3   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +P <sub>NAF</sub>      | 15           | 0.95         | 0.08    | 0.252          | 0.447             |
| 4   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +WAF                   | 14           | 1.01         | 0.08    | 0.250          | 0.448             |
| 5   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF                        | 13           | 1.07         | 0.08    | 0.244          | 0.446             |
| 6   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF                        | 12           | 1.08         | 0.08    | 0.243          | 0.447             |
| 7   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +P <sub>NAF</sub>      | 14           | 1.26         | 0.07    | 0.249          | 0.447             |
| 8   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +WAF                   | 13           | 1.30         | 0.07    | 0.247          | 0.448             |
| 9   | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +WAF +P <sub>NAF</sub> | 14           | 1.74         | 0.06    | 0.250          | 0.448             |
| 10  | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +WAF +P <sub>NAF</sub> | 15           | 1.88         | 0.05    | 0.252          | 0.448             |
| 11  | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +P <sub>NAF</sub>      | 14           | 1.91         | 0.05    | 0.248          | 0.446             |
| 12  | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF +P <sub>NAF</sub>      | 14           | 1.92         | 0.05    | 0.246          | 0.446             |
| 13  | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF                        | 12           | 1.92         | 0.05    | 0.240          | 0.446             |
| 14  | A +S +A*S +T <sub>N</sub> +P <sub>N</sub> +Eur +Y +NAO +IbP +NAF                        | 13           | 1.96         | 0.05    | 0.244          | 0.446             |
| RI  | 1.00 1.00 1.00  | –            | –            | –       | –              | –                 |
| Id. | Model (BIC)   | $\Delta BIC$ |              |         |                |                   |
| 1   | A +S +A*S +T <sub>N</sub> +IbP +P <sub>N</sub>  | 10           | 0.00         | 0.32    | 0.226          | 0.446             |
| 2   | A +S +A*S +T <sub>N</sub> +IbP  | 9            | 0.27         | 0.28    | 0.199          | 0.441             |
| 3   | A +S +A*S +T <sub>N</sub>   | 8            | 0.44         | 0.25    | 0.176          | 0.444             |
| 4   | A +S +A*S +T <sub>N</sub> +Eur  | 9            | 1.46         | 0.15    | 0.199          | 0.443             |
| RI  | 1.00 1.00 1.00  | –            | –            | –       | –              | –                 |

Models are linear mixed-effects models with individual identity and year as crossed random effects

A age, S sex, T<sub>N</sub> mean spring temperature at the breeding grounds, P<sub>N</sub> mean spring rainfall at the breeding grounds, MAO North Atlantic Oscillation index, Eur average April NDVI in central Europe, IbP average April NDVI at the Iberian Peninsula, NAF average March NDVI in North Africa, P<sub>NAF</sub> average April rainfall along the northwestern African coast, WAF average March NDVI in West Africa, K number of parameters, AIC Akaike's Information Criterion, BIC Bayesian Information Criterion, Weights Akaike weights, RI relative importance

\* Represents interactions



**Fig. 3** Partial regression plots showing the effects of environmental variables from the breeding grounds, the Iberian Peninsula and central Europe on arrival date (2485 arrivals) in a Norwegian pied flycatcher population during 1985–2014

the variability in arrival dates, whereas the entire model explained around 45%.

