

## Seasonal trends in the temporal plasticity of breeding in blue tits and great tits in the Loch Lomond area

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### ABSTRACT

Birds commonly increase their fitness by synchronising the emergence of their chicks with the peak in resource abundance in the environment. Climate change is driving earlier laying in many bird species, but within one season individuals may subsequently show additional plasticity. Presumably, birds benefit from being able to adjust the timing of their breeding activities according to environmental conditions. This plasticity in the timing of breeding is illustrated in blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) in the Loch Lomond area, Scotland. Birds use several mechanisms to fine-tune timing of breeding once laying has commenced. These include delays in clutch completion (laying gaps), modulating clutch size, and extending incubation periods beyond population average. We found a seasonal trend in these three mechanisms, with early breeding birds displaying larger laying gaps and extended incubation, and laying larger clutches, compared to later birds. Overall, we found increasing synchronicity with each breeding event across the population. No significant effects of delays in clutch completion and extended incubation period were found on hatching success or nestling weight. Whether the plasticity in the breeding process of tits arises due to a constraint (e.g. energy or nutrients), or a cue received from the environment is uncertain, but we need to improve our understanding of this plasticity in order to better predict the potential effects of climate change on breeding birds.

### INTRODUCTION

The timing of breeding in birds is crucial, as they must synchronise the time of resource abundance in the environment with the peak energy demands of the chicks (Drent & Daan, 1980; Van Noordwijk *et al.*, 1995). Although breeding too early may be disadvantageous due to unpredictable environmental conditions, birds breeding earlier in the season are often more successful than those breeding later (Perrins & McCleery, 1989). Clutch size tends to decrease as the season advances, as birds' breeding output has possibly evolved to match the seasonal decline in favourable environmental

conditions (e.g. food availability; Perrins & McCleery, 1989). However, reduced clutch size is also a means for birds to adjust the time of hatching of their clutch, because many species only fully incubate once a clutch is complete. Thus, smaller clutches advance hatching. Other breeding activities can also be adjusted with effects on hatching time, including laying patterns and intensity of incubation.

The peak of resources in the environment fluctuates on different time-scales. On an inter-annual time-scale, an increase in early spring temperatures caused by climate change is driving many changes in the seasonal emergence of resources. For instance, Polgar & Primack (2011) report a progressive shift to earlier timing of bud burst, resulting in earlier emergence of caterpillars, which may favour a hasty start to breeding in birds. Evidence for the advancement of breeding dates has been found in pied flycatcher (*Ficedula hypoleuca*; Both & Visser, 2001), spotted flycatcher (*Muscicapa striata*; Both *et al.*, 2004) and tree swallows (*Tachycineta bicolor*; Dunn & Winkler, 1999), amongst others. On a short time-scale, the progress of tree phenology can vary within one season; for instance, a cold-spell may delay leafing, consequently affecting the time of caterpillar emergence, an important resource for many breeding birds (Van Asch *et al.*, 2013).

Blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) are small passerine birds native to mixed woodland areas. These species have large clutches (10-12 eggs for blue tits, 6-11 eggs for great tits) which hatch altricial young, requiring food provisioning during approximately three weeks (Snow *et al.*, 1997). The total length of the breeding period is approximately 40 days (Snow *et al.*, 1997). Synchronising the emergence of chicks with environmental resources is complex, because there is a long time-span (at least ca. three weeks) between the laying of the first egg and hatching. This time-span, however, also offers opportunities for modulating breeding behaviour in response to environmental constraints or cues. Blue tits and great tits typically lay one egg per day (Perrins, 1979), and the incubation period lasts 13 days on

average (Snow *et al.*, 1997). However, variation in the timing of these two periods has been reported, in the form of “laying gaps” (Nilsson & Svensson, 1993) and an extended incubation period (White & Kinney, 1974; Haftorn, 1981).

Laying gaps, defined as interruptions in laying occurring between the laying of the first egg and the completion of the clutch, are reported by Dhondt *et al.* (1983), in a population of breeding blue tits and great tits. In this paper, the frequency of laying interruptions in blue tits was correlated to the preceding year’s winter temperatures, whereas interruptions in great tit laying were correlated to the feeding conditions during the laying period. Nilsson & Svensson (1993) observed gaps in laying in 27% of great tit clutches in a population in southern Sweden. Provisioning extra food to females before laying had a significant negative effect on the frequency of laying gaps, with only 8.3% of the provisioned females interrupting their laying (compared to the 27% in control birds).

