Latitudinal variation of arrival and breeding phenology of the pied flycatcher *Ficedula hypoleuca* using large-scale citizen science data.

ABSTRACT

Many species have advanced the timing of their annual reproductive cycles in response to climatic warming, sometimes leading to asynchrony between tropic levels and negative population consequences. Long-distance migratory birds that are reliant on short seasonal food pulses to provision nestlings are particularly susceptible to such disjunction because late arrival to breeding areas may preclude optimal timing of egg laying. It is unknown whether the interval between arrival and egg laying is sufficiently plastic, in time and space, to enable an adaptive response when arrival times change relative to food resources. We used citizen science data, describing pied flycatcher *Ficedula hypoleuca* arrival and egg laying dates, to explore temporal (2013-2016) and spatial (5 latitude degrees across Great Britain) variation in the phenology of arrival, laying and the interval between them. Data from a long-term field study were also used to assess the long-term trend in the phenology of arrival and laying at a single location. The arrival-laying interval was consistently shorter in the north, a pattern driven by the contrast between spatial variation in arrival date and spatial invariance in laying date. To understand whether a short arrival-laying interval may have consequences for productivity, we assessed the association between the interval and clutch size. We found no statistically significant correlation between the arrival-laying interval and clutch size. When examining longer-term changes in arrival and laying, we focussed on a single location. Arrival date of the first male and first egg laid in a season both advanced since 1986. However, the long-term arrival-laying interval demonstrated high inter-annual variability with no evidence of a long-term trend, providing no evidence of the interval shortening as a response to advancing spring and changes in life-cycle phenology. Together, our results showcase spatial and annual variation in the arrival-laying interval, with no effect on clutch size, indicating the potential for these migrant birds to adapt this interval to align with local conditions and mitigate the impacts of mismatch.

KEYWORDS

Arrival constraint, long-distance migrant, phenological mismatch, citizen science, laying date, spatial variation, Nest Record Scheme, BirdTrack

1. INTRODUCTION

One documented consequence of a warming climate is phenological mismatch, where previously aligned seasonal events have become disjunct as a result of differential adaptation to climate change across different trophic levels (Thackeray et al. 2016). Migratory birds are particularly susceptible to phenological mismatch because their migration and breeding strategies are adapted to match conditions at multiple locations throughout their annual cycle (Carey 2009, Saino et al. 2011), and so constraints at one stage of the cycle may lead to impacts on subsequent stages (Ockendon et al. 2012). For example, migration timing may constrain the timing of breeding schedules, potentially limiting birds' ability to adapt sufficiently to changes in timing in the availability of food resources. This may cause or exacerbate a phenological mismatch between tropic levels, associated with lower nest success (Verhulst and Nilsson 2008).

In migratory birds, studying temporal and spatial variation in the interval between arrival to breeding grounds and the start of egg laying may provide insights into the underlying mechanisms that enable phenological adaptations to climate change. Plasticity in arrival and egg laying date are well known (Both et al. 2005, Charmantier and Gienapp 2014, Valtonen et al. 2017). However, the interval between arrival and egg laying, while influenced by plasticity of either one, further encapsulates the variation in time taken to establish a territory, find a mate, build a nest and reach egg laying condition. Therefore, the length and variability of this interval is not only determined by variation in arrival and laying date, but also by the duration of the necessary activities to prepare for breeding.

If the arrival-laying interval remains constant across space and time, this suggests a fixed period of time is required between arrival and egg laying, and that the timing of laying is therefore closely linked to the timing of arrival. Such rigidity would mean that late arrival would lead to late breeding, increasing the chance of a phenological mismatch (Both and Visser 2001). Importantly, late arrival is relative to the peak of required breeding resources, so late arrival may be due to birds migrating later, or the peak of resources occurring earlier. On the contrary, if the arrival-laying interval shows spatial or temporal variation, it could suggest adaptive responses to compensate for the impacts of an earlier spring or late arrival, potentially avoiding any subsequent negative consequences. Because phenological constraints can happen locally, at restricted parts of the species range, the presence of spatial variation in the arrival-laying interval could further help reveal local plasticity in this interval (Low et al. 2019).

The pied flycatcher *Ficedula hypoleuca* is a single-brooded Afro-Palaearctic long-distance migrant that breeds in forest habitats. In highly seasonal habitats, such as deciduous forests, species including the pied flycatcher are at risk of phenological mismatch as they time breeding to coincide with short seasonal peaks in local food abundance (Visser et al. 2004, 2006, Both et al. 2009, Both 2010a). In response to an advance in spring phenology, some pied flycatcher populations have advanced their dates of both arrival and egg laying (Both and Visser 2001a, Ahola et al. 2004, Hüppop and Winkel 2006), whilst others have shown less plasticity (Both et al. 2004). There is some evidence that individual pied flycatchers can shorten the interval between arrival and egg laying when they arrive relatively late compared to other individuals (Lundberg and Alatalo 1992). However, in an English population, the first arrival date of a male pied flycatcher was considered not important in determining timing of breeding, which may have arisen from the large time difference between first arrival and first egg date in England compared to some other European populations (Goodenough et al. 2011). The variation in the phenology of pied flycatcher arrival and egg laying, shown from single site studies such as this, highlights the need to investigate the spatial structure in this interval at a larger scale, to identify if and how the interval varies across space, as well as over time. This information can subsequently be used to identify whether some populations are at greater risk of arrival related breeding constraints in relatively early years. As deciduous forest phenology is later at more northern latitudes (Smith et al. 2011, Burgess et al. 2018), risks will be expected to be greatest for populations breeding at more southern latitudes.

