Phenological responses of breeding birds to weather variation
- how does the flexibility of blue tits and great tits vary across Europe?

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Abstract

Many temperate living forest birds raise their chicks almost exclusively on a caterpillar diet, and synchrony of the breeding cycle with caterpillar prey abundance is under strong selection. Asynchrony results in increased foraging effort by parents to sustain their offspring, resulting in lower parental condition in addition to lower weight and lower survival of chicks. Most research on the timing of reproduction in insectivorous passerines has focused on the date of clutch initiation (i.e., the first day of egg-laying), as the main determinant of synchrony with peak food abundance. A less investigated aspect of avian phenological plasticity is the ability of the birds to readjust the timing of their reproduction after egg laying has started. These behavioural adjustments may help birds cope with weather fluctuations not easily predicted based on cues available ahead of the breeding season.

For this master thesis, I investigate the links between short-term variability in spring weather and flexibility in incubation behaviour in insectivorous forest birds. I assembled a meteorological dataset and used breeding data from eight European populations of sympatric blue tits, Cyanistes caeruleus, and great tits, Parus major. I hypothesise that flexibility in incubation behaviour is a response to weather fluctuations occurring after the onset of reproduction, and that this response has an effect on reproductive success. To test this I defined a variable, hereafter hatch gap, representing how early or late female birds start incubating their eggs relative to the end of egg laying. This variable therefore represents behavioural flexibility of females in the onset of incubation.

We find that hatch gap decreases with increasing temperatures occurring during the egg-laying phase, indicating that females advanced incubation in warmer weather. This association is found for both species and at all sites. Moreover, reproductive success was higher for earlier start of incubation.

We conclude how the observed flexible responses may result from energetic constraints leading to postponed incubation at low temperatures, but also adaptive advancement of incubation when weather is warm during egg laying that might help the birds track caterpillar abundance and therefore improve their reproductive success.

Introduction

In temperate environments seasonal fluctuations in food resources influence the phenology of species to an extent that varies among trophic levels. Because they are at a lower trophic level, primary consumers (herbivores), respond more rapidly to seasonal changes in the abiotic environment than the secondary consumers preying them (M. E. Visser, van Noordwijk, Tinbergen, & Lessells, 1998). In forest ecosystems, arboreal caterpillars rely on new tree foliage, which development hinge directly on local weather conditions, as the main food source in spring (Visser et al., 1998). For many insectivorous forest birds there is strong selection for phenological synchrony with caterpillar prey abundance, due to the fact that many passerine chicks are raised on an almost exclusive caterpillar diet (Verhulst & Tinbergen, 1991). Nestling provisioning is the most resource-demanding activity in the breeding cycle (Tomás, 2015). Failing to match the energetic demands of offspring with peak prey abundance increases the amount of foraging effort by parents needed to sustain their offspring, resulting in lower overall parental condition (Thomas, Blondel, Perret, Lambrechts, & Speakman, 2001), lower fledgling weight, and lower fledgling survival rate (Visser et al., 2006).

Insectivorous bird species have been shown to time their reproduction partly based on abiotic cues occurring prior to the breeding season. While late-winter changes in photoperiod facilitate physiological changes that initiate the breeding cycle (Dawson, King, Bentley, & Ball, 2016), temperature in early spring correlates with the start of egg-laying, and is considered to be used by the birds to anticipate when caterpillar availability will be at its highest (Schaper et al., 2012). Most research on optimal time of reproduction in insectivorous passerines has conventionally focused on the timing of clutch initiation, which is the first day of egg-laying, as the main determinant of synchrony between maximal food demand in nestlings and peak food abundance (Tomás, 2015), in addition to the underlying physiological mechanisms for this synchrony, as well as the adaptive value of phenotypic plasticity under changing environmental conditions (Charmantier et al., 2008; M. E. Visser et al., 1998).

A gradual increase in spring temperature across the European continent has led to a corresponding advancement in time of caterpillar peak abundance (Walther et al., 2002), which consequently advance the optimal time of clutch initiation. Whether the insectivorous passerines are able to sufficiently track the rapid phenological changes of their food resource, differs significantly among species and populations (Husby et al., 2010). All populations investigated display considerable individual variation in plasticity for clutch initiation, but only in some are the birds seemingly able to establish synchrony (Both & Visser, 2005; Husby et al., 2010).