An extended incubation period, defined as an incubation period longer than average for the population, could be due to two main reasons: a later start to incubation, or lower incubation temperature for example due to interruptions in incubation. Reduced incubation temperature may allow birds to further delay hatching date, but could also have significant costs associated. For instance, Nord & Nilsson (2011) report that reduced incubation temperatures result in lower hatching success and smaller tarsus length in blue tits. Modulation in incubation period has been reported in wild birds in inter-annual comparisons of populations of marsh tits (*Poecile palustris*; Wesolowski, 2000), and great tits (Cresswell & McCleery, 2003).

These modulations in breeding behaviour could be a physiological response resulting from a constraint imposed by environmental conditions, for instance a bird being too energy-constrained to lay a second egg immediately after the first, or to keep eggs at optimal incubation temperature. However, delays in breeding could also be a mechanism to maintain synchronisation after receiving certain environmental cues, as argued by Cresswell & McCleery (2003). In this scenario, the bird is able to lay a second egg but nonetheless delays laying in order to extend the breeding period to match the food peak in the environment. Potential cues in the environment that could modulate breeding in birds are temperature, food-availability, or tree leafing (Visser *et al.*, 2004). In both the “cue” and the “constraint” scenario, delays in breeding could result in fitness consequences in terms of breeding success, if, for instance, temperature during incubation has decreased below that necessary for embryonic development (Haftorn, 1981; Olson *et al.*, 2006). Our present study arose due to observations made during the breeding season of 2017 (April-June

2017). The breeding season started earlier this year than previously recorded in our study system (see below), prompting the question of whether birds would maintain a regular pace of breeding, or would extend the breeding process after the unusually early start. We aim to illustrate the delays observed in the breeding process of blue tits and great tits, and to assess if there are any resulting fitness correlates. Our report is the first mention of breeding delays in Scotland; it also demonstrates that a trend in the length of the laying and incubation periods can be observed within a single breeding season.

Our hypotheses were two-fold; our first hypothesis was that due to the early start in laying, we would encounter laying gaps and extended incubation amongst the population. Specifically, we predict that lags in laying and incubation will be observed more frequently amongst early breeders than later in the season. Our second hypothesis was that, in agreement with previous studies, the clutch size of tits would decrease through the season, as a result of selection to match the resource fluctuation, or due to an energy constraint. Finally, we predict that interruptions in laying and extended incubation will have consequences for the breeding success of birds.

## METHODS

The nests referred to in this report are all part of the Glasgow Gradient, an experimental set-up with a selection of sites across a gradient of urbanisation (Pollock *et al.*, 2017 and Capilla-Lasheras *et al.*, 2017 for details). The sites included in this report are those at the rural end of the gradient: the area of woodland surrounding the Scottish Centre for Ecology and the Natural Environment (SCENE; 56°07'34.4"N, 4°37'04.6"W), the area of woodland adjacent to Sallochay bay (56°07'34.7"N, 4°36'20.9"W), and the woodland surrounding Cashel farm (56°6'45.0"N, 4°34'32.9"W), all three on the banks of Loch Lomond. These three sites contain a total of 412 nestboxes (Woodcrete, Schwegler, Germany; dimension = 260H × 170W × 180D cm; hole diameter = 32 mm), commonly occupied by blue tits and great tits.

Starting on 9 March 2017, weekly checks were carried out on all the nest boxes, monitoring and recording nest building and egg-laying. Once egg-laying was completed, the earliest possible hatch date was calculated, by estimating the date of the final egg (assuming one egg/day), and adding 12 days of incubation (including day of clutch completion). Nestboxes were checked on the estimated hatch date and every other day after that if the eggs were still intact. Once hatching began (Fig. 1), the date was recorded along with the number of hatchlings. Hatching success was calculated by dividing the number of eggs by the number of hatchlings. For a subset of boxes (n=51 in SCENE, n=4 in Sallochay, n=34 in Cashel), nestlings were weighed and ringed on day 8 after hatching. After the

young had fledged, the nest boxes were cleared out and any dead chicks found were removed and recorded. The number of dead chicks found in the nest was used to calculate fledging success (fledglings/hatchlings).