Here we examine temporal and spatial variation in the arrival-laying interval, and its correlation with clutch size. A constant interval between arrival and laying would suggest less resilience to future advances in resource phenology, leading to increased potential for phenological mismatch. Spatial variation in the interval would suggest local adaptation to advances in resource phenology which may mitigate the impacts of any future advance of resource phenology. We use two citizen science datasets covering Great Britain, and a longer dataset at a single location, to jointly examine both temporal and spatial variation in the interval, as well as its possible association with fecundity.

2. MATERIALS AND METHODS

2.1 Estimation of arrival phenology

To model arrival phenology, we used data from the checklist-based BirdTrack database (BTO, RSPB, Birdwatch Ireland, SOC, & WOS, 2017), selecting records from 1st March to 15th July in each of four years 2013–2016. This database allows participants to report bird observations at different locations, subsequently validated to ensure high accuracy of the records. We selected complete checklists – those for which the participant reported all detected species – of up to five hours duration. Given our focus on arrival at breeding sites, we selected only checklists within known breeding areas, to minimise the inclusion of passage birds. In spring, Pied flycatchers migrate directly to breeding sites (Ouwehand and Both 2017) and are only rarely observed or captured on passage at coastal migratory bird observatories in the UK (Sparks et al. 2005, Goodenough et al. 2015), and so although passage birds cannot be fully excluded, instances will be rare. We defined the known breeding area as all those 10 km x 10 km squares identified as having breeding pied flycatchers by Bird Atlas 2007–2011 (Figure 1) (Balmer et al. 2013). The broad time period selected provided roughly a month margin around the time period where the species is expected to arrive, making sure we encompassed times without pied flycatcher presence (see Table S1 for the sample sizes).

To estimate arrival date on the breeding grounds, we fitted a separate Generalised Additive Model (GAM) to data from each of the four years, with the detection/non-detection of pied flycatcher on a BirdTrack checklist as the binomial response variable, using a logit link function. We selected three different groups of explanatory variables predicting the probability of pied flycatcher on a checklist: spatio-temporal, observer effort and environmental. The first group includes day of year and northing, modelled as a joint tensor product smooth (Wood 2017), to allow the arrival curve to vary with latitude. Northing is the latitudinal axis from the UK projection OSGB and is closely aligned with latitude. The second group comprises checklist duration, which measures variation in effort between checklists. The third group includes altitude and five landcover variables ecologically relevant for this species (percentages of broadleaf, coniferous, grassland, urban and suburban) selected from the 1km raster LCM2007 landcover map (Morton et al. 2007). BirdTrack records were each assigned to a 1 x 1km square. The landcover variables were the percentage area covered by each landcover type (%) within each 1km square. The altitude was the mean elevation within each 1km square (Jarvis et al. 2008). The equation defining the model of Detection on a BirdTrack checklist was

$$\mathrm{E}(logit(Detection_i)) = \beta_0 + t_1(dayofyear_i\,, northing_i) + f_1(duration_i) + f_2(altitude_i) + \textstyle\sum_{j=3}^{7} f_j(habitat_{ij})\ ,$$

where the f functions correspond to different thin plate regression splines applied to each covariate, the t function corresponds to a tensor product spline, i indexes the checklist and j indexes the landcover variable.

We fitted a separate model for each year. For model selection we used the shrinkage approach in the 'mgcv' R package (Wood 2017) which removes variables by shrinking their effective degrees of freedom (edf) below 0.1. The maximum edf for the joint smooth was set at 24 and at 4 for the effort and landcover covariates. After fitting the model, all the relationships between the covariates and the explanatory variables were individually checked for biologically plausible relationships.

To test the predictive abilities of the arrival models, we performed ten-fold cross validation, grouping the data by observer before aggregating into 10% subsets. This meant that each of the 10 subsets contained the records of 10% of the observers, with the records of a single observer being allocated to a single group. We used the data of 90% of the observers to predict to the remaining 10% of entirely different observers, doing this for each of the 10 possible combinations. The metric selected for validation was Area Under the Curve (AUC) (Sing et al. 2004), calculated with the 'PresenceAbsence' R package (Freeman and Moisen 2008).

To estimate arrival date, we predicted the probability of occurrence on a checklist from the GAM model, for each day and across a sequence of northings. All other covariates were fixed at their median values in 10 x 10 km squares where the species had been detected, hence effectively predicting the occurrence for a median habitat composition. This process resulted in a prediction matrix containing the probability of pied flycatcher occurrence on a checklist at each day and northing. To estimate the proportion of the population that had arrived by each date, we standardised the prediction matrix using the maximum estimated occurrence rate for each northing, assuming that the maximum corresponds to the date where all the individuals that could potentially arrive are present (arrival is a cumulative process). Given this point as a reference, we then estimated the date that corresponds to 50% of the population having arrived.

We performed 200 non-parametric bootstraps of our original data, randomly sampling checklists with replacement, maintaining the total number of checklists. We fitted the model described above to each of the bootstrapped datasets and extracted the metric corresponding to 50% of the arrival for the northing gradient.

2.2 Estimation of breeding onset phenology

To estimate timing of breeding onset, here defined as the clutch initiation date (i.e. the date of the first egg laid), we used data from the British Trust for Ornithology's Nest Record Scheme (NRS) (Crick et al. 2003). The NRS is a citizen science scheme that monitors bird nesting attempts, with observers recording nest contents at several times throughout a breeding attempt. As nests are not visited daily to determine the exact day of clutch initiation, minimum and maximum clutch initiation dates were calculated based on nest observations and known incubation length and laying rate parameters. We excluded nests where the uncertainty around the clutch initiation date exceeded ±5 days (only 14% of the records exceeded ±4 days uncertainty, with 61% being below ±1.5 days).