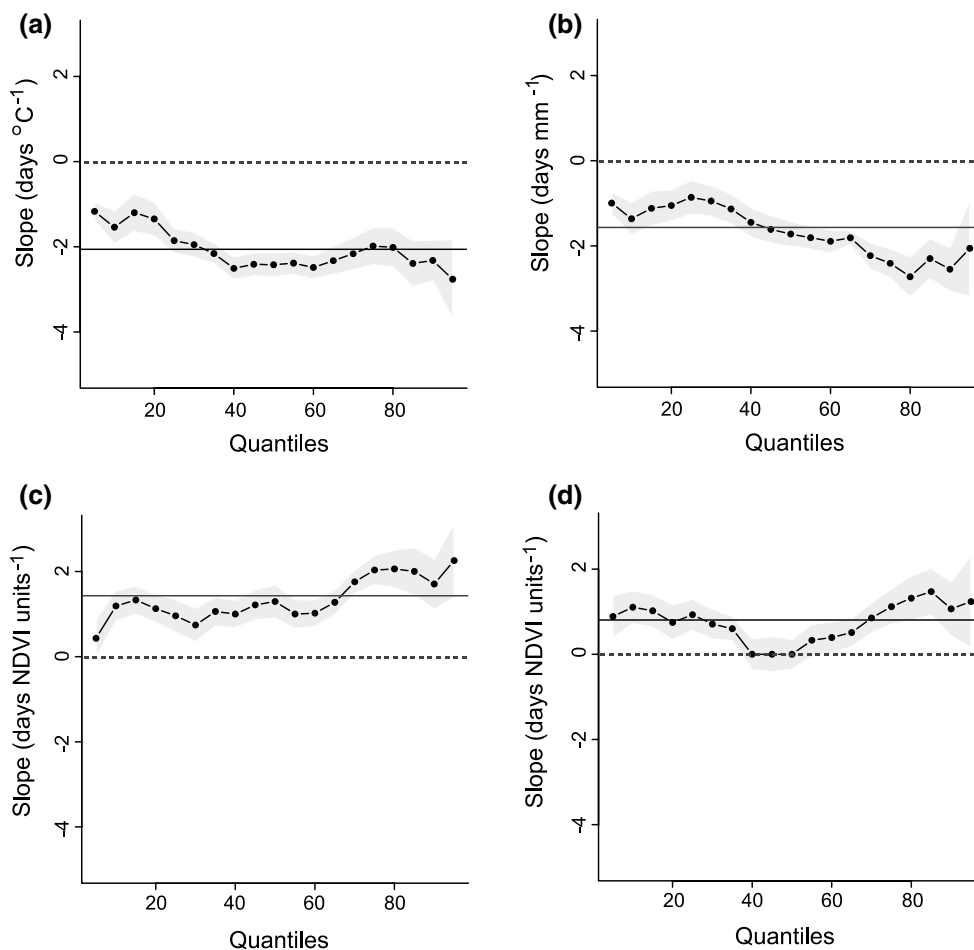
## Discussion

### Temporal changes in arrival

The population of pied flycatchers in southern Norway advanced its spring arrival by 5.4 days over a period of 30 years. This is in agreement with previous studies that

described advancing phenology in this species (Hüppop and Hüppop 2003; Jonzén et al. 2006; Both 2010). However, there are noticeable differences between populations; while some have shown advancing arrival or passage date (Germany: Hüppop and Hüppop 2003; Hüppop and Winkel 2006; Italy: Jonzén et al. 2006), others have shown either no change (central Europe: Hüppop and Winkel 2006) or changes within populations or areas, with only some individuals advancing arrival (Finland: Ahola et al. 2004; Fennoscandia: Jonzén et al. 2006). These population-specific responses may arise as a consequence of several factors,





**Fig. 4** Intra-population heterogeneity in the responses to the environment in a Norwegian pied flycatcher population during 1985–2014. Relationships between the top environmental predictors and arrival date at the different fractions of the population: **a** temperature and **b** rainfall at the breeding grounds, **c** NDVI at the Iberian Peninsula and

**d** in central Europe. *Dots on the line* show the slope values of specific regressions of arrival on the corresponding variable carried out at 5% intervals of the arrival distribution (quantile regressions); *grey fields* indicate 95% confidence intervals; the *straight lines* show the population's mean slope

**Table 2** Parameter estimates with standard error (SE) based on the top models (with  $\Delta AIC < 2$  and  $\Delta BIC < 2$ ) testing environmental influence on migration phenology in the pied flycatcher (see Table 1)

|                                   | Estimate | SE   | <i>t</i> value |
|-----------------------------------|----------|------|----------------|
| Intercept                         | 138.26   | 0.54 | 257.42         |
| Sex                               | -5.59    | 0.44 | -12.60         |
| Age                               | 2.25     | 0.51 | 4.38           |
| Spring mean temperature           | -2.03    | 0.45 | -4.56          |
| Spring mean rainfall              | -1.18    | 0.43 | -2.72          |
| Mean April NDVI Iberian Peninsula | 1.18     | 0.46 | 2.56           |
| Mean April NDVI central Europe    | 0.85     | 0.48 | 1.78           |
| Sex* age                          | 2.75     | 0.64 | 4.28           |