**Fig. 1.** Blue tit chicks on the day of hatching, from the woodlands around SCENE. Photograph by Crinan Jarrett.

An extended data set from the Glasgow Gradient was used to compare timing of breeding in 2014-2017. These data had been collected following the same protocol of nestbox checks mentioned above. From this extended data set, a mean start of laying and a mean start of hatching was extracted, along with the data of the first egg and the first hatchling in the population (defined below). Data on the bud burst of trees in the forests of SCENE and Cashel were collected on a weekly basis by observing the canopy of each nestbox-carrying tree through binoculars, and scoring bud burst from 0 to 5, using the categories detailed by Derory *et al.* (2006). Data for the daily mean temperature at Gartocharn Portnellan Farm (56°2'55.9"N, 4°34'0.2"W), 9.4 km from SCENE, were obtained from the Met Office Library & Archive.

The following arguments were used during the analysis:

**At population level**

- a) Date of first egg in population: estimated based on weekly visits to nests, assuming daily laying. Maximum error = 6 days.
- b) Mean start of laying: calculated from data from SCENE, Cashel and Sallochty.
- c) Date of first hatchling in population: estimated from visits to nestboxes on the estimated date of hatching, and then every two days after that. Maximum error = 1 day.
- d) Mean start of hatching: calculated from data from SCENE, Cashel and Sallochty.

**At individual nestbox level**

- e) Date of first egg: estimated based on weekly visits to the nests, assuming daily laying. Maximum error = 6 days.
- f) Date of laying completion: estimated based on the number of eggs in the complete clutch

and the information from the weekly visits to the nests. Maximum error = 6 days.

- g) Delay in laying completion or “laying gaps”: defined as any days beyond those necessary to lay a complete clutch assuming one egg per day (i.e. for a clutch of 7 eggs, 7 days would be the estimated laying period, whereas 9 days would imply 2 days of delay).
- h) Delay in hatching or “extended incubation”: defined as any days beyond the 13 day incubation period, the average for blue tits and great tits (Snow *et al.*, 1997), assuming incubation starts with the last egg. A negative figure for delay in incubation implies an incubation period of less than 13 days, a start of incubation prior to clutch completion, or estimation error based on the above.

All bird sampling was conducted following the directions and legislations of the Scottish Natural Heritage (52463 to BH) and the British Trust for Ornithology (Scientific C licence to BH). Statistical analyses were performed in R (version 3.3.3) using the platform RStudio (version 1.0.136). General linear models (GLMs) were constructed using the package *stats* (R Core Team, 2017). Models were selected by backward elimination of variables from full models, where the starting point was a model containing all variables deemed biologically plausible (Table 1), and potential interactions between them. The best-fit model was selected based on its performance being significantly better ( $p < 0.05$ ) when compared to the model resulting from dropping an additional variable (chosen based on lowest Akaike’s Information Criterion). This selection was done using Likelihood Ratio Tests (LRTs), with the package *lmerTest* (Zeileis & Hothorn, 2002). Residuals of the best-fitting model were plotted and visually assessed to ensure that parametric assumptions were met. The reported LRT output is that obtained by comparing the best-fit model with the model resulting from dropping an additional variable in the step-by-step deletion process. We used a binomial distribution for modelling hatching success. The package *moments* (Komsta & Novomestky, 2015) was used to calculate kurtosis and skewness in the long-term Glasgow Gradient data set. The package *ggplot2* (Wickham, 2009) was used to create the plots.

**RESULTS**

The date of the first egg in the population and the mean start of laying were earlier in 2017 than the three previous years (2014-2016, Table 2). The date of first hatchling in the population and the mean start of hatching were also earlier in 2017 than in previous years. For the 2017 breeding season, clutches laid earlier in the season tended to have more laying gaps compared to clutches laid later, for both blue tits (Fig. 2e) and great tits (Fig. 2f).

<b>Response variable</b>	<b>Explanatory variables</b>	
	<b>Full model</b>	<b>Best-fit model</b>
Delay in laying completion	Date of first egg Species Clutch size Site Site*Date of first egg Species*Date of first egg Temperature	Date of first egg Clutch size
Delay in hatching	Date of laying completion Clutch size Species Site Site*Date of laying completion	Date of laying completion Clutch size Site*Date of laying completion
Clutch size (Blue tits)	Date of laying completion Site	Date of laying completion Site
Clutch size (Great tits)	Date of laying completion Site	
Hatching success	Delay in laying completion Clutch size Site Species Date of laying completion	
Nestling weight	Delay in laying completion Delay in hatching Clutch size Site Date Species	Clutch size Site Species
Nestling weight range	Delay in laying completion Delay in hatching Clutch size Site Date Species	Species

**Table 1.** Response variable and explanatory variables for all models used in analysis. An asterisk (\*) between two terms indicates an interaction. The full model contains all variables deemed biologically plausible, and the best-fit models contain all variables remaining after backwards selection.