The midpoint between the minimum and maximum clutch initiation dates was used as our estimate of the clutch initiation event. Events were aggregated within the same 10km squares used for the arrival analysis and two-day periods. Our response variable was the detection/non-detection of a clutch initiation event within a 10km square, during a two-day period, with a logit link function. Any 10km squares without any pied flycatcher nest records were excluded from the analysis (see Table S1 for sample sizes). The equation defining the model was:

$$\mathrm{E}(logit(Detection_i)) = \beta_0 + t_1(day_i, northing_i) + f_1(altitude_i) + \sum_{j=2}^{5} f_j(habitat_{ij}) \quad ,$$

where, as before, the *f* functions correspond to different thin plate regression splines applied to each covariate, the *t* function corresponds to a tensor product spline, *i* indexes the checklist and *j* indexes the landcover category: broadleaf, coniferous, grassland and suburban (urban was absent). The upper limit of edf was again set at 24 for the joint variable and 4 for the environmental covariates.

Breeding onset is a single event, the first egg a pair lays in a season. This is in contrast with arrival which is a cumulative process, in the sense that when an individual arrives, it is available for detection throughout the breeding season. Subsequently, to obtain the date when 50% of the population have initiated clutches, we assume clutch initiation of first nesting attempts follow a normal distribution (Lundberg and Alatalo 1992). Assuming a symmetrical distribution, the peak of clutch initiation will therefore give us the median date when 50% of birds have initiated laying. Thus, to estimate the peak laying date, we computed the date which the most clutch initiation events were detected, corresponding to the peak of the laying distribution.

Repeating the same procedure described for arrival, we fitted a separate model for the data from each year and we performed ten-fold cross-validation and used AUC to assess the model fit. We performed 200 non-parametric bootstraps on each year of data, extracting the estimated median clutch initiation date at each northing.

2.3 Estimation of the arrival-breeding interval

The estimated interval between population arrival and breeding onset is the difference between the median arrival date and the median clutch initiation date. We calculated this interval difference at each northing, for one bootstraped arrival model and one bootstraped breeding onset model. Repeating this for 200 randomly-assembled pairs of bootstraps, we produced bootstrap estimates of the arrival-breeding interval. This enabled us to estimate the difference between arrival and breeding with confidence intervals that reflect the uncertainty in both the arrival and breeding estimates.

2.4 Link between clutch size and the estimated arrival-breeding interval

To investigate a possible relationship between the arrival-breeding interval and fecundity, we modelled clutch size as a function of the estimated interval for that location. Clutch size is a nest-level variable from the NRS dataset. The estimated interval is a population-level estimate from the previous models. To relate the two, we used a Generalised Estimating Equation (GEE), accounting for the correlation in the estimated interval between nests with similar northings. We split the data into 24 clusters, each containing the observations belonging to a single year and 100-km latitudinal band (measured with northing). We assumed independent structure between the clusters, such that observations within each cluster were correlated, but those between clusters were independent. The response variable was clutch size with a Poisson distribution and the predictor variable was the estimated median arrival-laying interval at that northing. The GEE model was fit using R package ‘geepack’ (Halekoh et al. 2006).

2.5 Comparing population estimates to individual birds

To test how our modelled estimates of arrival date and breeding onset phenology related to individual data, we compared our metrics derived from the large-scale population analysis, to data collected on individuals, available at one breeding location. Arrival dates of individual male pied flycatchers from a population in Devon (East Dartmoor, 50°36'N, 3°43'W) were estimated from field observations, providing approximate individual arrival dates for 66 males in 2015 and 2016. Individuals were identifiable through unique ring combinations and plumage features. Estimated male arrival date on a territory was calculated as the midpoint between the first observation of each individual and the previous survey where the bird was not detected (see Bell et al. (2017) for further details). Individual nesting attempts were subsequently closely monitored, and breeding onset dates calculated for each individual. We used these values to calculate the median arrival-breeding interval for each year, as well as associated binomial-based confidence intervals (Conover 1999). We compared these values to the population metrics estimated from our models for the corresponding northing in Devon.

2.6 Long-term changes in arrival and breeding onset

We also used data from the East Dartmoor population to examine long-term temporal change in arrival date of the first male each year, the earliest first egg laying date of each year and the interval between these. East Dartmoor is a well visited nature reserve, and first males have been recorded since 1986 by staff and visitors. From 2009, more intensive (daily) visits were made due to concurrent studies, which indicate that in most years on the day of first male arrival more than one individual was observed and a large proportion arrived within a week of the first male (personal observations). Without arrival data of male arrival to individual territories in earlier years it was not possible to use metrics that capture the mean arrival date, but the same method is reliably used in other studies of the species (Both and Visser 2001b, Goodenough et al. 2011). First females in the population are observed within a few days of the first male, and as pairing and nest building occurs on the day of arrival (Potti and Montalvo 1991) female arrival date was taken as the day that nest building started which was recorded by at least weekly nest-box monitoring as described by Visser et al. (2015). For years (2015-2018) when male arrival was recorded to territories we calculated the mean protandry, with the range (9-12.5 days) within the range found by other studies (Ouwehand and Both 2017, Cadahía et al. 2017, Tomotani et al. 2018). From the nest monitoring we used the earliest recorded nest building date (female arrival) and first egg date recorded for each year. Linear temporal trends were fitted separately to the population first male arrival and first egg dates. Although observations of the first male and first nest building are both influenced by size of the population, over this time period (1986 – 2018) the population remained stable at this site, so we do not expect temporal trends due to changing population size.