\*Represents interactions

including (a) adaptation to local conditions (e.g. Sparks et al. 2007), (b) different sensitivity to climatic changes (e.g. Gordo and Sanz 2010), or (c) differences in population

trends, especially when population declines may affect the detectability of the earliest individuals (e.g. Gordo and Doi 2012). In addition, heterogeneity in climatic trends across the planet (IPCC 2013) may cause birds to experience changes with different intensity and direction. This can be especially relevant when birds' life cycles comprise movements at continental scales (Newton 2008), as is the case for the pied flycatcher. Different climatic cues between wintering and breeding grounds may cause mismatches between arrival time and the peak of food availability, and this has been suggested as a possible mechanism causing population declines on migratory birds (Both et al. 2006a; Møller et al. 2008; Saino et al. 2011). In the pied flycatcher, different European populations winter in different areas in Africa (Ouwehand et al. 2016), and differences between these areas, both in climate or other environmental factors, may help explain the diversity of phenological responses found among populations. For example, Ouwehand and Both (2017) found

that departure from the African wintering grounds, rather than migration speed, determines variation in spring arrival in Dutch pied flycatchers. Other examples may be extreme events that impact the birds during migration, affecting only some populations in specific instances, causing delays in arrival and lower survival (Briedis et al. 2017).

Changes in bird migration phenology have traditionally been studied using temporal trends in measures of central tendency (mean, median or mode) or in arrival dates of first individuals (Gordo 2007; Knudsen et al. 2007). In the pied flycatcher, the 5–10, 50 and 90–95% quantiles have often been investigated (e.g. Ahola et al. 2004; Jonzén et al. 2006), with studies finding that early individuals were advancing their arrival at faster rates than later ones. This is in contrast with our results, which show a consistent change in timing throughout the entire distribution of arrivals. Possible reasons for this difference include (1) population-specific responses; (2) the different periods considered between our and other studies; our study includes more recent years than previous investigations, which might either better capture the warming trend (see Fig. 1) or simply reflect differences between sampled periods; or (3) the fact that we sampled the entire distribution of arrivals at 5% intervals, which provides a more comprehensive approach than only considering the median, the very early or the very late individuals.

Annual variation in male and female arrival was closely correlated. Males arrived, on average, five days before females throughout the study period. The absence of temporal changes in protandry has been found previously for the pied flycatcher (Rainio et al. 2007; Tøttrup and Thorup 2008). In contrast, Harnos et al. (2015) found an increasing degree of protandry, with only males arriving earlier. In other species, previous studies observed both increases and decreases in protandry in response to global warming (e.g. Spottiswoode et al. 2006; Tøttrup and Thorup 2008; Bauböck et al. 2012). Direct comparisons with other studies are difficult because of differences in sample periods, regions sampled and in migration routes; however, the observed differences may also be attributed to population-specific responses. These population differences may explain the results by Harnos et al. (2015), who studied flycatchers from Hungary, which are likely to follow a more easterly route on their spring migration, where they experience different environmental conditions than populations like ours that use more westerly routes (Ouwehand et al. 2016).

Adult birds arrived on the breeding ground, on average, five days before yearlings, and this difference did not change throughout the study. Earlier arrival of adult flycatchers with similar time lags for yearlings has been documented before (Potti 1998; Both et al. 2016), and it may arise from a number of factors: (1) less experience, e.g. lower foraging efficiency at the stopover sites (Lundberg and Alatalo 1992); (2) higher susceptibility to environmental variability *en route*

(Saino et al. 2004; Sergio et al. 2014); (3) dominance of adults at the stopover sites; or (4) slower rates of progress due to wing shape where juveniles have shorter and less pointy wings (e.g. Potti 1998; de la Hera et al. 2014).