	<b>Date of first egg in population</b>	<b>Mean start of laying</b>	<b>Date of first hatchling in population</b>	<b>Mean start of hatching</b>	<b>Mean temperature of previous winter</b>
2017	12-April	25-April	8-May	17-May	5.0°C
2016	20-April	1-May	16-May	24-May	4.5°C
2015	21-April	5-May	18-May	28-May	3.5°C
2014*	24-April*	1-May*	15-May*	20-May*	4.8°C

**Table 2.** The timing of different breeding events in blue tits and great tits in the years 2014-2017: for years 2015-2017, data were extracted from all the boxes in SCENE, Cashel and Salloch. For 2014 (\*), only the data from Cashel were used. Mean temperature (°C) of the winter (Dec, Jan and Feb) previous to breeding season is for W. Scotland.

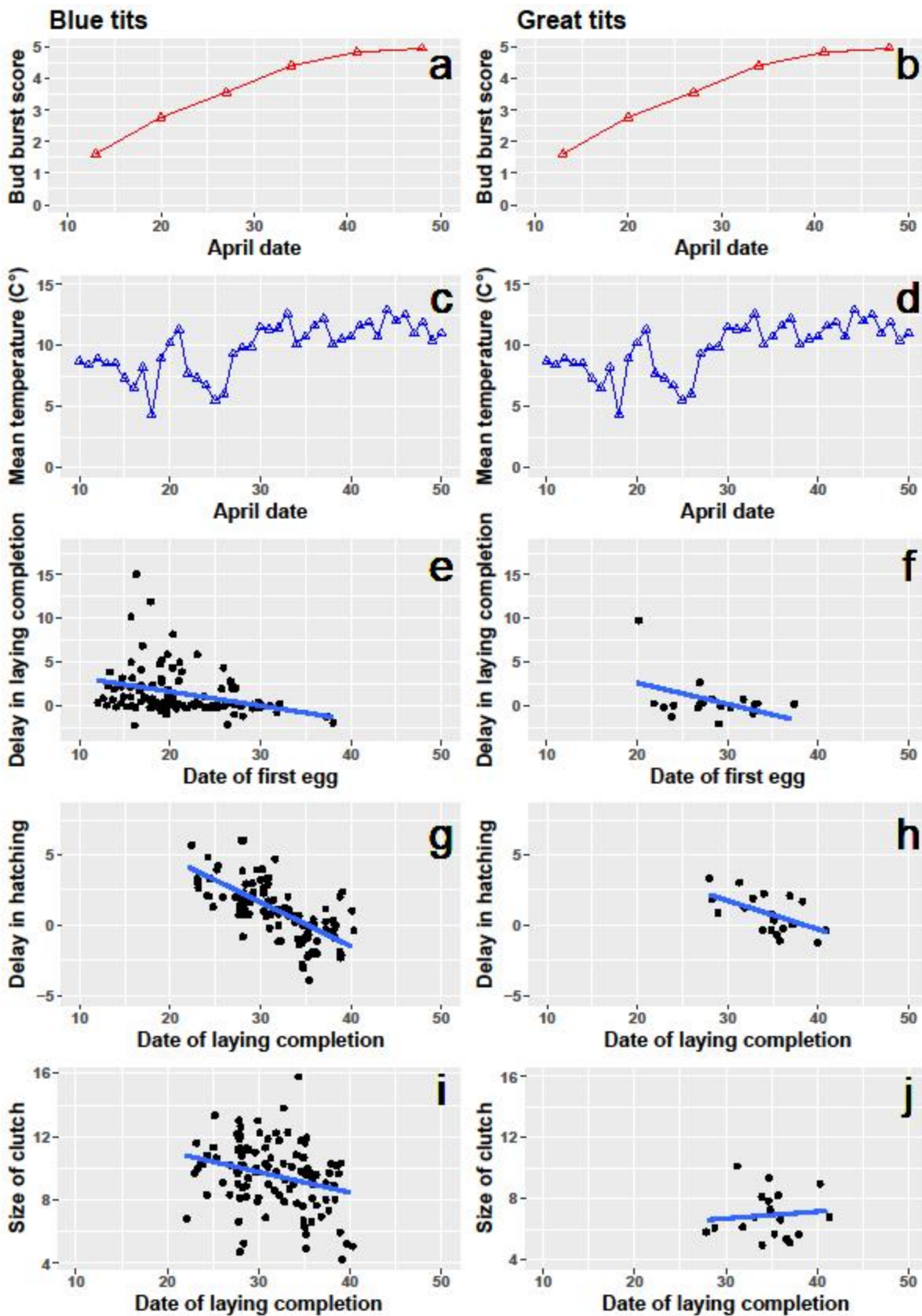


Fig. 2. Phenology: mean bud burst score for SCENE and Cashel, between 10 April and 20 May 2017 (a and b). Average daily temperature between 10 April and 20 May 2017 (c and d). The delay in laying completion (number of extra days taken to complete clutch beyond 1 egg/day) plotted against the date of first egg for blue tits (e) and great tits (f) in Cashel and SCENE. Clutch size (number of