Effects of variability in climatic conditions on the phenology of the migratory European pied flycatcher (*Ficedula hypoleuca*)

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Abstract

During the last few decades the phenology of many passerine birds have shifted, a trend that has been seen throughout the world. This has led to an increasing fear that the birds are having trouble adapting, and experiencing an increasing mismatch between the timing of food requirements and their breeding. This fear has been highlighted in migratory birds who, in contrast to resident birds, are unable to respond to local climate cues to adapt to this mismatch. The consequences of changes in climate means for ecology has already attracted plenty of interest and highlighted important questions. But less work has been done looking at how climate variability affects populations dynamics and other aspects of ecology. We used a sliding window approach through the R package *climwin* to identify potential periods of climate sensitivity. This was done on a pied flycatcher population in Southern Norway with a dataset going from 1985-2017 looking at both temperature and precipitation. Measures of standard deviation for temperature and coefficient of variation for precipitation was then used as a metric for climate variability, and their influence on both laying date and breeding success was investigated using linear mixed-effect models. While no effect of the variability in temperature was found, the results showed that the population of flycatchers experienced an effect of variability of precipitation both directly and indirectly.

Contents

1. Introduction

With a changing climate we expect to see changes in weather both in regards to its mean, variability and extremes (Parmesan and Yohe, 2003; Jackson *et al.*, 2009; Fischer, Sippel and Knutti, 2021). As a result intensive research has been conducted in the last few decades to look at the potential consequences for different ecological and evolutionary processes. From the early 2000s ecological responses to climate change have been clearly visible (Walther *et al.*, 2002), and shifts in mean climate parameters have had a part to play in population dynamics, affecting living systems (Parmesan and Yohe, 2003; Oliver and Morecroft, 2014). Looking at mean climate parameters has been the go-to way of trying to find explanations for potential ecological changes for years (Parmesan and Yohe, 2003; Chen *et al.*, 2011). In the last few years research on climate variability has become more and more prominent. This variability is explained as irregular shifts in the environment caused by both natural and human activity (Lawson *et al.*, 2015). This could lead to species being unable to track shifting phenotypic optima due to more fluctuating selection pressures (Kopp and Matuszewski, 2014). The fear is that these changes in environmental variability may be harder to adapt to than altered mean conditions (Huntingford *et al.*, 2013), and potentially pose a greater risk to living organisms than mean climate warming (Vasseur *et al.*, 2014). The responses to this increase in climate variability are predicted to be hard to generalize, as they are complex depending on both individuals, populations or communities, as well as the physiological, ecological or evolutionary process (Vázquez *et al.*, 2017). Therefore the need to understand impacts on both stationary environments with constant mean conditions, along with more non-stationary environments, needs to be investigated (Lawson *et al.*, 2015).

During the last decades the spring arrival of many species of migratory passerine birds has shifted (Gordo, 2007). They are arriving earlier at their breeding grounds, and this change has been attributed to a change in climate and corresponding rises in temperatures in Europe and West Africa (Gordo, 2007; Both *et al.*, 2010; Remisiewicz and Underhill, 2020). Studies have also shown similar trends in other parts of the world, e.g. North America (Travers *et al.*, 2015) and Australia (Beaumont, McAllan and Hughes, 2006), indicating that this is a global development. Because long-distance migratory birds cannot accurately predict the phenology at their breeding grounds, and have evolved clock mechanisms to start their spring migration (Both and te Marvelde, 2007), they are potentially more vulnerable to climate changes. An increasing mismatch between the timing of food requirements and food availability is expected in these birds, especially in habitats with seasonal food peaks (Both *et al.*, 2010).This could have great ramifications in different species' ability to provide enough food for their fledglings at their breeding grounds. These phenological mismatches have been associated with lower nest success (Verhulst and Nilsson, 2007) and has become a cause for population declines in long-distance migrants in seasonal habitats (Both et al., 2010; Burger et al., 2012; Doiron, Gauthier and Lévesque, 2015; Lameris et al., 2018; Ross et al., 2018). Even though passerine birds are arriving earlier, signs are still pointing to some birds arriving too late at their breeding grounds to time the annual food peaks (Both and Visser, 2001). Especially forest birds have shown strong synchronization with these peaks (Charmantier et al., 2008). Both et al., (2009) showed that

over 20 years, passerine hatching dates advanced slower than caterpillar peak dates, caterpillars being one of the more popular food items for passerine birds. Interestingly enough though, great tits in Oxford, England have adjusted their breeding to be completely in synch with their most reliant food source (Charmantier et al., 2008). There is thus variation within the trophic dependencies between different predator species. However, this difference between long-distance migrants and residents or short distance-migrants might be due to the fact that the residents can respond to local cues, while long-distance migrants have to rely on circannual clocks or cues unrelated to their breeding grounds (Both and Visser, 2001; Both and te Marvelde, 2007; Hubálek, Hubálek and Čapek, 2008; Rubolini, Saino and Møller, 2010). Phenological mismatches might not be a problem, as long as food availability does not fall below a threshold (Veen et al., 2010). It has been expected that habitats differ in the penalties of being late due to differences in seasonality of food availability (Both et al., 2010). One option to minimize the mismatch between timing of breeding and seasonal pulses in food availability might be to select for morphological changes to increase migration speed (Zimova et al., 2021). This, or other changes, might be necessary as migratory bird species have seen stronger declines when not showing any form of phenological response to climate change (Møller, Rubolini and Lehikoinen, 2008). As climate change has not yet abated, nor is it likely to in the future, it remains to be determined whether populations will be able to meet the requirements from a changing climate (Both and te Marvelde, 2007).

As a long-distance migrant overwintering south of the Sahara Desert, the pied flycatcher (Ficedula hypoleuca), is one of the long-distance passerine species potentially affected by climate change. Arriving from Africa at their breeding grounds in Europe as cavity-nesting birds, they readily breed in nest boxes, producing 5-7 eggs (Lundberg and Alatalo, 1992).The species prefer to breed in deciduous forests from May into July, but they do breed in most forest habitats if there are available nest holes (Lundberg and Alatalo, 1992). This readiness for box-nesting has made them a popular study species among researchers trying to answer various ecological questions.

Mean temperature has been used to explain potential changes in flycatcher's phenology (Källander et al., 2017; Helm et al., 2019) related to both laying date and reproductive success. Precipitation has also been used, from looking at how mean precipitation affect adult or fledgling survival (Chernetsov et al., 2009), and how the sum of precipitation affects the health of nestling pied flycatchers (Skwarska et al., 2022). Less work have been directed at how populations are affected by increased climate variability (Vázquez et al., 2017), but a recent study has shown that the relationship between population dynamics in different organismal groups and climate variability depend largely on the season and the organismal group in question (Le Coeur, Storkey and Ramula, 2021). LeCoeur et al., (2021) identified a major challenge in ecology, namely to understand how populations are affected by increased climate variability. Even though long-term population growth rates are partially associated with short-term interannual climate variability, the responses might be population specific (Le Coeur, Storkey and Ramula, 2021), as some studies have found strong declines in areas with early food peaks (Sanz et al., 2003; Both et al., 2006; González-Braojos,) while areas without the same peaks have managed quite well (Eeva, Ryömä and Riihimäki, 2005; Both et al., 2006). In this thesis, the potential effect of climate variability on a population of pied flycatchers in Southern Norway is investigated.