Repeatability is the fraction of total phenotypic variance that could be attributed to the individual, and thus it depends on how consistent individuals are and on the amount of phenotypic variance present (Conklin et al. 2013; Both et al. 2016). Even though the repeatability estimates for relative and for absolute arrival dates were not different, relative arrivals reflect better whether birds are consistent in arriving earlier or later than the average, regardless of the specific annual conditions that may advance or delay the general phenology of the entire population. In general, the repeatabilities we found were slightly lower than those from other studies, both for flycatchers and other migrant species (see Table 1 at Both et al. 2016). Both et al. (2016) consider consistent individual variation in departure dates from the wintering grounds as the most likely cause of repeatability in arrival dates. This initial individual variation can be balanced out by environmental conditions during migration, which might synchronize the entire population's arrival in some years, leading to lower repeatability. Accordingly, this synchronization effect might be higher in our study population than in other areas. The overlapping confidence intervals between the male and female repeatability estimates indicate no sex-related difference, which is in agreement with other studies on the same species (Both et al. 2016). Repeatability shows how consistent a phenotypic trait is within individuals and may, thus, be a first pointer towards understanding its genetic basis (Both et al. 2016). The low repeatability values we found might suggest that the advancement in arrival dates we observed might be caused by phenotypic plasticity. Indeed, this would be in agreement with the results of Tarka et al. (2015), who find that phenotypic plasticity best explains the advancement of arrival date in a great reed warbler *Acrocephalus arundinaceus* population.

### Climate and NDVI influence on arrival dates

Contrary to other studies (e.g. Saino et al. 2004; Both et al. 2006b; Ouwehand and Both 2017), conditions at the wintering grounds and departure from West Africa, along with those at potential stopovers in Northern Africa, contributed relatively little to variation in arrival phenology. The likelihood of targeting the right geographical areas, where flycatchers actually are or fly through, is lower on these wintering and passage regions than on the breeding grounds. This difference might be part of the reason of the results we found. In addition, recent studies have shown that flycatchers migrate relatively fast and with little variation in migration speed (Ouwehand et al. 2016; Ouwehand and Both 2017). If this is, indeed, a general pattern, it would

mean that conditions *en route* may contribute relatively little to variation in arrival phenology.

Birds arrived earlier in years with warmer springs and more rainfall at the breeding grounds (Fig. 3). Advancement in arrival date with increasing temperature is probably the most reported effect of climate change on migratory birds (Knudsen et al. 2011; Saino et al. 2011). Higher temperature can influence the progress of migration and arrival date directly by increasing migration speed through better weather conditions and more efficient use of migratory fuel (Ahola et al. 2004). Alternatively, temperature could influence migration progress indirectly via propagation of phenological effects through the food chain (Knudsen et al. 2011). In this case, milder temperatures would favour an earlier development of vegetation and, hence, the availability of food (Hüppop and Hüppop 2003), thus facilitating arrival. Such an effect might be noticed by earlier arrival phenology following high NDVI values when passing through central Europe. However, this is the opposite of what we found in this study (Fig. 3), suggesting that temperature affects migration directly by enabling higher speed. We also found that flycatchers arrived earlier during rainy springs, which may be counterintuitive, since rain is expected to slow down progress and delay arrival (Newton 2008). However, the low-pressure systems associated with rainfall and higher temperatures may explain early arrival in southern Norway. These systems bring southerly tailwinds that would speed up the last stage of the migratory journey while minimizing energy expenditure (e.g. Alerstam and Lindström 1990).

Flycatchers arrived later in years with higher greening (high NDVI), and, presumably, higher food abundance both at the Iberian Peninsula and in central Europe (Fig. 3). This is somewhat counterintuitive, because faster refuelling rates would be expected under improved foraging conditions, facilitating earlier arrival. Previous research on the effects of NDVI on the timing of arrival and passage is mixed (Saino et al. 2004; Gordo and Sanz 2008; Tøttrup et al. 2008; Balbontín et al. 2009; Robson and Barriocanal 2011), and delayed arrival has been suggested as a response to improved foraging conditions *en route* (e.g. Møller and Merilä 2004). Several hypotheses may explain this pattern: (1) If NDVI and, hence, foraging conditions are good *en route*, birds would spend more time at stopover areas, but with low NDVI and poor conditions birds would skip those areas and arrive earlier. If this is true, birds would arrive in better condition on years with high NDVI than otherwise, which would be reflected by a positive correlation between body condition and NDVI values. We computed body condition by two different methods and performed ad hoc correlations with NDVI both at the Iberian Peninsula and in central Europe, but we observed, contrary to expected, negative, very low, but significant correlations (see Supplement S6). This relationship, thus, deserves further investigation.