eggs) of blue tits (g) and great tits (h) plotted against the date of laying completion. The delay in hatching (number of days exceeding the expected 13 day period) plotted against the date of laying completion for blue tits (i) and great tits (j). The dates are expressed using the April Date system, where number 1 = 1 April 2017.

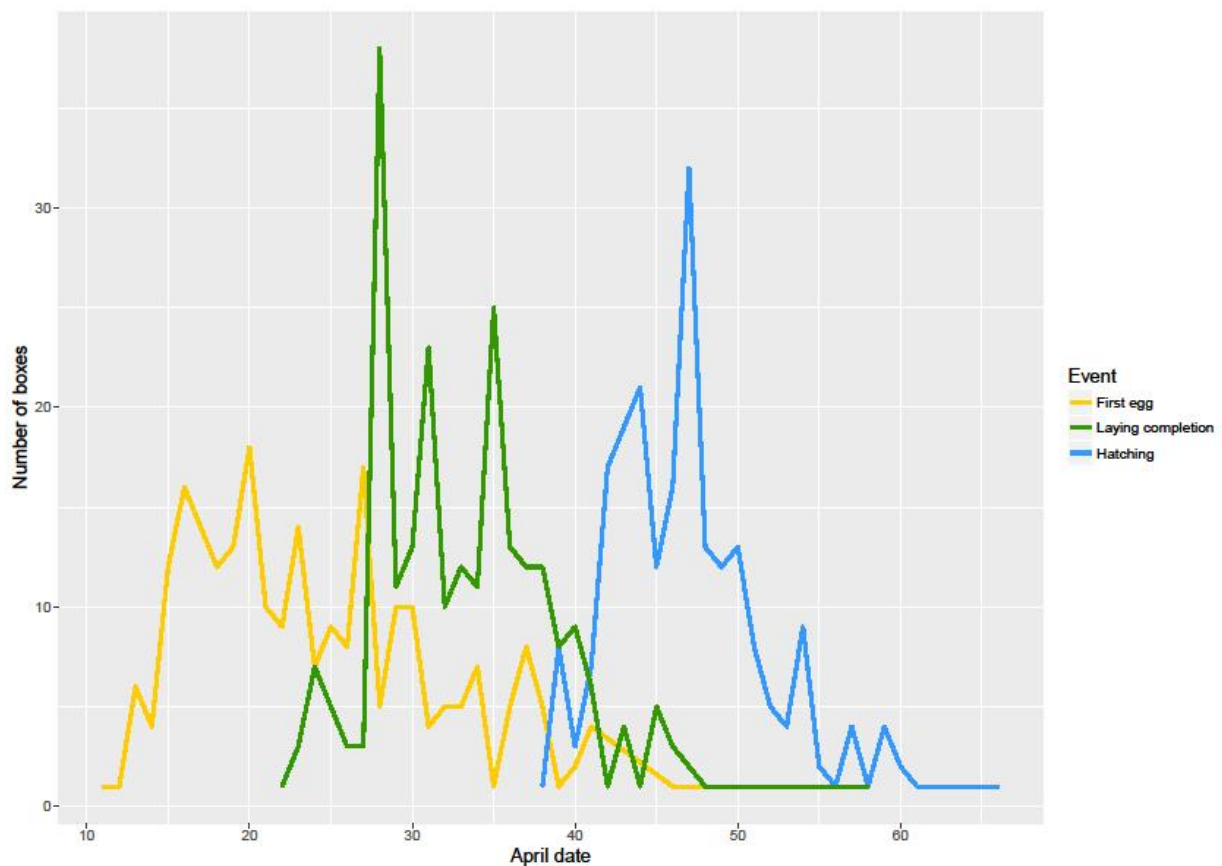
The later clutches, in some cases, shortened the estimated laying period duration expected from daily laying, by maximally three days. The model best explaining the *delay in laying completion* (LRT:  $\chi^2(1)=39.66$ ,  $p<0.0001$ ), contained the explanatory variables *date of first egg* (slope $\pm$ SE =  $-0.22\pm 0.02$ ,  $p<0.0001$ ) and clutch size ( $-0.52\pm 0.1$ ,  $p<0.0001$ ; Table 1). The variables site, species, temperature at date of first egg and the interaction between species and *date of first egg* did not explain significant amounts of variation ( $p>0.05$ ) and were dropped from the final model. There was a correlation found between temperature and date (correlation coefficient = 0.62), with temperature increasing as the season advances.