With the aforementioned knowledge, the present study tests the following hypotheses:

1) The variation in flycatcher's laying dates is affected by the variability in climatic conditions
2) The breeding success of the flycatchers is influenced by the variability climatic conditions

2. Materials and method

2.1 Study site

The study area (Sinober in Sørkedalen; 59°59'N, 10°38'E) (Figure 1) is located near Oslo, in Southern Norway. It comprises mixed coniferous forest with mainly pine (Pinus sylvestris), spruce (Picea abies), birch (Betula pubescens) and the occasional rowan tree (Sorbus aucuparia) with some open patches. This is an area that covers around 72 ha (Cadahía et al., 2017). Wooden nest boxes have been available for flycatchers in the forest since 1985, when nest boxes started being placed on trees 1.5m above ground. The boxes had an inner depth of 13-16 cm from the base of the entrance hole to the bottom, with an entrance hole of about 32mm in diameter. Worn-out nest boxes were replaced when necessary. During the study period the number of nest boxes varied between 225-275 with the number of nests ranging between 22 and 109.
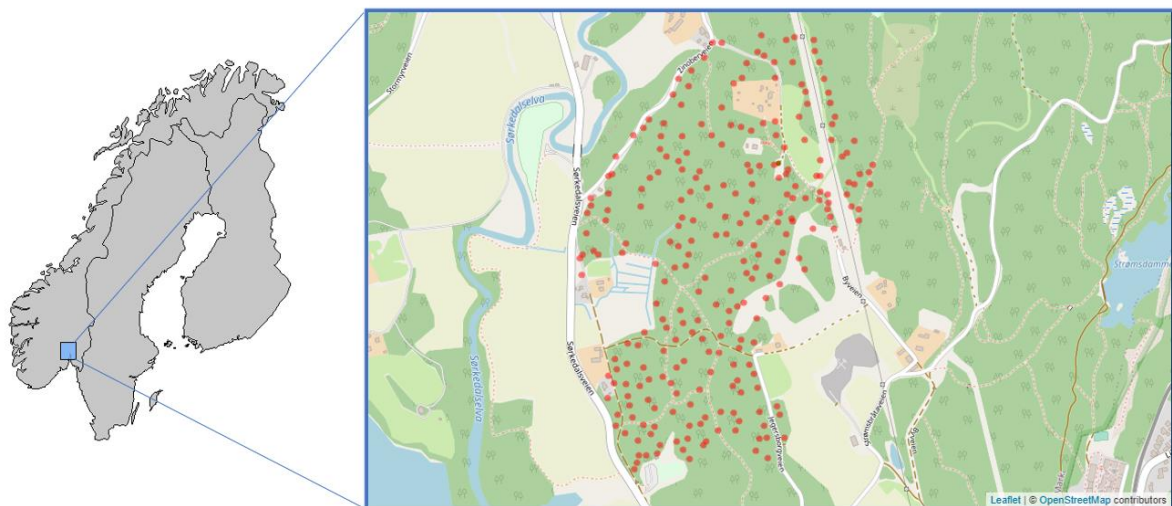

Figure 1: The location of the study site at Sinober in Sørkedalen, Oslo, Norway. The red dots represent the locations of the different nest boxes used during the years of data collection (1985-2017). The GPS coordinates were distributed on a map using the Leaflet package in R.

2.2 Breeding data

The study area was visited from late April to early July, with slightly varying frequency between years (Table 1), usually around a week before the first birds started to arrive. Other cavities with possible flycatcher nests were investigated in parallel, with very few nests being found other than in nest boxes (Lampe pers com.). The data used in this study are long term data collected from the period of 1985-2017. The arrival data for females were not available or of poor quality for five years (1989, 2001, 2002, 2004, 2005).

Table 1: An overview of the frequency of visits during the period of 1985-2017 of data collection at the study site at Sinober Sørkedalen.

Years (periods)	Frequency of visits
1985-2002	Daily visits
2003	Every 3-4 days
2004	Every 4-5 days
2005	Only sporadic visits -> No data available
2006-2010	Daily visits
2011-2013	Every other day
2014-2015	Daily visits
2016	Daily visits in early season, declining visits at the end of May
2017	Daily visits

For males, the arrival time was defined as the day a male was first observed in the area. Males occupy a territory soon after arrival, where they start singing to attract a mate (Lundberg and Alatalo, 1992). If the male had not been previously ringed, the male could be identified by judging what nest box he is sitting at, his dorsal plumage color and the size of his white forehead patch (Lundberg and Alatalo, 1992), before he was ringed. During this period of singing, males are readily attracted to nest boxes and were trapped using song playback to be ringed. The male mating status was defined depending on whether he mated with one (monogamous), two (bigamous) or three (trigamous) females.

Most nest-building is started by females shortly after they arrive; thus, the start of nest construction was used to define female arrival dates. Using building start as a proxy for arrival was deemed appropriate as (Dale et al., 1992) found that the time between the female arriving and the start of nest building lasted a median time of 9.8 hours, with a range of 0.9-30 hours, where only a quarter of the females used over 24 hours. In addition, a study showed that in the 179 field observations, only 1 of the observed arrival dates of females matched the actual arrival date measured with geolocators (Both et al., 2016). This demonstrates that just observing the females at the breeding grounds is not sufficient to accurately calculate their arrival.

The accurate determination of the laying dates was possible due to the fact that the flycatcher produces one egg a day. The nest boxes were visited frequently enough to be able to backtrack and calculate the laying date. The final number of eggs observed in the nest boxes was defined as the clutch size. The female mating status was defined depending on whether the female mated with a monogamous or polygynous male. A female mating with a monogamous male was labeled a primary female, and mating with a polygynous male

labeled either secondary or tertiary female. All dates were converted into Julian dates (1st of January = 1) and, after taking leap years into account, used in the subsequent analyses.

Males were trapped upon arrival and females while they were incubating. Each bird was given a metal ring with a unique number combination in addition to 2-3 colored rings. If previously unringed, the age (yearling or adult) was determined according to (Svensson, 1992). All nestlings were also carefully handled and ringed on day 13 with a numbered metal ring. The day of ringing was important so that the chicks were old enough to be ringed, but not old enough to fledge. The breeding success was defined as the number of chicks that left the nest box, and this number was corrected for if chicks were found dead between ringing and fledging.

2.3 Climate data

Climatic data was used to identify potential climatic signal periods where temperature and precipitation might have the greatest influence on the laying date and breeding success of the study species. This data was downloaded from the Norwegian Meteorological Institute (Meteorological Institute, 2022). The weather station closest to the study site Tryvannshøgda (SN18950) did not provide sufficient data for the study period, so the station Oslo-Blindern (SN18700) around 9km from the study site was chosen to provide the necessary data. The site at Blindern was still missing 8 days of data (0.1% of the data), so the station at Tryvannshøgda was used to complete the dataset. The station at Blindern is situated at a similar elevation to the study site (94 m.a.s.l) making it a comparable substitute. The time resolution was chosen as 'day'. The weather elements selected were 'precipitation' (mm/day) and the 'average daily temperature'. A period from 1st of December to late July for each year of the study period (1985-2017, excluding 2005) was downloaded.

2.4 Statistical analysis

All statistical analyses were conducted using the statistical programming environment R, version 4.1.2 (R Core Team, 2021). Linear mixed-effect models (LMM) with Gaussian error structures were used to study phenological and climatic effects on laying date and breeding success. Both models included a random intercept effect for individual identity to account for the fact that some birds were caught several years whereas others were caught only once, and this imbalance can provide issues of pseudo replication and non-independence of the data. A random intercept for year was also included to account for variation between years not captured by the climate variables. The R package climwin (van de Pol et al., 2016) was used to identify spring time windows ("climate windows") in which climate could affect laying dates and breeding success. The package performs a sliding window analysis, comparing two separate datasets: one for climate data, and one containing information on the response variable, as well as any covariates. A key feature of the package is the ability to define a baseline model into which climate data will be added. This allows for the analysis of data with a variety of error distributions, the inclusion of multiple covariates and the use of mixed-effects modelling (van de Pol et al. 2016). Climwin tests for different statistical parameters

(e.g. mean and standard deviation) simultaneously. The package does not however give any indication of how well the different covariates and the response variable relate, so it was only used as a tool for identifying windows of potential climate sensitivity. So an automated model selection had to be performed through the package MuMIn in the later part of the statistical analysis.