(2) If ecological conditions during the winter have led to poorer body condition, migrants might spend more time at stopover sites increasing their condition (Gordo 2007; Gordo et al. 2013). However, we found no effects from the wintering grounds on phenology, and, in addition, whether and why this would correlate with NDVI in southern and central Europe remains unknown. (3) Some studies show that birds that either lose or increase fuel stores at a high rate would leave a stopover site quickly, whereas birds increasing fuel stores at intermediate rates would stay longer (Schaub et al. 2008); this would account for the observed pattern only if high NDVI entails intermediate refuelling rates. (4) Delayed arrival may also indicate difficult progress in the north if mild weather in southern Europe correlates with severe weather in Scandinavia as might occur in winters with positive NAO (Stenseth et al. 2003). However, none of the correlations performed ad hoc to test this, between the NDVI on the Iberian Peninsula and, respectively, the NDVI in central Europe, temperature and rainfall on the breeding grounds, were significant (see Supplement S6). (5) In many flycatcher populations, a large fraction of young individuals skips breeding the first year (Both et al. 2017), which could be because they arrive too late. It could be the case that profitable conditions during migration (high NDVI) allow more young individuals to arrive at the breeding grounds in time, but, since these individuals are later, this would result in a positive slope between NDVI and arrival. In conclusion, reasons for the positive arrival-NDVI relationships are still unclear and further research on this issue needs to be carried out.

We found intra-population heterogeneity in responses to environmental conditions with later arriving birds showing greater sensitivity to temperature, rainfall and NDVI (Fig. 4a–c). Saino et al. (2004) and Tøttrup et al. (2008) also found intra-population differences in how migration phenology varied with environmental conditions in differing age classes and during different phases of migration, respectively. The explanation for this diverse intra-population sensitivity to the environment may lie in a combination between different selective pressures and individual experience. In males, competition for suitable nest sites is severe, and they are, thus, under pressure to arrive early (Newton 2008), which provides greater opportunities for polygyny (“mate opportunity” hypothesis; Canal et al. 2012). This pressure affects both adult and yearling males, but the less experience of the latter may make them more dependent upon environmental conditions. Arriving early is a trade-off between costs and benefits, where the territory-holding males have more to gain than the females (Newton 2008), which are not subject to the same selective pressures. Females do compete for partners, but a male without a nest site would lose the opportunity to breed, while a late-arriving female could still mate with hitherto unpaired and/or polygynous males.

Here, we showed advanced arrival date in the pied flycatcher in southern Norway following environmental conditions on the breeding grounds and *en route* in southern and central Europe. However, in contrast to other studies, we found little influence from the wintering quarters or other passage areas. We also showed that different population fractions vary in their response, highlighting the importance of studying the entire population to achieve a more realistic understanding of the responses to environmental variation.

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**Author contribution statement** LC, AL, AN, HML, TS and NCS conceived the idea. HML and TS conducted fieldwork. EK analysed part of the data. LC analysed the rest of data and did the statistical modelling. LC, AL, EK and AN wrote the manuscript. HML, TS and NCS provided editorial advice.