All modelling was conducted in R (R Development Core Team 2018) and GAMs were fitted using package 'mgcv' version 1.8-31 (Wood 2017). Sections 2.1 and 2.2 are represented schematically in Fig S1 in the supplementary material.

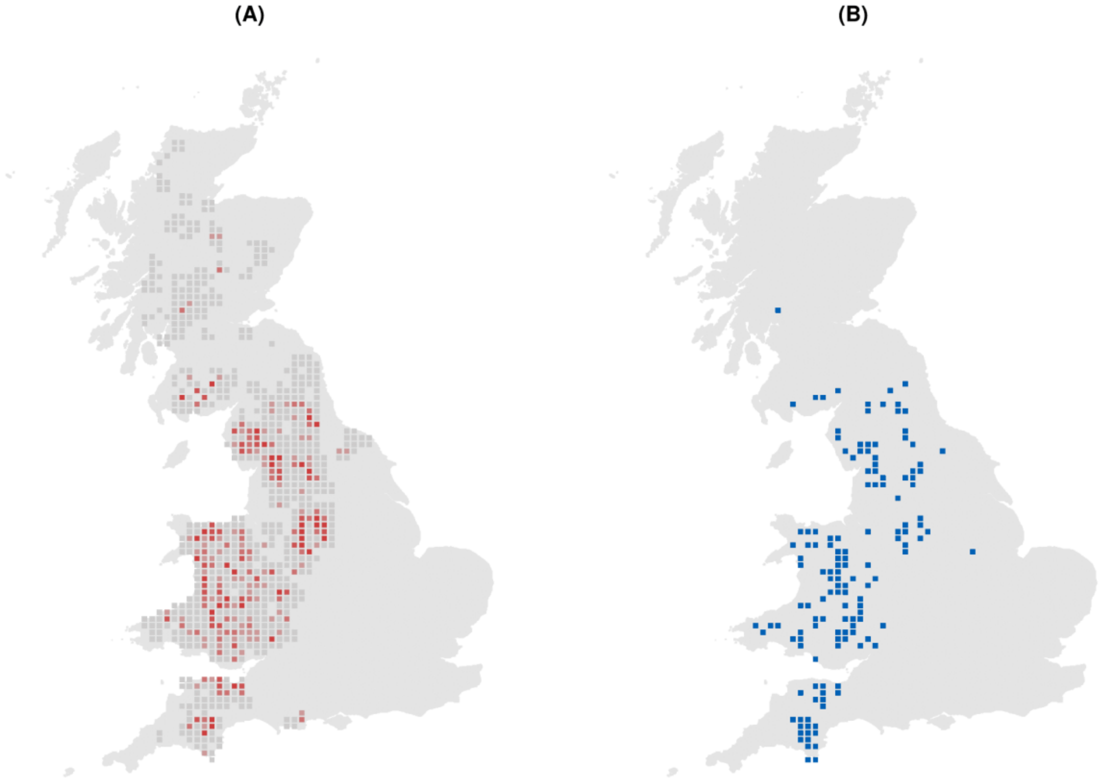

FIGURE 1 (A) Distribution of BirdTrack records in all years combined (2013–2016) in 10 km x 10 km squares where the species was detected breeding between 2007-2011 (Balmer et al.

2013). Red squares correspond to squares where the species was detected in any of the years, varying from palest shade of red (only one year detection) to that darkest (detected in all 4 years). Dark grey squares correspond to squares which were sampled but had no pied flycatcher detections. (B) Distribution of monitored nests in all combined years (2013–2016). Each blue 10 km x 10 km square contained at least one monitored nest in each of the four years. Table S1 contains the detailed sample sizes plotted in these maps.

3. RESULTS

We present estimates from both arrival and breeding onset models for the 50-600 km northing range in Great Britain covering approximately Plymouth (50°N latitude) to Moffat (55°N latitude). Arrival date and breeding onset values in this section refer to median estimates at different values of northing.

3.1 Estimation of arrival phenology

In each of the four years arrival in the north occurred at a similar date, whereas arrival in the south was earlier and more variable (Figure 2, Table S2). In 2014, the early arrival in the south led to a large (15 day) difference between the south and the north. Conversely, the late arrival in the south in 2015 led to a small (four day) difference between the south and the north. Therefore, later arrival in the south led to more synchronised arrival across the British breeding range (Figure 2). The explained deviance of the four models, from each year 2013 to 2016, was 34–40%. All models performed very well in the cross-validation, with AUC values between 90–92%. Details of the models are shown in the supplementary information (Table S3).

3.2 Estimation of breeding onset phenology

As with arrival, breeding onset was consistently later in the north, however, latitudinal variation in breeding onset was smaller than latitudinal variation in arrival date. In 2014 there was almost synchronous breeding onset throughout the full latitudinal range, with females laying only two days later in the north compared to the south (Figure 2). At the other extreme, 2015 showed the largest latitudinal breeding onset difference, with females laying six days later in the north. Across years, the median breeding onset date was consistently within a narrow eight-day period, between the second and third week of May. Uncertainty in the median breeding onset date was much lower than uncertainty in median arrival (Figure 2). The explained deviance of the breeding models ranged between 27–38%. The models performed well in the cross-validation, with AUC values between 79–88% (Table S3).