All climate windows with a duration of one week or longer were searched, from the 1st of April to the 30th of June. The 30th of June was set as the reference date for climwin to be able to create a data matrix with the relevant climatic and biological data. The best window was selected based on a difference in Akaike Information Criterion (AIC) values (ΔAIC) provided in climwin. The 90 day period from to 1st of April to the 30th of June was chosen to decrease the likelihood of getting a false positive result with no actual biological influence, as searching a vast amount of windows increases this likelihood (Helm et al., 2019). Climwin would then search 4000+ windows to find the preferred window (models = (range*(range+1))/2). To confirm the validity of the window, and account for potential overfitting, the randwin function was used to create 1000 randomized datasets along with the subsequent pvalue function. This was done to exclude the possibility of discovering a relationship between the climate data and the biological data by chance. If an appropriate window was not detected, the overall start and end dates would be calculated by taking an average across windows. This was done using the medwin function in climwin that uses the Akaike weights provided by climwin during the initial sliding window search. The choice of the type of time window – absolute or relative – was important when traits could be expressed at different times among individuals (Gienapp, Hemerik and Visser, 2005). Assuming the same absolute time windows for all individuals is unlikely to be appropriate if the timing of trait expression varies substantially among individuals and if the time-lag is short (van de Pol et al. 2016). Even though we know that the breeding season of the flycatcher is short (Lundberg and Alatalo, 1992), we did not expect the birds to express a substantial variation in trait expression, and the birds are therefore expected to be influenced by the same climate. This makes an absolutely window the favoured choice, and it also makes interpretation of results easier than a relative window would have (van de Pol, 2016). The aggregate statistics chosen were both the mean and the standard deviation to see which one provided the preferred window. They were chosen as they were going to be used as parameters in future model selection, and we could then compare the windows with differing statistics to see if there were any major differences in periods of climate sensitivity that needed to be taken into account. A linear function was used as a linear relationship between the climate and biological data was expected more than a quadratic or a logarithmic one.

The analysis in climwin provided four windows. Two for laying date and two for breeding success, one for each of the climatic variables on each response variable. The climate data relevant to these different time periods were downloaded from the seklima server of the Norwegian Meteorological Institute, and subsequently used to provide climate covariates in further analyses. This was done by calculating new metrics for variability in the data from the climate data downloaded. The standard deviation and coefficient of variation were used as metrics for variability in precipitation. The standard deviation provides a measure of variability as it is the square root of the variance in the data. The coefficient of variation was used to compare the relative amounts of variation across variables with different means, as it measures the ratio between the mean and the standard deviation (Le Coeur, Storkey and

Ramula, 2021). This means that the coefficient of variation for precipitation gives us a standardized way to compare variability between years which can have different means. For the temporal variability in temperature, only the standard deviation could be used as a metric for variability. Temperature is an interval scale where 0 is not informative. This means that because one can have both negative and positive temperature values, the mean can end up being zero. This would make it impossible to provide a coefficient of variation, since this is calculated by dividing the standard deviation by the mean.

LMM were run through an R package called 'lme4' (Bates et al., 2014). These models were used to explain the variance in the response variables. To provide the proportion of variance explained by the different models, R2 was used as implemented on the R package 'MuMIn' (Nakagawa and Schielzeth, 2013; Johnson, 2014; Bartoń, 2015). In LMM the R2 is divided into two parts, the marginal R2 where the variance is only explained by the fixed effects, and the conditional part in which the variance is explained by the full model (fixed and random effects). The automated model selection was now conducted using the dredge function in the MuMIn package. This provided an overview of which covariates to include or exclude from the final model, depending on the Bayesian Information Criterion (BIC) provided. The final covariates included were the ones included in models with ΔBIC of ≤ 4. The analysis was based on 842 breeding events.

For the laying date model a normal distribution of the response variable was assumed, making a LMM with a gaussian error distribution appropriate. The pre-dredge model for laying date was constructed using a linear mixed-effect model with laying date as the response variable, and female age, female mating status, female arrival, male arrival, mean temperature and precipitation, standard deviation for temperature and precipitation and coefficient of variation for precipitation as predictor variables. Year and female ID were set as the random effects. The response and predictor variables were identical to the baseline model used in the climwin sliding window analysis, excluding the climate variables.

For the breeding success model a poisson distribution would be a likely assumption with count data. But as we had no data on failed breeding attempts, no zeros were present in the dataset for either clutch size or number of fledglings produced. This made an assumption of either poisson or a negative binomial distribution impossible. A normal distribution was therefore also assumed for the breeding success.The pre-dredge model for breeding success was constructed using a linear mixed-effect model with number of fledglings as the response variable, and clutch size, female age and mating status, male mating status, laying date, mean temperature and precipitation, standard deviation of temperature and precipitation and the coefficient of variation for precipitation as predictor variables. Year and female ID were set as the random effects. The response and predictor variables were identical to the baseline model used in the climwin analysis, excluding the climate variables.

3. Results

3.1 Laying date analysis

3.1.1 *Climwin* exploration

There were 2 preferred windows for temperature, and 2 preferred windows for precipitation (Table 2). Both climatic parameters had one preferred window with the statistic 'mean' and one preferred window with the statistic 'standard deviation (SD)'.

For the laying date temperature window, the most preferred window was the one for mean temperature (ΔAICc = -17.5) and had an opening 67 days before the reference date (30th of June), and closing 27 days before the reference date. This corresponds to a window opening on the 24th of April and a closing on the 3rd of June. The second most preferred window was for SD, and looked quite different from the one for mean temperature. To account for this difference in the mean and SD windows and if those showed any big differences in potential climate sensitivity, we used the *medwin* function for both parameters, which provides a median start and close date for the windows within the 95% confidence interval. This revealed that the median of the temperature windows for SD was very similar to the preferred mean temperature window (mean: 71-27 days before reference date; SD: 67-25 days before reference date). This gave confidence in exploring the most preferred mean window originally discovered (67-27 days before reference date). When validating the preferred window and accounting for overfitting using the randomization and p-value option in climwin (n = 1000), the results showed a p-value of 0.001, indicating a clear window for climatic sensitivity.

The same analysis for the preferred mean precipitation window provided a p-value of 0.3, indicating that the observed climate signal might have been obtained due to chance. An appropriate window was not detected, so the overall start and end dates were calculated by taking an average across alternative windows using the medwin function. This provided a period for potential climate sensitivity opening 69 days before the reference day and closing 26 days before, equaling a window opening on the 22nd of April and closing on the 4th of June.

Table 2: Preferred windows for potential climate sensitivity on the response variable laying dates identified in climwin. The windows are absolute windows with either precipitation or temperature as the explanatory variable, and the values are either mean or standard deviations with a linear function. The ΔAICc values are the AICc of null model – AICc of climate model. The numbers for window open and window close are the number of days before the reference date of June 30th.

Response	Climate	Type	Stat	Func	ΔAICc	WindowOpen	WindowClose
Laying date	Precip	absolute	mean	lin	-5.9	90 (April 1st)	69 (April 22nd)
Laying date	Temp	absolute	mean	lin	-17.5	67 (April 24th)	27 (June 3rd)
Laying date	Precip	absolute	sd	lin	-7.3	90 (April 1st)	52 (May 9th)
Laying date	Temp	absolute	sd	lin	-5.7	90 (April 1st)	37 (May 24th)