The initial model to explain variation in clutch size in blue tits and great tits contained as explanatory variables *date of laying completion*, site and species. However, there was a significant effect of the interaction between species and *date of laying completion* ( $p=0.001$ ) on clutch size, and therefore further analysis was done using a separate model for each species. For blue tits, the best-fit model (LRT:  $\chi^2(1)=9.5$ ,  $p=0.002$ ) contained the variables *date of laying completion* ( $-0.13\pm 0.04$ ,  $p=0.002$ ) and site ( $-1\pm 0.37$ ,  $p=0.008$  for SCENE; Table 1). Average clutch size per nest was larger for the birds laying early in the season, and smaller for those laying later (from ca. 11 to 7 eggs; Fig. 2g). The *date of laying completion*

did not have a significant effect on the clutch size of great tits ( $p>0.05$ , Fig. 2h).

The *delay in hatching* decreased significantly with date in both blue tits (Fig. 2i) and great tits (Fig. 2j). Birds starting incubation earlier tended to have a longer incubation period than those starting later in the season. The model best explaining variation in *delay in hatching* (LRT:  $\chi^2(2)=95.39$ ,  $p<0.0001$ ) contained the explanatory variables *date of laying completion* ( $-0.27\pm 0.02$ ,  $p<0.0001$ ), clutch size ( $-0.22\pm 0.05$ ,  $p=0.0001$ ), site ( $-2.8\pm 1.3$ ,  $p=0.03$  for SCENE) and an interaction between site and the *date of laying completion* ( $0.08\pm 0.03$ ,  $p=0.03$ ; Table 1). Species had no significant effect on *delay in hatching* ( $p>0.05$ ), nor did the interaction term between species and *date of laying completion*.

Overall, the synchrony within the population in the timing of breeding activities increased through the season (Fig. 3). This increase in synchrony can be seen in the decreasing standard deviation, range and coefficient of variation of the data (Table 3). The coefficient of variation drops from 32.2 for date of first egg, to 10.2 for date of hatching. Kurtosis is higher in the two later events, indicating curves with less weight on the tails (Sokal & Rohlf, 1981). All three curves are positively skewed, indicating a higher frequency of events early in the range.



**Fig. 3.** Frequency plot illustrating the number of boxes on each day for the three main breeding events (date of 1<sup>st</sup> egg, date of laying completion and date of hatching).

Event	Mean±sd	Range	CV	Kurtosis	Skewness
1st egg	24.4±7.8	43 (11-54)	32.2	3.2	0.75
Laying completion	33.5±5.9	36 (22-58)	17.8	3.9	0.78
Hatching	46.9±4.8	28 (38-66)	10.2	3.9	0.84

**Table 3.** For three breeding events (date of first egg, date of laying completion and date of hatching): mean and standard deviation (sd), range, coefficient of variation (CV), kurtosis and skewness of data.