## References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E (2004) Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob Change Biol* 10:1610–1617
- Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E (ed) *Bird migration: the physiology and ecophysiology*. Springer, Berlin, pp 331–351
- Balbontín J, Møller AP, Hermosell IG, Marzal A, Reviriego M, de Lope F (2009) Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *J Anim Ecol* 78:981–989
- Bartoń K (2015) MuMin: Multi-Model Inference. R package version 1.15.1. <http://CRAN.R-project.org/package=MuMin>
- Bates D, Maechler M, Bolker B, Walker S (2013) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-5. <http://CRAN.R-project.org/package=lme4>
- Bauböck L, Miller-Rushing AJ, Primack RB, Lloyd Evans TL, Wasserman FE (2012) Climate change does not affect protandry in seven passerines in North America. *Wilson J Ornithol* 124:208–216
- Both C (2010) Flexibility of timing of avian migration to climate change masked by environmental constraints *en route*. *Curr Biol* 20:243–248
- Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migratory bird. *Nature* 411:296–298
- Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T et al (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc R Soc Lond B* 271:1657–1662
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006a) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83
- Both C, Sanz JJ, Artemyev AA, Blaauw B, Cowie RJ, Dekhuijzen AJ et al (2006b) Pied flycatchers *Ficedula hypoleuca* travelling from Africa to breed in Europe: differential effects of winter and migration conditions on breeding date. *Ardea* 94:511–525
- Both C, Bijlsma RG, Ouwehand J (2016) Repeatability in spring arrival dates in pied flycatchers varies among years and sexes. *Ardea* 104:3–21
- Both C, Burger C, Ouwehand J, Samplonius JM, Ubels R, Bijlsma RG (2017) Delayed age at first breeding and experimental removals show large non-breeding surplus in pied flycatchers. *Ardea* 105:43–60
- Briedis M, Hahn S, Adamík P (2017) Cold spell *en route* delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecol* 17:11
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, New York
- Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Front Ecol Environ* 1:412–420
- Canal D, Jovani R, Potti J (2012) Male decisions or female accessibility? Spatiotemporal patterns of extra pair paternity in a songbird. *Behav Ecol* 23:1146–1153
- Chan K-S, Ripley B (2012) TSA: time series analysis. R package version 1.01. <http://CRAN.R-project.org/package=TSA>
- Conklin JR, Battley PF, Potter MA (2013) Absolute consistency: individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS ONE* 8:e54535
- Dale S, Rinden H, Slagsvold T (1992) Competition for a mate restricts mate search of female pied flycatchers. *Behav Ecol Sociobiol* 30:165–176
- de la Hera I, Pulido F, Visser M (2014) Longitudinal data reveal ontogenetic changes in the wing morphology of a long-distance migratory bird. *Ibis* 156:209–214
- Dunn PO, Winkler DW (2010) Effects of climate change on timing of breeding and reproductive success in birds. In: Møller AP, Fiedler WP, Berthold P (eds) *Effects of climate change on birds*. Oxford University Press, London, pp 113–128
- Fox J, Weisberg S (2011) *An {R} companion to applied regression*. 2nd Edition. Thousand Oaks CA: Sage. <http://socserv.socsci.mcmaster.ca/~fox/Books/Companion>
- Gienapp P, Bregnballe T (2012) Fitness consequences of timing of migration and breeding in cormorants. *PLoS ONE* 7:e46165
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58
- Gordo O, Doi H (2012) Drivers of population variability in phenological responses to climate change in Japanese birds. *Clim Res* 54:95–112
- Gordo O, Sanz JJ (2008) The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *J Ornithol* 149:199–210
- Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. *Glob Change Biol* 16:1082–1106
- Gordo O, Tryjanowski P, Kosicki JZ, Fulín M (2013) Complex phenological changes and their consequences in the breeding success of a migratory bird, the white stork *Ciconia ciconia*. *J Anim Ecol* 82:1072–1086
- Gwinner E, Helm B (2003) Circannual and circadian contributions to the timing of avian migration. In: Berthold P, Gwinner E, Sonnenschein E (eds) *avian migration*. Springer, Heidelberg, pp 81–95
- Harnos A, Nóra Á, Kovács S, Lang Z, Csörgő T (2015) Increasing protandry in the spring migration of the pied flycatcher (*Ficedula hypoleuca*) in Central Europe. *J Ornithol* 156:543–546