The climwin exploration (Figure 2) shows that the most preferred window found for temperature is in an area around the windows with the strongest climatic sensitivity (top left graph). It also shows that we can be 95% confident that the best climate window falls within 25% of the total fitted windows. The middle top graph shows this distribution. The beta linear plot (top right) shows the spread of model coefficients across all fitted climate windows. It shows that windows around our best model show a negative relationship between temperature and our covariates (red), while others show little response (blue). The final plot shows the overall start and end days calculated by taking an average across windows. This corresponds well with our best window determined using ΔAICc (Table 2).
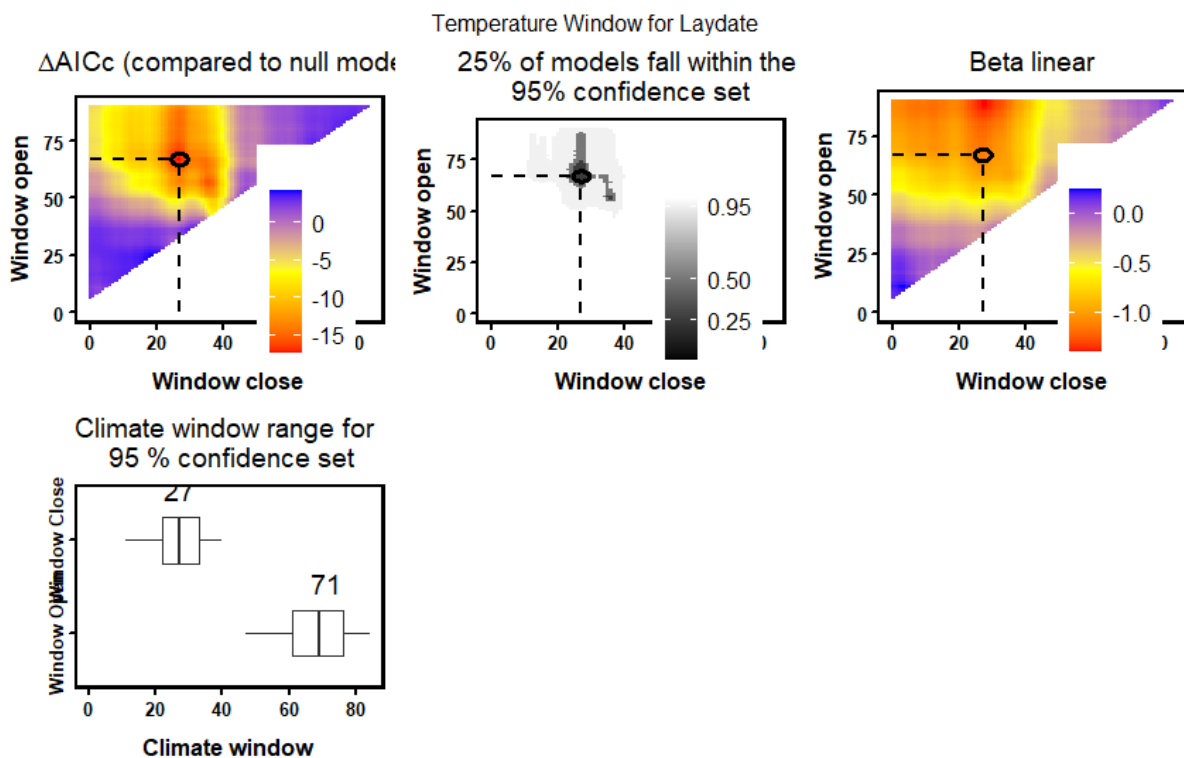

Figure 2: Output of the absolute sliding window analysis on the preferred temperature model in the climwin package in R. Analysis testing the relationship between mean temperature and laying date in the pied flycatcher (Ficedula hypoleuca) using a reference date of June 30th. (Top left) Heat map of ΔAICc (AICc of null model – AICc of climate model) for all fitted climate windows. The red area indicates the area of most climatic sensitivity, and blue the least. (Top middle) 95%, 50% and 25% confidence sets for all fitted climate windows. (Top right) Plot of model coefficients showing the spread of model coefficients across all fitted windows. Estimating the relationship between climate and the biological response laying dates. (Bottom left) Boxplots of the start and end point of all climate windows that make up the 95% confidence set. In all plots, the best fitted climate window (lowest value of AICc) is circled. Plots generated using the plotall function.

3.1.2 Model exploration

The dredge function from the MuMIn package provided one single model inside the threshold of ΔBIC ≤ 2 (Table 3) (n.models run = 1024). This model included three different covariates included in the final model. These were the arrival date of the female (AF), the arrival date of the male (AM) and the mean temperature for the window provided by climwin (TM). Two models had a coefficient inside a ΔBIC = four, and we considered them to be high enough to be included in the final model (based on the «rule of thumb» by Kass and Raftery,

1995). The additional covariates were the coefficient of variation for precipitation for the window provided by climwin (PCV) and the different years of the study(Y). The random effect for female ID was removed as it caused singularity issues and showed no impact on the model.

	Component models					BIC	ΔBIC	Weight
1	A_F	$+A_M$	$+T_M$			4242.8	0	0.51
2	A_F	$+A_M$	$+T_M$	$+P_{CV}$		4246.4	3.55	0.09
3	A_F	$+A_M$	$+T_M$	$+Y$		4246.6	3.82	0.08
4	A_F	$+A_M$	$+T_M$	$+P_{CV}$	$+Y$	4247.5	4.66	0.05
5	Ag_F	$+A_F$	$+A_M$	$+T_M$		4247.7	4.91	0.04
6	A_F	$+A_M$	$+T_M$	$+T_{SD}$		4248.1	5.27	0.04
7	P_{CV}	$+A_F$	$+A_M$	$+T_M$	$+P_{SD}$	4248.5	5.68	0.03
8	A_F	$+A_M$	$+P_M$	$+T_M$	$+P_{SD}$	4249.0	6.14	0.02
9	A_F	$+T_M$	$+T_M$	$+P_{SD}$		4249.0	6.19	0.02
10	A_F	$+A_M$	$+T_M$	$+P_M$		4249.5	6.67	0.02
11	P_{CV}	$+A_F$	$+A_M$	$+P_M$	$+T_M$	4249.9	7.06	0.01
12	A_F	$+T_M$				4251.0	8.16	0.01

Models are linear mixed-effects models with individual identity and year as random effect A_F arrival female, A_M arrival male, Ag_F age female, T_M temperature mean, Y year, T_{SD} temperature standard deviation, P_M precipitation mean, P_{SD} precipitation standard deviation, P_{CV} precipitation coefficient of variation

The final model provided estimates of the different parameters female arrival, male arrival, coefficient of variation for precipitation and the mean temperature on the laying date (Table 4). The estimates show a strong, positive relationship between female arrival and the laying date (Figure 3a), indicating that earlier female arrival facilitates earlier laying dates. The estimates also show a positive relationship between male arrival and laying dates (Figure 3b), indicating an effect of males arriving earlier facilitating earlier laying dates. Next, the estimates show a negative relationship between the coefficient of variation of precipitation on laying date (Figure 3c), indicating that higher variation in precipitation leads to birds laying their eggs earlier. Second to last, the estimates show a negative relationship between mean temperature and laying dates (Figure 3d), showing that warmer mean temperatures in the relevant period lead to earlier laying dates. Finally, a negative relationship between year and laying date (Figure 3e) was found, showing that the birds are generally breeding earlier at roughly half a day per decade. The R^2 of the final model on laying date showed a fixed R^2 of 0.74 and a conditional R^2 of 0.77. This indicates that 77% of the variance in the data is explained by the model. The random effects contribute with the additional 3% of the explained variation.

Table 4: Model estimates from the full linear mixed-effects model on laying date in the Pied Flycatcher. The model shows the estimates of the different parameters female arrival, male arrival, mean temperature, coefficient of variation for precipitation and year on the response laying date.