Hatching success of the birds was not significantly affected by laying gaps, nor by the variables site, clutch size, species, or date of laying completion ( $p > 0.05$ ). After dropping these variables one by one, the null model proved to be best fit (LRT:  $\chi^2(1) = 1.8$ ,  $p = 0.17$ ; Table 1). The same results were obtained using a Gaussian and a binomial distribution. The best-fit model to explain nestling weight at day 8 (LRT:  $\chi^2(1) = 7.9$ ,  $p = 0.004$ ) contained the explanatory variables species ( $5.7 \pm 0.17$ ,  $p < 0.0001$  for great tit), clutch size ( $-0.08 \pm 0.02$ ,  $p = 0.005$ ) and site ( $-1.42 \pm 0.35$ ,  $p < 0.0001$  for Salloch; Table 1). The delay in laying completion and the delay in hatching did not have a significant effect on the weight of the chicks on day 8 ( $p > 0.05$ ), and were dropped from the final model. The best-fit model to explain within-nest variation in chicks, calculated as the standard deviation of the weights of all chicks from one nest, contained only species as an explanatory variable (LRT:  $\chi^2(1) = 11.9$ ,  $p = 0.0005$ ; effect of species  $0.3 \pm 0.08$ ,  $p = 0.0007$  for great tit; Table 1). Clutch size, site, date, delay in laying completion and delay in hatching were non-significant ( $p > 0.05$ ) and were dropped from final model.

## DISCUSSION

The breeding season of 2017 started earlier than in the three previous years, which was reflected both in the start of laying, and in the date of hatching. The mean temperature of the 2016-17 winter was higher than the three previous years, indicating a possible correlation between milder winters and earlier spring breeding. Under a climate change scenario, there is contrasting evidence showing that birds either sufficiently change their breeding timing to match environmental resources (McCleery & Perrins, 1998) or do so insufficiently, resulting in a mismatch between the timing of breeding and maximum resources (Visser *et al.*, 1998). The time-lapse between the start of laying and hatching adds complexity to the synchronisation of breeding in birds.

The main predictor for laying gaps was the date. Specifically, laying gaps decreased throughout the 2017 breeding season, meaning that late-breeding birds showed little delays, whereas birds breeding earlier tended to lay at a slower rate. Temperature was found to be a poorer predictor than date for explaining delay in laying completion, and was consequently dropped from the final model. This finding is not fully consistent with most of the literature on laying gaps, which emphasises a

correlation between temperature and the frequency of gaps (Dhondt *et al.*, 1983; Nilsson & Svensson, 1993; Cresswell & McCleery, 2003). An experimental set-up by Yom-Tov & Wright (1993), where boxes were heated artificially, resulted in a lower frequency of laying gaps in heated boxes. To our knowledge, the correlation between date and frequency of laying gaps has been documented only by Lessells *et al.* (2002) in a population of great tits. However, the variables temperature and date are difficult to separate. Indeed, there was a relatively strong correlation between these variables in our data-set. Thus, our results on a minor role of temperature as a driving factor for delays in laying are tentative. Various factors should be taken into account: for example, the weather data included are only a mean temperature, and this may not be the driving factor for birds' breeding pattern, and it is unsure whether the determining temperature for laying gaps is that of the first day of laying. These queries would benefit from high resolution weather information and a longer time-series of data on birds' breeding activity (e.g. Cresswell & McCleery, 2003 and Visser *et al.*, 1998).

Delay in laying completion was also affected by clutch size, with less delay occurring in boxes with larger clutches. Larger clutches will naturally take a longer time to lay, and thus (all else being equal) hatching is pushed back with every added egg. Laying a small clutch but at a slow rate (with laying gaps) could be a "budget" version of this same behaviour, the outcome being the delay in hatching date. This mechanism could be a result of a constraint on the ability of some birds to produce eggs on a daily basis, and could entail fitness consequences. However, clutch size and laying delays decreased throughout the season. Therefore, the longer delay in larger clutches could simply be re-iteration of the shared trend to decrease through the season.

The modulation in clutch size by birds according to laying date has long been discussed in the literature (Lack, 1968; Perrins & McCleery, 1989), and is seen as an adaptive behaviour to better match environmental resources. In this report, clutch size was found to decrease throughout the season in blue tits, as expected. There was also a significant effect of site on clutch size, with SCENE having smaller clutches than Cashel. This phenomenon has been observed in previous years in the Glasgow Gradient (Helm *et al.*, unpublished data), and may be a result

of a more mature and resource-rich woodland in Cashel. The lack of a correlation between clutch size and date of the first egg in great tits may be a result of a smaller sample size (n=41 breeding pairs for great tits, n=159 for blue tits).