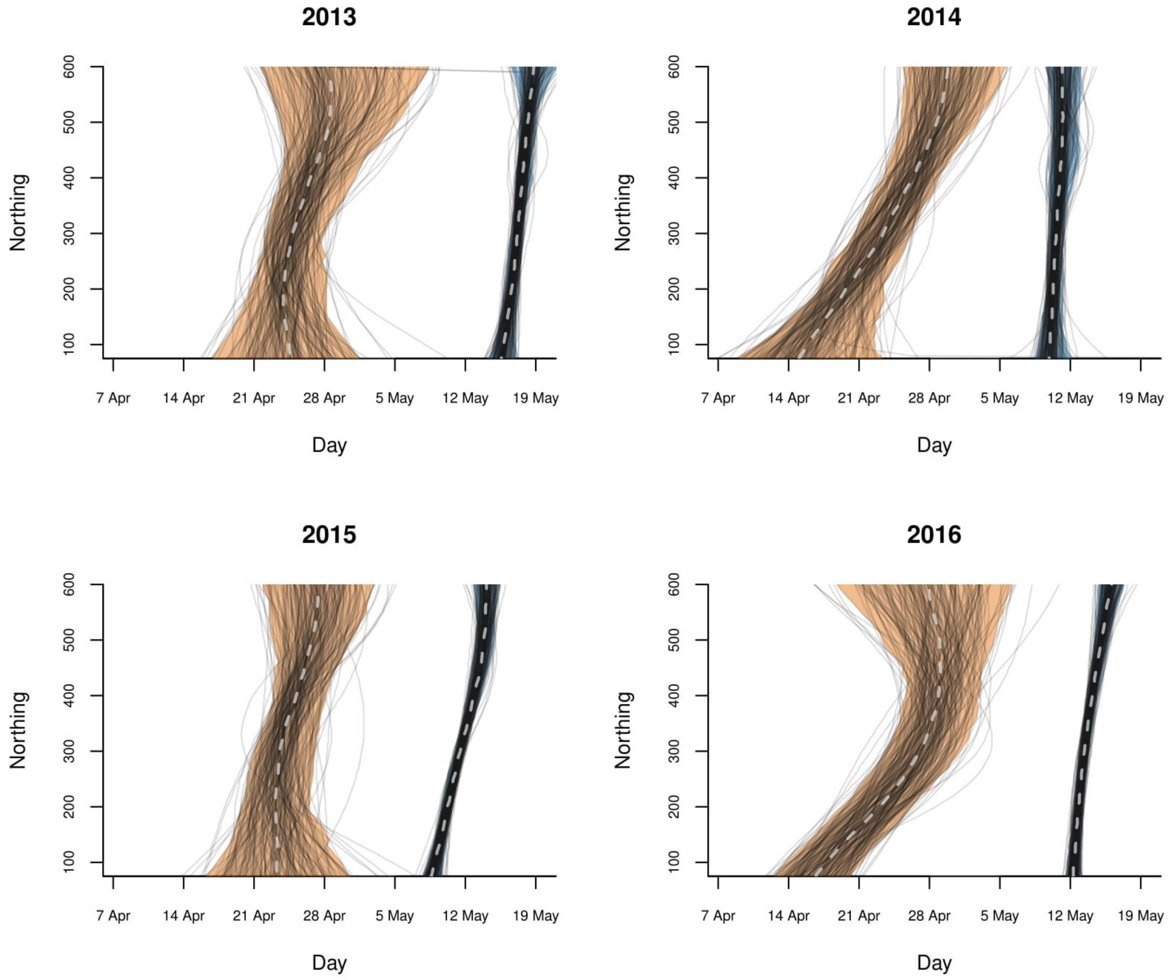

FIGURE 2 Variation of arrival and first egg dates with northing, across years (2013–2016). Each grey line represents an estimate from a single bootstrap resample. Bootstrap estimates for median arrival date are plotted on the left of each plot, with the orange background indicating the 95% confidence intervals. Bootstrap estimates for median breeding onset on the right of each plot, with a blue background indicating the 95% confidence intervals. The dashed line provides the median value across all bootstraps, for each of the estimated parameters.

3.3 Estimation of the arrival-laying interval

The estimated interval between arrival and egg laying varied across years and latitudes between 11 and 27 days. The largest latitudinal difference was in 2014, with southern populations taking an additional 13 days to lay after arrival compared to northern populations. This latitudinal pattern in interval was a consequence of the differential arrival date and constant laying date across the range. 2013 and 2015 showed similar intervals across all latitudes (Figure 3).