A less investigated yet potentially equally important aspect of avian phenological plasticity is the ability of the birds to readjust the timing of their reproduction after clutch initiation. Once egg laying has begun the birds typically lay one egg each day, and will normally not begin full incubation of the eggs before the clutch has been completed (Simmonds, Sheldon, Coulson, & Cole, 2017). Under ideal conditions, full incubation is initiated shortly after clutch completion and the average incubation period requires a minimal duration of time, characteristic for each species (Álvarez & Barba, 2014; Cresswell & Mccleery, 2003). By behaviourally altering the transitions between the consecutive intervals of egg-laying and incubation, female birds can further advance or postpone time of hatching. There are several ways in which these readjustments can be achieved. By increasing clutch size or postponing the start of incubation by a few days after all eggs are laid, females can delay the time of hatching (García-Navas & Sanz, 2011; Tomás, 2015). Inversely, they can advance hatching by producing a smaller clutch then what they would under optimal circumstances, increase incubation intensity or beginning incubation before all eggs are laid (Tomás, 2015).

These behavioural adjustments, supplement or partially compensate for the limitation of flexibility in time of clutch initiation, at least in some populations (Both & Visser, 2005; Cresswell & Mccleery, 2003), but could additionally have another vital function related to optimal time of breeding. They could also help birds cope with sudden weather fluctuations not easily predicted based on cues ahead of the breeding season. Cold spells, heat waves and heavy rainfall occurring after clutch initiation can shift the time of peak caterpillar abundance (Vedder, 2012). In the absence of any additional plastic adjustments from the breeding females, such a shift could disrupt the established synchrony between nestling food demand and prey availability. Behaviourally altering the length of the interval between clutch initiation and hatching may allow birds to fine-tune their phenology to current conditions, potentially reducing any phenological mismatch caused by short-term weather fluctuations (Tomás, 2015).

Generalizing the response of species to environmental variation based on one study population can be challenging due to large variation among populations in ecological (Husby et al., 2010). For this master thesis, I investigate the links between short-term variability in spring weather and flexibility in incubation behaviour in insectivorous forest birds. Using nest box breeding data from eight populations of sympatric blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*, across the European continent, I address the hypothesis that flexibility in incubation behaviour is an adaptive response to weather fluctuations occurring after the onset of reproduction. More specifically, I predict that:

1. *Flexibility in incubation behaviour differs among populations at the continental scale*

2. *Within populations, temperature and rainfall occurring after time of clutch initiation correlate with incubation behaviour; hatching should be postponed when weather is colder or rainier, and advanced when it is warmer or dryer.*

3. *Because of largely similar ecological niches, both study species should display comparable levels and patterns of flexibility.*

4. *Flexibility in incubation behaviour should increase reproductive success, but whether advancing or postponing hatching is optimal, will depend on weather conditions*

Materials and method

1. Study species

The great tit, *Parus major*, and the blue tit, *Cyanistes caeruleus,* are small non-migratory passerines widely distributed throughout the Palearctic. Both species are secondary cavity nesters, meaning that they reuse cavities previously excavated by other species. They also readily adopt artificial nest boxes and tolerate moderate levels of disturbance at the nest (Perrins, 1979), which makes them ideal model species for ecological research in the wild. During the winter season the two species feed on various food sources, but during the breeding season they both rely exclusively on arboreal caterpillars as prey for their young (Dhondt, 1977). Their optimal nesting habitat is therefore deciduous forest where caterpillars are very abundant during spring (Dhondt, 1977), but they also breed in mixed or coniferous forests. Interspecific competition occurs, but their ecological niches do not completely overlap, as there are slight differences in body and bill size that result in marginal differences in optimal prey size. Their foraging habits also differ somehow, with great tits foraging closer to the ground, (Perrins, 1979), which allows the two species to coexist in sympatry over most of their distribution range (Dhondt & Eyckerman, 1980).