- Hüppop O, Hüppop K (2003) North Atlantic oscillation and timing of spring migration in birds. *Proc R Soc Lond B* 270:233–240
- Hüppop O, Winkel W (2006) Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *J Ornithol* 147:344–353
- Hurrell JW (1995) Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* 269:676–679
- IPCC (2013) Climate Change 2013: the physical science basis. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Johnson PCD (2014) Extension of Nakagawa & Schielzeth's  $R^2$  GLMM to random slopes models. *Meth Ecol Evol* 6:133–142
- Jonzén N, Lindén A, Ergon T, Knudsen E, Vik JO, Rubolini D et al (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961
- Kanamitsu M, Ebisuzaki W, Woollen J, Yang S-K, Hnilo JJ, Fiorino M, Potter GL (2002) NCEP-DOE AMIP-II reanalysis (R-2). *Bull Am Meteor Soc* 83:1631–1643
- Knudsen E, Lindén A, Ergon T, Jonzén N, Vik JO, Knappe J et al (2007) Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Clim Res* 35:59–77
- Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N et al (2011) Challenging claims in the study of migratory birds and climate change. *Biol Rev* 86:928–946
- Koenker R (2015) Quantreg: Quantile Regression. R package version 5.19. <http://CRAN.R-project.org/package=quantreg>
- Lundberg A, Alatalo RV (1992) The pied flycatcher. T & AD Poyser, London
- Martínez-de la Puente J, Merino S, Lobato E, Moreno J, Tomás G, Morales J (2009) Male nest-building activity influences clutch mass in pied flycatchers *Ficedula hypoleuca*. *Bird Study* 56:264–267
- Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R et al (2006) European phenological response to climate change matches the warming pattern. *Glob Change Biol* 12:1969–1976
- Møller AP, Merilä J (2004) Analysis and interpretation of long-term studies investigating responses to climate change. *Adv Ecol Res* 35:111–130
- Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc Natl Acad Sci USA* 105:16195–16200
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev* 85:935–956
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from Generalized Linear Mixed-effects Models. *Meth Ecol Evol* 4:133–142
- Newton I (2007) Weather-related mass-mortality events in migrants. *Ibis* 149:453–467
- Newton I (2008) The migration ecology of birds. Academic Press, London
- Ouwehand J, Both C (2016) Alternate non-stop migration strategies of pied flycatchers to cross the Sahara desert. *Biol Lett* 12:20151060
- Ouwehand J, Both C (2017) African departure rather than migration speed determines variation in spring arrival in pied flycatchers. *J Anim Ecol* 86:88–97
- Ouwehand J, Ahola MP, Aulsems ANMA et al (2016) Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *J Avian Biol* 47:69–83
- Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510
- Potti J (1998) Arrival time from spring migration in male pied flycatchers: individual consistency and familial resemblance. *Condor* 100:702–708
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Rainio K, Tøttrup AP, Lehikoinen E, Coppack T (2007) Effects of climate change on the degree of protandry in migratory songbirds. *Clim Res* 35:107–114
- Robson D, Barriocanal C (2011) Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. *J Anim Ecol* 80:320–331
- Saino N, Szép T, Romano M, Rubolini D, Spina F, Møller AP (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7:21–25
- Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K et al (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc R Soc B* 278:835–842
- Schaub M, Jenni L, Bairlein F (2008) Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behav Ecol* 19:657–666
- Sergio F, Tanferna A, De Stephanis R, López Jiménez L, Blas J, Tavecchia G et al (2014) Individual improvements and selective mortality shape lifelong migratory performance. *Nature* 515:410–413
- Sparks T, Tryjanowski P, Cooke A, Crick H, Kuźniak S (2007) Vertebrate phenology at similar latitudes: temperature responses differ between Poland and the United Kingdom. *Clim Res* 34:93–98
- Spottiswoode CN, Tøttrup AP, Coppack T (2006) Sexual selection predicts advancement of avian spring migration in response to climate change. *Proc R Soc Lond B* 273:3023–3029
- Stenseth NC, Ottersen G, Hurrell JW et al (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc R Soc Lond B* 270:2087–2096
- Studds CE, Marra PP (2011) Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proc R Soc Lond B* 278:3437–3443
- Svensson L (1992) Identification Guide to European Passerines. Fingraf AB, Södertälje
- Tarka M, Hansson B, Hasselquist D (2015) Selection and evolutionary potential of spring arrival phenology in males and females of a migratory songbird. *J Evol Biol* 28:1024–1038
- Taylor B, Christie DA (2015) European pied flycatcher (*Ficedula hypoleuca*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds) Handbook of the birds of the world alive. Lynx Edicions, Barcelona, pp 128–129
- Tøttrup AP, Thorup K (2008) Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *J Ornithol* 149:161–167
- Tøttrup AP, Thorup K, Rainio K, Yosef R, Lehikoinen E, Rahbek C (2008) Avian migrants adjust migration in response to environmental conditions en route. *Biol Lett* 4:685–688