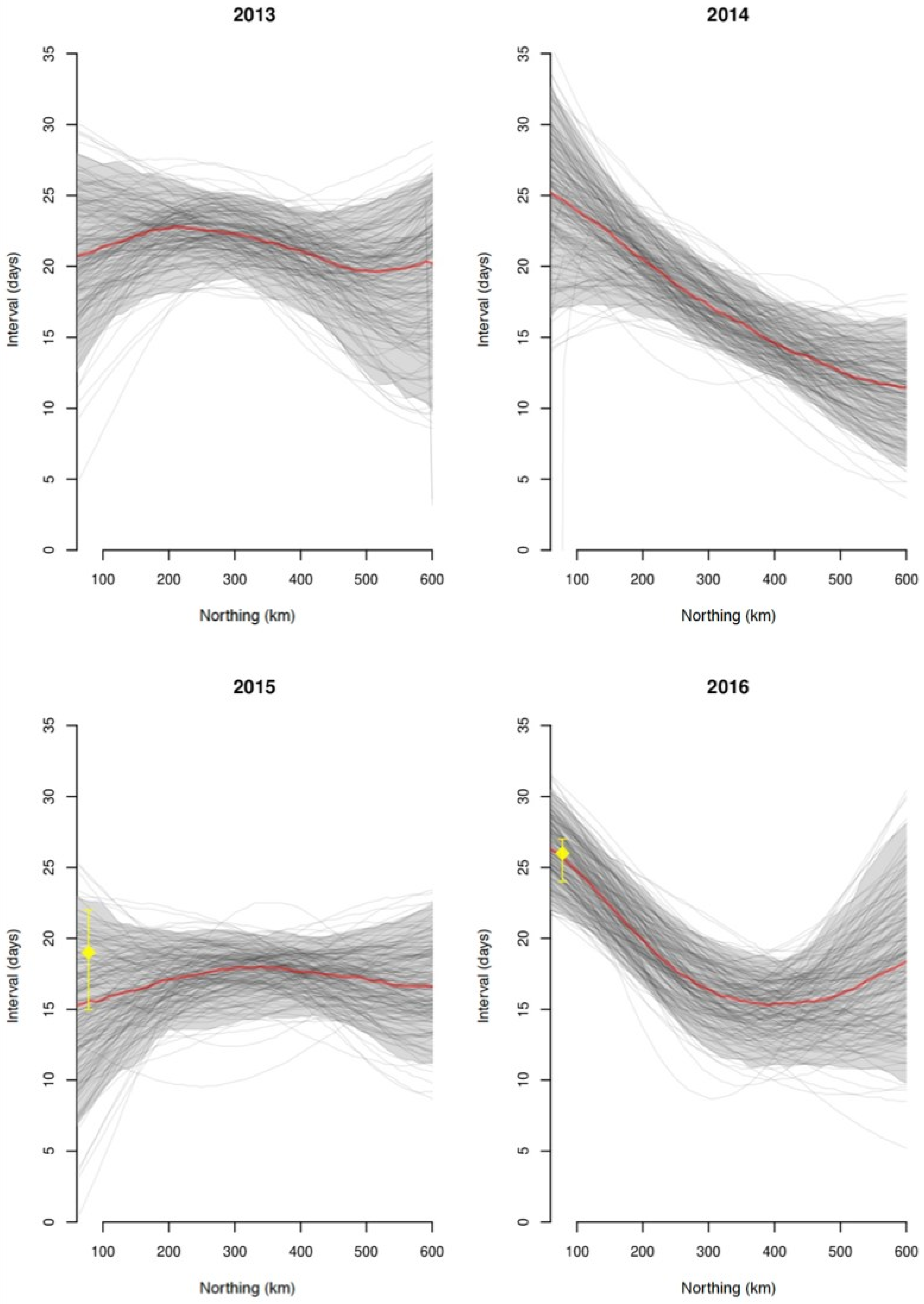

FIGURE 3 Variation of the estimated interval between arrival and breeding (in days) with northing, across years (2013–2016). Each line corresponds to the difference between randomly paired sets of bootstrapped values for arrival and breeding onset. 95% confidence intervals are shown by the grey band, with the red line showing the median interval. The yellow diamond corresponds to the point estimates for the interval using field data collected from Devon, southern England, with the respective 95% confidence intervals.

3.4 Link between clutch size and the estimated arrival-breeding interval

We found no evidence of a link between clutch size and the estimated arrival-breeding interval. The estimated coefficient in the GEE model for the effect of the estimated interval on clutch size was -0.0229 with p-value = 0.14, suggesting no statistically significant evidence of a population-level association between clutch size and estimated interval.

3.5 Comparing population estimates to individual birds

Individual pied flycatchers within the Devon study population had a median interval between arrival and breeding of 19 days (95% C.I.: 16–23 days) in 2015 and 26 days (25–28 days) in 2016. The median estimates of the population models at this latitude were intervals of 16 days (8–23 days) in 2015 and 26 days (22–30 days) in 2016. Therefore, our model estimates of the population intervals overlapped with the confidence intervals for the individual intervals collected from field data. This shows good agreement between the individual and population estimates.

3.6 Long-term changes in arrival and breeding onset

In Devon both the arrival date of the first male and the first egg of the season significantly advanced since 1986 (Figure 4a, $r^2 = 0.28$, slope = -0.30, $P<0.001$; $r^2 = 0.35$, slope = -0.24, P<0.001). However, the interval between the first male arrival and the earliest egg did not change over time (Figure 4b, $r^2 = 0.03$, slope = 0.08, P=0.37).