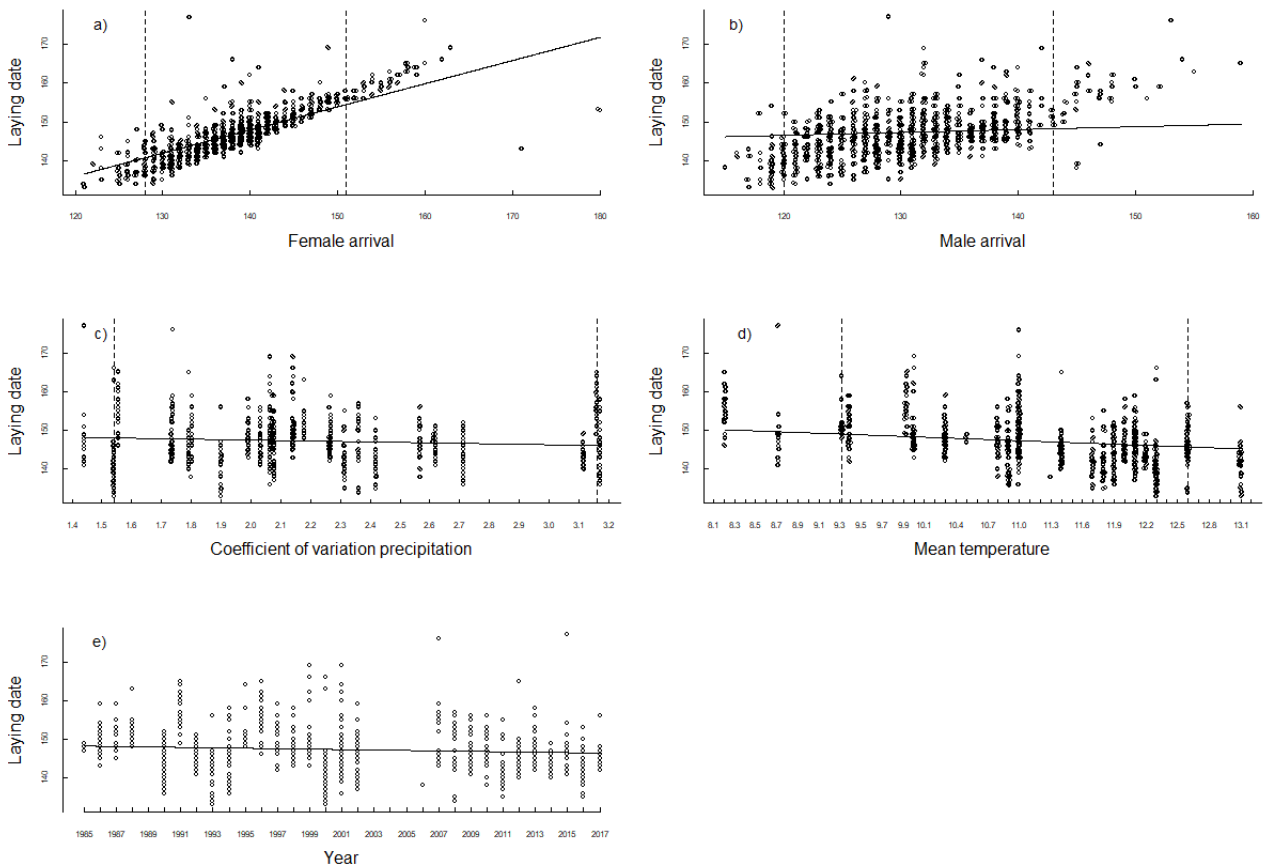| Parameters	Estimates	Std. error	t-value
Female arrival	0.60	0.02	32.0
Male arrival	0.07	0.02	4.0
Mean temperature	-1.01	0.19	-5.2
Coefficient of variation precipitation	-1.21	0.51	-2.4
Year	-0.06	0.02	-2.3

Figure 3: The effect of the different predictive variables on the response variable laying date. a) Female arrival b) Male arrival c) Coefficient of variation of precipitation d) Mean temperature e) Year. The individual effects of each predictor variable are shown while all other variables are set at their average values. The points are jittered for increased visibility.

3.2 Breeding success analysis

3.2.1 *Climwin* exploration

There were 2 preferred windows for temperature, and 2 preferred windows for precipitation (Table 5). Both climatic parameters had one preferred window with the statistic 'mean' and one preferred window with the statistic 'standard deviation (SD)'.

For temperature, the most preferred window was the one for mean temperature (ΔAICc = -10.8) which had an opening 75 days before the reference date (30th of June), and closing 35 days before the reference date. This corresponds to a window opening on the 16th of April and a closing on May 26th. The second most preferred window was for SD, and looked quite different from the one for mean temperature. To account for this difference in the mean and SD windows and if those showed any big differences in potential climate sensitivity, we used the *medwin* function for both parameters, which provides a median start and close date for the windows within the 95% confidence interval. This revealed that the median of the temperature windows for SD was similar to the preferred mean temperature window (mean: 77-31 days before reference date; SD: 68-23 days before reference date). This gave confidence in exploring the most preferred window (75-35 days before reference date). When validating the preferred window and accounting for overfitting using the randomization and p-value option in climwin (n = 1000), the results showed a p-value of 0.001, indicating a clear window for climatic sensitivity.

The same analysis for the precipitation windows provided a p-value of 0.74, indicating that the observed climate signal was might have been obtained due to chance. An appropriate window was not detected, so the overall start and end dates were calculated by taking an average across windows using the medwin function. This provided a period for potential climate sensitivity for precipitation opening 68 days before the reference day and closing 25 days before, equaling a window opening on the 23rd of April and closing on the 5th of June.

Table 5: Preferred windows for potential climate sensitivity on breeding success (number of fledglings = n_fledglings) identified in climwin. The windows are absolute windows with either precipitation or temperature as the explanatory variable, and the values are either mean or standard deviations with a linear function. The ΔAICc values are the AICc of the null model – AICc of climate the model. The numbers for window open and window close are the number of days before the reference date of June 30th.

Response	Climate	Type	Stat	Func	ΔAICc	WindowOpen	WindowClose
n.fledglings	Precip	absolute	mean	lin	-0.06	59 (May 2nd)	53 (May 8th)
n.fledglings	Temp	absolute	mean	lin	-10.8	75 (April 16th)	35 (May 26th)
n.fledglings	Precip	absolute	sd	lin	-2.2	10 (June 20th)	3 (June 27th)
n.fledglings	Temp	absolute	sd	lin	-0.3	86 (April 13th)	61 (April 30th)

The climwin exploration (Figure 4) shows that the most preferred window found for temperature is in an area around the windows with the strongest climatic sensitivity (top left graph). It also shows that we can be 95% confident that the best climate window falls within 35% of the total fitted windows. So it does not provide as strong confidence as in the laying

date window. The beta linear plot (top right) shows the spread of model coefficients across all fitted climate windows. It shows that windows around our best model show a negative relationship between temperature and our covariates (red), while others show little response (blue). The final plot shows the overall start and end days calculated by taking an average across windows. This corresponds well with our best window determined using ΔAICc (Table 5).
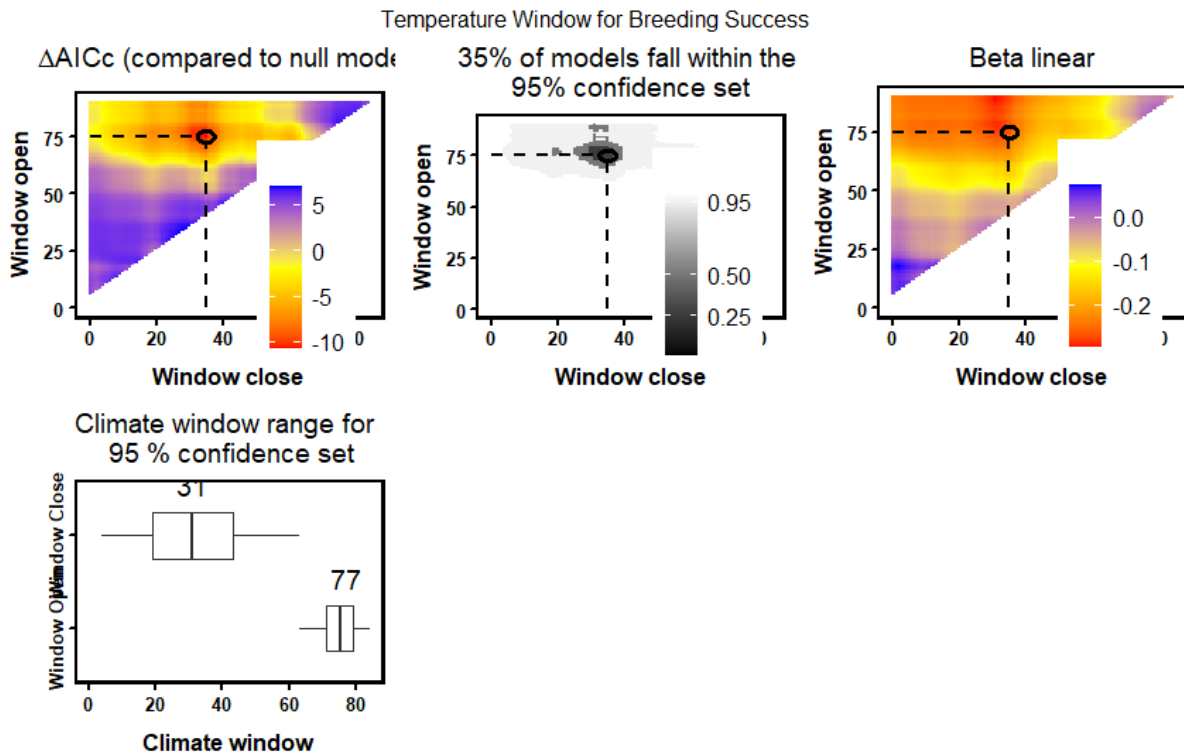