The delay in hatching followed a seasonal pattern similar to the delay in laying completion, decreasing progressively as the season advanced. Thus, birds breeding earlier had an extended incubation period compared to birds breeding later, matching our initial predictions. The decrease in incubation period with advancing spring dates has been documented previously in marsh tits (Smith, 1993; Wesolowski, 2000), both within seasons and between seasons. Cresswell & McCleery (2003) find no seasonal trend in total incubation period in great tits in the mixed deciduous woodland of Wytham Woods. However, they identified the extent of incubation on the day of clutch completion (percentage of time spent on nest) as one defining factor for incubation period: the more time a bird spent incubating on that specific day, the shorter the total incubation period was. Consistent with these results, Wang & Beissinger (2011) review the concept of "partial incubation", defined as a reduced amount of time during egg laying or full incubation that parents sit on and warm their eggs. Partial incubation is found to be present in multiple species of bird including great tits (Wang & Beissinger, 2011), and could be one potential explanation for a modulation in the time-span between laying initiation and hatching.

Other variables explaining delay in hatching were clutch size, site, and the interaction between site and date of laying completion. Larger clutches tended to have less delay in hatching, matching the results for delay in laying completion. An extended incubation period could be an alternative behaviour adopted by birds with small clutches, resulting in a later hatching date possibly beneficial to adjust to environmental fluctuations. Also, as clutch size decreases with the season, the effect of clutch size on delay in hatching could simply be a re-iteration of the temporal trend. Site has a significant effect on the delay in hatching, with SCENE having less delay than Cashel. As the interaction between site and date of laying completion is significant, we can assume that the breeding process at SCENE is later, resulting in less delay.

The fitness consequences of delaying laying completion and delaying hatching are hard to predict. On the one hand, if these mechanisms allow greater synchronisation with environmental resources, one would expect breeding success to be higher in birds who display plasticity in the timing of breeding. Additionally, if delaying allows parents to better budget their energy reserves, this may be beneficial for parent fitness as well (Wang & Beissinger, 2011). On the other hand, it has been shown that egg viability decreases with time of

exposure to ambient temperature (Beissinger *et al.*, 2005; Wang *et al.*, 2011), and that reduced temperature during incubation results in lower hatching success (Nord & Nilsson, 2011), indicating that delays in both laying and incubation could be detrimental to breeding success.

In this report neither the delay in laying completion nor the delay in hatching had clear consequences on breeding success. Birds who did delay the breeding process had neither higher nor lower hatching success. Nor did they produce smaller nestlings compared to birds who did not delay. One possible way to explain this is that the fitness correlates analysed were not the ones affected by delays in breeding. For instance, the main consequences of delaying could be seen in the body condition of the parents, which could be assessed in future studies (Wang & Beissinger, 2011). A second possible explanation is that the penalty for delaying birds was masked because of good environmental conditions. In this case, in a year with very poor environmental resources, the constrained birds could suffer direly for their delays.

In this study, there appears to be a general trend to greater synchronicity as the breeding season advances. The start of laying is a lot more variable compared to the hatching date of birds in the population. This trend supports the idea that the main event which requires synchronisation with environmental resources is hatching, rather than the initiation of the whole breeding process (Cresswell & McCleery, 2003). It is possible that a long-term trend to earlier warm springs due to climate change selects for birds to start breeding early, however it will be beneficial for birds to be able to "tailor" their behaviour once laying has started, to be able to cope with unexpected short-term conditions such as a cold spell.

In this study we document a clear temporal trend in the delay of laying completion, clutch size, and the delay in hatching, which adds evidence to the use of these three mechanisms to synchronise breeding within a population, presumably to match the peak in environmental resources. In a highly fluctuating environment, both within and between seasons, it is yet unclear whether the plasticity in breeding phenology of birds results from an environmental cue or from an imposed constraint. In our study we detected no fitness consequences of breeding delays. Although we cannot fully rule out these consequences, it may be that plasticity in breeding activities is sufficient to counteract environmental fluctuations. The timing of breeding in birds may indeed benefit from a degree of plasticity, but these benefits may be context dependent. We are entering uncharted territory, and a wider understanding of the range of responses available for birds to survive a changing climate is necessary.

## ACKNOWLEDGEMENTS

We would like to thank Paul Jerem, Kate Griffiths, Nanette Verboven and the whole Bird Group for their help in the field. We would also like to thank the staff at SCENE, and the Trustees of the RSFS Forest Trust for access to Cashel Forest.

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