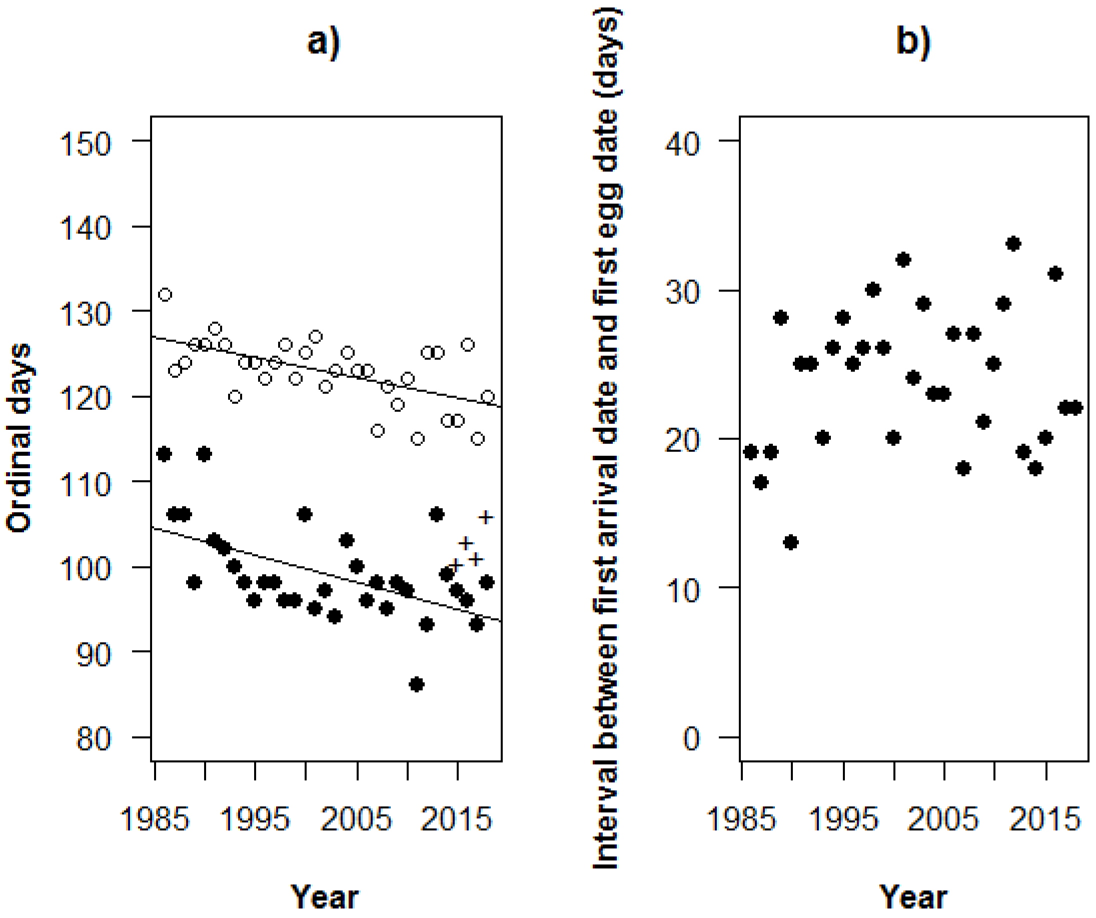

FIGURE 4 Long term trends from field data collected at East Dartmoor, Devon, for a) first male arrival (closed circles) and mean annual first egg laying date (open circles), and b) the interval in days between arrival to a territory by a male and the laying of the first egg in that nest. Trend lines show significant linear regressions. Population size ranged from 49- 87 pairs.

4. DISCUSSION

We describe the spatial and inter-annual variation in the timing of pied flycatcher arrival and egg laying onset across a large spatial extent. Although our results corroborate previous work in finding that arrival is later in the north and shows considerable variation between years, importantly we find differences in the variability of arrival date compared to egg laying onset. Arrival date showed greater spatial and inter-annual variation compared to egg laying onset, particularly in the south of our study region. The combination of variation in arrival with a consistent onset of egg laying led to spatial and temporally variable interval between arrival and laying. We observed that the arrival-laying interval was consistently shorter in the north, but there was no correlation between the length of the arrival-laying interval and clutch size, suggesting no detectable consequence on fecundity resulting from a shorter interval. Data from a single site showed a long-term temporal trend in first male arrival and the first egg laid in a season, with both advancing over time, but the time interval between them, although variable between years, did not show a temporal trend. Together our results suggest that there is no temporal shortening of the time between arrival and egg laying as a response to advances in phenology, but that migratory birds are able to adapt to local conditions, at least to some extent, by shortening the interval in years or locations where arrival is late relative to egg laying phenology. However, because the period between first arrival and first egg laid has not shortened over time, this suggests there may be a limit of this adaptation to future advances of spring resulting from climate warming.

Arrival to breeding locations was consistently later at northern latitudes, but even across four years, the latitudinal discrepancy in arrival dates showed high inter-annual variation. The two years when arrival was early in the south corresponded with a greater variation in arrival date across Great Britain. Inter-annual variation in arrival date may be caused by variation in departure date from non-breeding areas in sub-Saharan Africa, as indicated from tracking of pied flycatchers in the Netherlands, conducted over some of the same years as our work (Ouwehand and Both 2017), and from studies of other Afro-Palaearctic migrants (Saino et al. 2004). Weather conditions and extreme events encountered *en route*, such as sand-storms over the Sahara desert or weather in southern Europe, are also likely to play a role in determining arrival date (Hüppop and Winkel 2006, Strandberg et al. 2009, Both 2010a).

Like arrival, the onset of egg laying was also consistently later in the north, as shown in previous work across the breeding range (Lundberg and Alatalo 1992, Sanz 2008). The NRS dataset we used to examine laying date across Great Britain for four years has previously been used to show this spatial pattern over more than 50 years (Burgess et al. 2018). However, in contrast to arrival date, we found laying date showed relatively little variation across latitude and between years, with 2–6 days variation across latitudes and 2–8 days between years. Spatial variation in egg laying onset will arise from variation in the determinants of laying cues across latitudes, elevations and between habitats, such as from temperature, vegetation phenology and food abundance (Sanz 2008, Smith et al. 2011, Burger et al. 2012).