Figure 4: Output of the absolute sliding window analysis on the preferred temperature model in the climwin package in R. Analysis testing the relationship between mean temperature and breeding success in the pied flycatcher (Ficedula hypoleuca) using a reference day of June 30th. (Top left) Heat map of ΔAICc (AICc of null model – AICc of climate model) for all fitted climate windows. The red area indicates the area of the most climatic sensitivity, and blue the least. (Top middle) 95%, 50% and 25% confidence sets for alle fitted climate windows. (Top right) Plot of model coefficients showing the spread of model coefficients across all fitted windows, estimating the relationship between climate and the biological response breeding success. (Bottom left) Boxplots of the start and end point of all climate windows that make up the 95% confidence set. In all plots, the best fitted climate window (lowest value of AICc) is circled. Plots generated using the plotall function.

3.2.2 Model exploration:

The dredge function from the *MuMIn* package provided one model inside the threshold of a ΔBIC ≤ 2 (Table 6). This model included four different covariates included in the final model. These were the clutch size (C), mating status of the female (M_F), the laying date (L) and the mean temperature for the window provided in *climwin* (T_M). One more model had a ΔBIC ≤ 4, but did not include any additional covariates.

Table 6: Top models (∆BIC ≤ 2) from the model exploration on breeding success and its initial covariates. This was calculated using the dredge function in the MuMIn package. It shows the different models produced with different covariates and their inclusion or exclusion from the models. The covariates from the models of a ∆BIC ≤ than 4 were included in the final model.

	Component models					BIC	∆BIC	Weight
1	C	$+M_F$	$+L$	$+T_M$		2948.4	0.00	0.58
2	C	$+M_F$	$+T_M$			2950.7	2.30	0.18
3	C	$+M_F$				2953.4	4.97	0.05
4	C	$+M_F$	$+L$	$+T_M$	$+T_{SD}$	2954.9	6.41	0.02
5	C	$+P_{CV}$	$+M_F$	$+L$	$+T_M$	2954.9	6.44	0.02
6	C	$+M_F$	$+T_M$	$+L$	$+P_M$	2954.9	6.47	0.02
7	C	$+Ag_F$	$+M_F$	$+L$	$+T_M$	2955.2	6.71	0.02
8	C	$+M_F$	$+L$	$+T_M$	$+P_{SD}$	2955.2	6.72	0.02
9	C	$+M_F$	$+L$			2956.3	7.83	0.01
10	C	$+P_{CV}$	$+M_F$	$+T_M$		2956.9	8.40	0.01
11	C	$+M_F$	$+P_M$	$+T_M$		2957.1	8.63	0.01
12	C	$+Ag_F$	$+M_F$	$+T_M$		2957.3	8.81	0.01

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

C clutch size, M_F matingstatus female, L laying date, T_M temperature mean, P_{SD} precipitation standard deviation, P_M precipitation mean, P_{CV} precipitation coefficient of variation

The final model built using the dredge function in *MuMIn* provided estimates of the different parameters clutch size, female mating status, laying date and the mean temperature on the breeding success (Table 7). The estimates show a strong, positive relationship between clutch size and the breeding success (Figure 5a), indicating that a bigger clutch size naturally increases the chance of having more nestlings leaving the nest box. Next, a strong and negative relationship between mean temperature and breeding success was found (Figure 5b), indicating that increasing mean temperature decreases the chance of more nestlings leaving the nest box. Additionally, a negative relationship between laying dates and breeding success was found (Figure 5c), indicating that laying earlier increases the probability of having more nestlings leaving the nest box. The estimates also show a strong and negative relationship between female mating status and breeding success (Figure 6), indicating that mating first with male leads a higher probability of successfully having more nestlings leaving the nest box. The R^2 of the final model on breeding success from the exploratory analysis in *MuMIn* showed a fixed R^2 of 0.20 and a conditional R^2 of 0.28. This indicates that 28% of the variance in the data is explained by the model. The random effects contribute with the additional 8% of the explained variation.

Table 7: Model estimates from the final mixed-effect model on breeding success in the Pied Flycatcher. The model shows the estimates of the different parameters clutch size, female mating status, laying date and mean temperature on the breeding success.

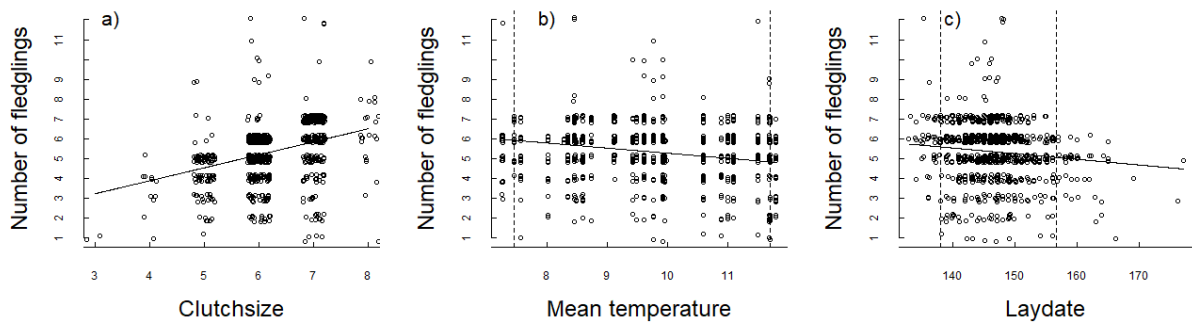| Parametric coefficients	Estimates	Std. error	t-value
Clutch size	0.67	0.07	9.9
Female mating status	-0.64	0.16	-4.0
Laying date	-0.03	0.01	-3.0
Mean temperature	-0.25	0.06	-4.2