The estimated arrival-laying interval reached 26 days in some years and locations, and was never less than 11 days. The population interval estimated by our models was within the range of long-term observations of the interval between first arrival and first egg laying date at our Devon field site (Fig 4), and in range of the intervals found in other studies of pied flycatchers across their breeding distribution (Lundberg and Alatalo 1992, Both and Visser 2001a, Goodenough et al. 2011). Upon arrival at breeding territories, after migrating, females are assumed to need to gain condition for egg laying. However, we are aware of no studies of this on small migratory passerines, and so how long this may take and which factors may cause this to vary is unknown (Low et al. 2019). In pied flycatchers this may be no longer than the 10 days necessary for the growth of ovaries and oviduct, a process that can start during migration before arrival to breeding grounds (Silverin 1980). Our finding of egg laying onset showing less spatial and inter-annual variation compared with arrival date indicates that, in years with early arrival, individual birds pair and build nests well in advance of egg laying, which starts when cues and/or female fitness allow.

Our arrival phenology data likely better represent male arrival, as females arrive later and have lower detection rates because they are less conspicuous due to plumage and behaviour. Mean protandry in pied flycatchers varies across Europe, falling within the range 5–17 days (Rainio et al. 2007, Both 2010b, Both et al. 2016, Ouwehand and Both 2017, Cadahía et al. 2017, Tomotani et al. 2018), with protandry at our Devon field site over four years (2015–2018) being 9–12 days. While the protandry of the species is around 5–17 days, typically the first females arrive within a few days of males (Goodenough et al. 2011 and personal observations). Thus, despite males having higher detection rates, we still have a reliable and systematic metric of population arrival dates. Our study was not able to examine the interval between individual female arrival and laying, and so our estimation of arrival-laying interval is longer than will be the case in reality.

The long arrival-laying interval we found across latitudes, and no reduction trend in the interval between one population's first arrival and first egg laid, over 33 years, could suggest that timing of arrival is not constraining the timing of egg laying onset in Great Britain, despite advances in spring phenology. That would support the conclusion of a single-site study that proposed no arrival constraint on laying for a British population (Goodenough et al. 2011). However, a true test of that hypothesis would require the study of individual female arrival and laying times rather than population firsts or means. Furthermore, any biological constraints may act in subtle ways across space, with arrival-laying intervals influenced by spatial variation in food resources or by the longer photoperiod in the north, providing longer foraging hours.

The relationship between the arrival-laying interval and arrival constraint has been studied on individuals in another long-distance migrant, the northern wheatear *Oenanthe oenanthe* (Low et al. 2019). The authors found that the arrival-laying interval changed very little over time, and was shorter in late years for late arriving individuals, concluding that breeding was constrained by arrival only for the latest arrivals, and that for earlier arrivals, laying was determined by local conditions. East Dartmoor has one of the most southern populations of pied flycatcher in Great Britain, and so where arrival date would be most likely to constrain breeding in years requiring early laying to maximise breeding success, compared to more northern populations. Therefore, the absence of a reduction in the first male arrival and first egg laying interval, over a period when laying advanced by around 10 days (Figure 4a), could suggest a similar scenario to the northern wheatear's. However, future climate projections predict spring will become earlier and warmer, increasing selection for earlier breeding (Both and Visser, 2001). A lack of corresponding advances in arrival date could result in a future constraint on breeding onset.

Although the precise cues to egg laying in forest birds remain largely unknown, it is well established that first egg laying date is strongly related to spring temperature (Both and Visser 2001a, Schaper et al. 2011, Phillimore et al. 2016, Samplonius et al. 2018), and is constrained by photoperiod (Lambrechts and Perret 2000, Caro et al. 2007) and environmental conditions (Shutt et al. 2019). In our study, in years with early arrival, the arrival-laying interval was longer, which may result in advantages to females from having longer to improve their condition. Later arrival and a shorter interval between arrival and the optimal laying time may negatively impact on populations, potentially reducing the number of pairs able to nest or impact on individual fitness (Franks et al. 2018). However, we found no evidence of a relationship between the length of the interval and clutch size, suggesting no consequence on fecundity of variation in this interval. We were unable to test effects on nestling survival or reproductive success as too few nests are followed to conclusion in the NRS dataset, and this would be necessary to understand consequences to productivity, recruitment and population persistence.

This study highlights the value of examining patterns of arrival across large spatial scales at multiple locations. In particular, we were able to estimate arrival to breeding locations rather than to locations along migration routes, such as from migratory bird observatories as many previous studies of arrival date have relied upon (Tøttrup et al. 2006, Rubolini et al. 2007). Bird observatory datasets can be less suited to species like the pied flycatcher that tend to migrate directly to breeding sites in spring (Ouwehand and Both 2017), and so are observed or captured in small numbers at many bird observatories (Sparks et al. 2005, Goodenough et al. 2015). Our study also highlights the opportunities of using citizen science data to enable the estimation of arrival date to areas across breeding distributions for many species. We found that modelled population averages were aligned with individual measures of arrival and breeding intervals, for both of the two years that we were able to compare model results with measures at a single location, providing an indication of the validity of the models.

Overall, we further demonstrate the value of examining relationships between different life cycle stages of migratory birds at a population scale. Understanding temporal constraints and their spatial variation is important in assessing the impact of climate change on migrant birds and their capacity to adapt. Exploring potential mechanisms underpinning the latitudinal variation in interval length, for example spatial variation in invertebrate abundance, is a key area for future research. Determining whether there are adult fitness or reproductive costs to differing intervals is also needed to further inform studies of phenological mismatch.

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CONFLICT OF INTEREST

Authors declare no conflict of interests.

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