Figure 5: Effect of the different predictive variables on the response variable breeding success (number of fledglings raised). a) Clutch size b) Mean temperature c) Laying date. The individual effect of each respective variable is shown while all other variables are set at their average values. The points are jittered for increased visibility.
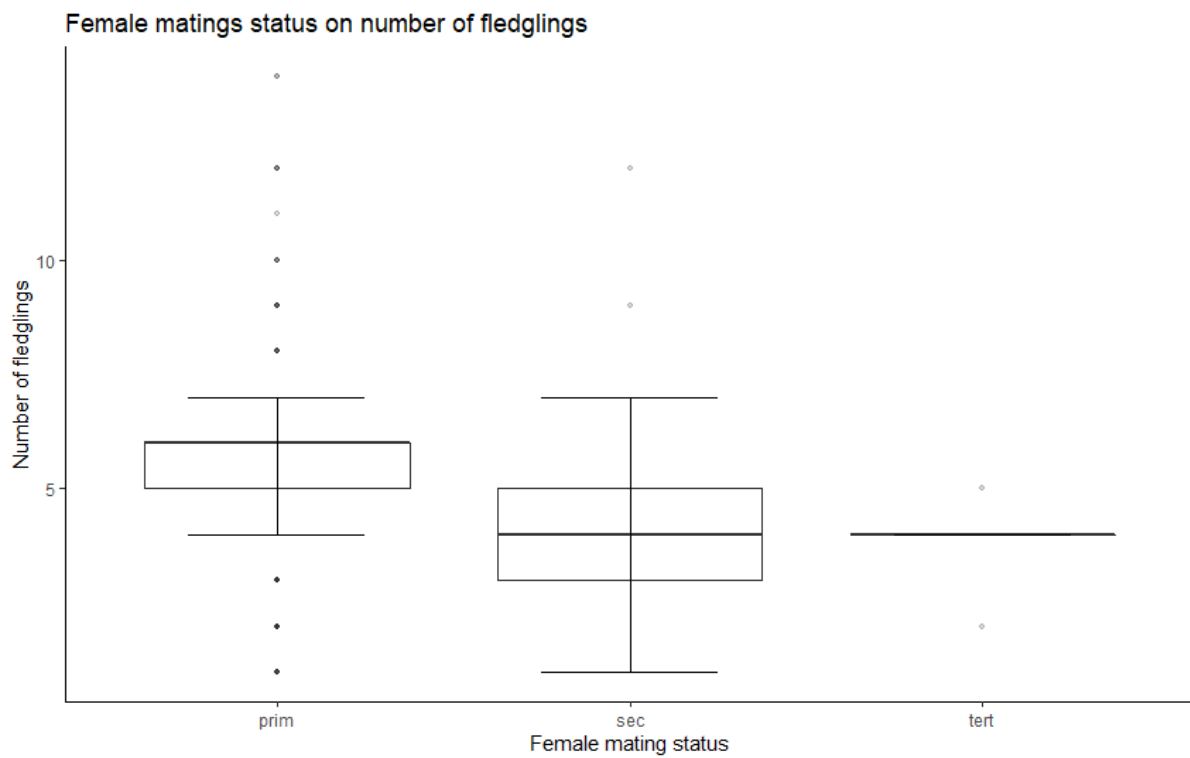

Figure 6: Boxplot with the distribution of the different female mating statuses and the number of fledglings produced for each status. «prim» represents the primary females that mated first with a male. The «sec» represents the secondary females which mated with an already mated male. And «tert» represents females that mated with males that already had mated with 2 females.

4. Discussion

The main goal of this thesis was to study whether variability in climate could affect the laying dates and breeding success of the pied flycatcher. Variability in precipitation had an effect on the laying dates in the flycatcher population. However, it was not found that variability in either temperature or precipitation affected the breeding success.

Laying date

Our results showed that earlier arrival in females leads to earlier laying dates. This is in line with research showing that laying date is indeed constrained by arrival of females (Both, Bijlsma and Visser, 2005). This is obvious as earlier arriving males are not capable of breeding before the females arrive. Earlier arrival in both males and females enhances an individual's chance to both acquire a high-quality territory and mate (Lundberg and Alatalo, 1992; Kokko, 1999), making the transition from migration to breeding more rapid. There has been differences in observed arrival in relation to breeding though, as some authors have found no earlier arrival but earlier breeding (Both & Visser, 2001; Coppack & Both, 2002), while others have found earlier arrivals with no earlier breeding (Valtonen *et al.*, 2017). This could indicate that pied flycatchers are changing the stages of their annual cycles at different rates (Coppack and Both, 2002). As female arrival is most important for laying date, male arrival naturally contributes less. Later arriving males have a harder time attracting a mate, as later arriving females often prefer to mate with high quality males, at times at the cost of becoming the secondary female (Slagsvold and Lifjeld, 1994; Tomotani *et al.*, 2021).

Variability in precipitation affected laying dates and indicates that periods with more variation in precipitation are related to earlier breeding in the flycatcher population. This result could be another case for birds using rain as a cue for breeding (Hau *et al.*, 2004; Saunders *et al.*, 2013), although a positive association between variability in precipitation and long term population growth rates has only been found for non-breeding season (fall – winter) (LeCour et al., 2021). Studies on the lesser kestrel have shown that the mean number of chicks per successful nest is positively influenced by precipitation during the winter, arrival, courtship, and incubation periods (Rodríguez and Bustamante, 2003). Flying insects are inactive during cold, wet or windy conditions (Cox *et al.*, 2019) which is in theory negative for the flycatcher. At the same time, an increase in spring precipitation might be necessary for the production of different insect species relevant to the pied flycatcher and create an abundance of food for the flycatcher females to prepare for egg-laying. Late arriving females are known to start their egg-laying 5 days after pair formation, while early females might wait several weeks (Lundberg & Alatalo, 1992). This indicates that they might be waiting for a more suitable period for breeding. It might be that some variation in precipitation increases the likelihood of high food availability compared to longer and more stable periods of rain or drought. The implications of this certainly depend on the expected future changes in precipitation variability. This has been difficult to predict due to the role of the natural variability of the climate system, also called internal climate variability (Deser *et al.*, 2012; Poschlod and Ludwig, 2021). However, it is known that the contribution of convective precipitation (water evaporation due to the sun's energy) to extreme precipitation has been projected to increase in Scandinavia due to temperature rises with few limitations related to moisture availability (Poschlod & Ludwig, 2021), and that precipitation variability has only been expected to

increase in a warming climate (Pendergrass *et al.,* 2017). This increase in variability inherently leads to the occurrence of extreme weather or climate events (van der Wiel and Bintanja, 2021), which in turn could decrease the predictability of climate conditions, and have negative consequences for the flycatchers.

Variability in temperature did not affect the laying date in our study. In contrast, Laaksonen et al. (2006) found that variability in temperatures at the breeding grounds increased among-year variation in both mean and skewness of laying dates. Later studies have found no increase in global temperature variability (Huntingford *et al.*, 2013), and this might contribute to explain our results. Other studies have even predicted a reduction in temperature variance in mid-to-high latitudes in the Northern hemisphere due to the greater warming of the Arctic (Screen, 2014). This might change future responses to climate change.

Our results showed higher mean temperatures resulting in earlier laying dates, which has been found in previous studies (Laaksonen *et al.*, 2006; Both and te Marvelde, 2007; Källander *et al.*, 2017). It is not surprising that the flycatchers might be more affected by climatic conditions in the early stages of breeding, as several studies have shown spring temperature to directly impact laying dates (Slagsvold, 1976; Both *et al.*, 2004; Dunn, 2004; Visser, Holleman and Caro, 2009; Verhagen *et al.*, 2020). Indications that seasonal increase in temperature, not mean temperature or daily temperature, is a cue for avian timing of reproduction have been found in great tits (Schaper *et al.*, 2012). There also seems to be an indication of geographical differences in response to temperatures, with more advancing breeding in northern latitudes (64.1°N– 68.4°N) (Vega, Fransson and Kullberg, 2021). This is in contrast to the findings from Both et al. (2004) which found that northerly populations delayed their laying date between 1980 and 2004. This could however indicate that the flycatchers are more responsive to weather cues at higher latitudes. Both and te Marvelde (2007) did however also find that there has been an increase in migration temperatures (better circumstances on their way to their breeding grounds) for northern populations (Both and te Marvelde, 2007). This could lead to them arriving at their breeding sites in better shape, perhaps closer physiologically to start breeding. This is supported by the fact that the arrival-laying interval has been found to be shorter in the north (Nicolau *et al.*, 2021). The difference in results might come from the fact that we have an additional 10+ years of data, and that the processes might have changed since the early 2000s.

The results also showed a negative yearly trend indicating that the flycatchers are laying their eggs slightly earlier each year. This has been a trend for years (Both *et al.*, 2004; Both, Bijlsma and Visser, 2005; Both and te Marvelde, 2007), although studies have also indicated that during the last decade (2005-2015) the selection on laying date has weakened considerably (Visser *et al.*, 2015). This is thought to be because of a cooling of arrival temperatures weakening the strength of the directional selection on laying dates. Thus, it will be interesting to observe the future patterns in laying date phenology and selection, which will be dependent upon the strength, direction and variability of climate change.

Breeding success

Our results showed the higher the clutch size, the higher the number of nestlings leaving the nest as fledglings. This comes as no surprise as experimental studies have shown that flycatcher females evaluate future conditions for incubating eggs and feeding nestlings based on food availability at laying (Sanz and Moreno, 1995). In addition, laying date is a strong determinant for clutch size (Laaksonen *et al.*, 2006). This corresponds with the knowledge that earlier arrival gives an increased chance for acquiring quality territory and males. A territory of high quality induces the female flycatcher to produce larger clutches, and thus more fledglings. That female flycatchers could evaluate potential success can be further supported by later breeding woodpecker females laying smaller clutches, but with no consequence to reproductive success (percentage wise) (Wiebe and Gerstmar, 2010). The consequences to this reproductive success should there be big changes in climate variation from the time of laying date to the climate after hatching could be substantial. Strong, consistent precipitation or a sudden drop in temperature could lead to a crash in food availability and to subsequent drops in breeding success. At worst, it could lead to very few nestlings reaching fledgling state that year. Studies have shown that females incubating larger clutches lost significantly more mass relative to those incubating reduced clutches (Moreno and Carlson, 1989), indicating that the females with larger clutches could be more vulnerable to failed breeding attempts.

Female mating status was found to be an important factor in establishing how many nestlings were likely to reach fledgling state. This makes sense as the male flycatcher also contributes into feeding the young (Lundberg & Alatalo, 1992), and if the male has more clutches to fend for it is fair to assume some consequences for these clutches. If a male would have a secondary female, he would have to fend for two clutches, with a possible overlap (Lundberg & Alatalo, 1992). He would then perhaps not be able to provide the same amount of food for the second brood, as bigamous males are known to give more support to their primary broods than to their secondary broods (Huk and Winkel, 2006). But laying date is nevertheless very much a female trait, and secondary females should by default lay later than primary females (Nilsson *et al.*, 2019). This might not be observed in our results because primary females are mixed with monogamous females into the category 'primary' so that late arriving monogamous females might «dilute» the expected difference. This is a shortcoming of the study, although other studies have found no difference in phenology between primary females of monogomous or bigamous male (Nilsson *et al.*, 2019). Furthermore, Huk & Winkel (2006) found that the number of fledglings was lower in females that mated with bigamous males, but where the secondary brood were more affected than primary broods. So, if a male is already mated, it will most often negatively affect female reproductive success. This might, though, be compensated for if the already mated male is of high quality (Slagsvold and Drevon, 1999).

The breeding success was negatively affected by mean temperature, meaning that higher mean temperature during the period from 16th of April to the 26th of May resulted in a lower reproductive output. This is in line with findings where mean temperature in May was negatively correlated with breeding success for a flycatcher population in Spain (Sanz *et al.*, 2003). The results from Spain were attributed to increasing spring temperatures leading to the growth up caterpillars speeding up, which made the window of food availability even shorter. This result was a little surprising as the breeding success for our population has

been stable, with a slight positive trend for each year. In addition, the forest in Norway consists of a mixed coniferous forest in contrast to the oak forest in Spain. The populations in coniferous forests are mentioned as less reliant on caterpillar peaks than their oak forest counterparts (Burger *et al.*, 2012). This could also be connected to the fact that temperature has direct effects on the thermoregulation in birds and their ability to maintain viable eggs (Stevenson and Bryant, 2000). Should either of these be the case, with temperature expected to only increase going forward, we could be seeing potential drops in the reproductive output of the pied flycatchers in Oslo. There has been indications that flycatchers could be more responsive to weather cues at higher latitudes combined with generally lower competition, and that the more southern populations are unable to match breeding time to earlier and warmer springs (Vega, Fransson and Kullberg, 2021). How long until that is also the case for the more northern populations remains to be seen given future climate warming and variability. This also highlights the importance of investigating populations of flycatchers at more than one geographical location, at different latitudes and longitudes.

Laying date was found to have a negative effect on breeding success. Earlier laying dates increased the chances of having more nestlings leaving the nest box, thus increasing the reproductive output. This corresponds well to others studies finding increased reproductive success with earlier laying dates (Verhulst and Nilsson, 2007; Vega, Fransson and Kullberg, 2021). The same indications have also been found in Great tits, with lower breeding success in later breeding individuals (Verhulst and Tinbergen, 1991). This corresponds well with the knowledge that earlier arriving individuals are more likely to acquire high quality males and territories (Lundberg & Alatalo, 1992), which would give those individuals a solid platform for increased breeding success. Even though we did not find anything indicating an effect from variability in climate on the breeding success directly, we do have results indicating laying dates having an effect on breeding success, thus an indirect effect of climate variability. Also, variability in precipitation along with mean temperatures influence the laying dates. This in turn could mean that even though variability in climate is not found to affect the breeding success directly, there is an indirect effect on the breeding success through laying date. This would make sense when flycatchers laying their eggs expecting a positive peak in food availability, only to experience cold weather with long periods of steady rain, decreasing insect activity and thus food availability. This could again lead to loss of body mass in the adult flycatchers, and decreased reproductive output.

The model for breeding success did not explain as much of the variation in the data as the one for laying date. This could be due to the fact that breeding success must be explained by additional factors to climatic and phenological ones. Factors like male and female quality, quality of territory as shown with the white throated dipper (Nilsson *et al.*, 2020), breeding densities with inter-and intra-specific competition, food availability and quality. With this said, it could also be an indication of why we did not find any influence of climate variability on the breeding success directly. As mentioned earlier, climate has already been shown to be an important factor for when the flycatchers start to lay their eggs. But, when they have arrived and reached their threshold to initiate breeding, the climate at the breeding site to this point might not have enough of an effect on the reproductive success. This is hard to quantify, although data on male quality is available for this study from 1990 and forward, which could be used in further studies to evaluate whether it is possible to detect potential significant

effects of male quality on breeding success, or look at interactions between male quality and arrival, and how that could potentially have an effect on phenology.

A note on the methods

The package *climwin* was used in this study because it provides a structured process to identify periods of potential climate influence on biological data. The main advantage the method offers is the possibility to increase the number of time windows to be tested, without arbitrarily selecting climate windows with little *a priori* knowledge on the relationship between climate and the biological response (van de Pol *et al.*, 2016). To test the same number of windows manually would be very time consuming. Even if a relationship was found this way, it would be hard to conclude whether this is the period with the most biologically meaningful impact. On the other hand, the drawback to the predominantly exploratory approach of *climwin* is the risk of overfitting and the bias that can occur at low sample and effect sizes, though these might be addressed with the right tools (van de Pol *et al.*, 2016).Searching for windows over a long-time span can easily lead to more false positive results (Helm et al., 2019), which means finding periods of climatic sensitivity that may not be ecologically relevant. In this study, finding windows of potential climate sensitivity to precipitation proved more challenging than finding those for temperature. The most likely reason for this is the fact that temperature tends to vary more gradually, whereas precipitation may be more stochastic. We found an effect of variability in precipitation in our study, even though this window was not supported by climwin. This shows that even though *climwin* is a useful tool, it has challenges with parameters such as precipitation. The package *climwin* offers standard deviation as a measure of variability, but it would be interesting to see how the implementation of other parameters could influence the ability to find periods of climatic sensitivity directly, such as the coefficient of variation for precipitation. Using a combination of the exploratory approach with *climwin* while resorting to common biological sense might be sensible. This seems to be a common approach by other ecologists using *climwin* as a tool for discovering periods of climate sensitivity (James *et al.*, 2019; Samplonius and Both, 2019; Camarero and Rubio-Cuadrado, 2020; Dominoni *et al.*, 2020).

In this study we found that a Norwegian population of flycatchers is affected by variability in precipitation both directly and indirectly, but not by variability in temperature. To better understand the implications of these results, future studies should continue to address changes in climate variability and how they are affecting population dynamics in passerine birds. This is especially true regarding the predicted increase in precipitation variability, as we need the complete picture in order to understand the consequences of changes in climate variability. Such increases in the understanding and knowledge could help avoid potential population declines.

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