2. Study sites

The study area consists of eight different sites around Europe (Figure 1, Table 1). The Bergen site, established in 2017, is situated at the University gardens (arboretum and botanical garden) outside the city of Bergen, western Norway. In Germany two sites located in Southern Bavaria, about 50 km away from each other, were selected to complement each other. In the Ammersee-Starnbergersee site, established in 2009 and located between Herrsching and Starnberg, southwest of Munich, the majority of the nest boxes are occupied by great tits (see Stuber et al. 2013 for details). In the Westerholz site, located further west close to the city of Landsberg am Lech and established in 2007, the nest boxes are dominated by blue tits (see Schlicht & Kempenaers 2016 for details). The Sekocin site was established in 2012 and is located in the Kampinos national park in central Poland (see Pepłowska-Marczak 2018 and Corsini et al. 2021). Two of the sites are located in the south of France. The Rouvière site is situated in Montarnaud, about 30 km north of Montpellier, and was established in 1991. The Corsica site, located north-west on Corsica, was established in the Fango valley in 1979 and further expanded to an adjacent valley in the 1990s (see Porlier et al. 2012 for details). The Wytham site near Oxford, England, was established in 1947 in a section of Wytham woods, and expanded to the whole woodland area in the 1960s. See Perrins & McCleery (1989). The Vlieland site was established in 1955 and covers the entire island of Vlieland, which is one of the Dutch Frisian islands situated in the Wadden Sea outside the Netherlands (see Kluyver 1970 for details).

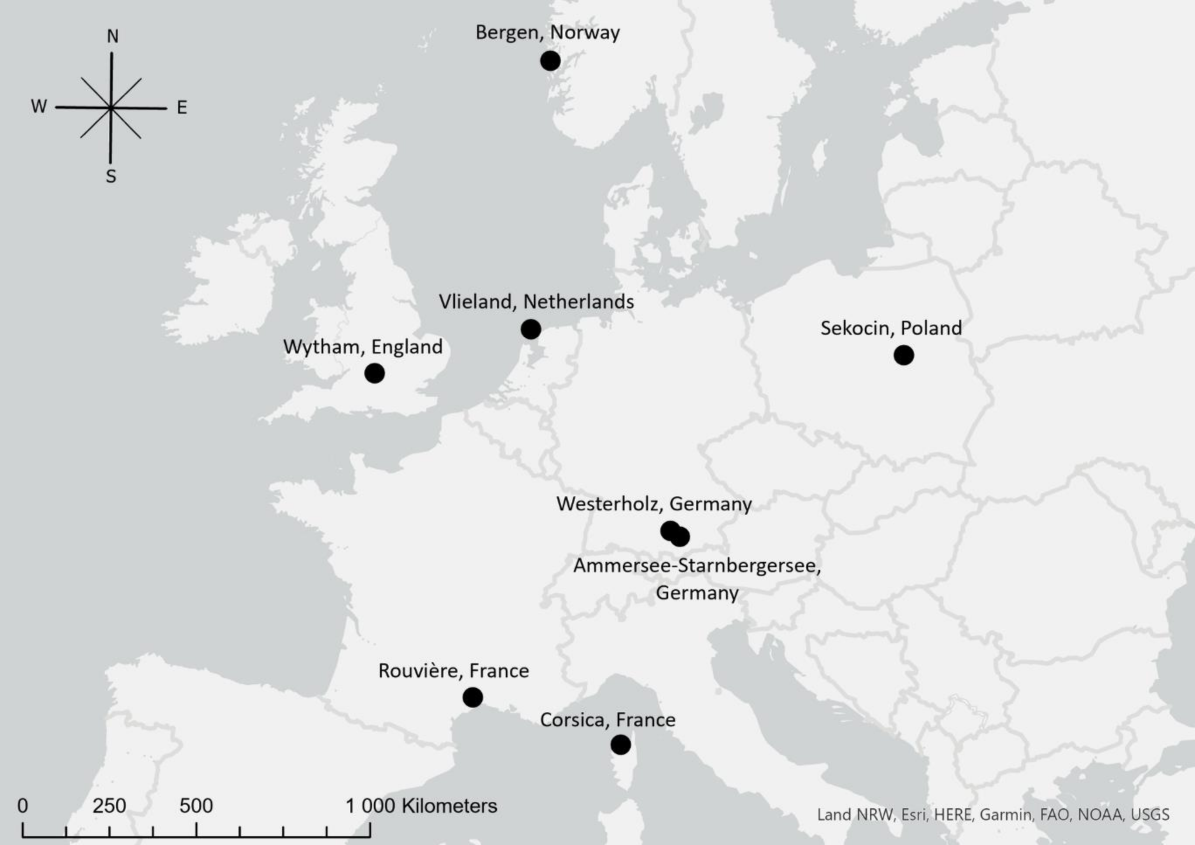

Figure 1. Locations of the eight European populations included in this study. Data from all other sites than Bergen were shared by collaborators via the SPI-birds research network. Data rights: Corsica and Rouvière - Anne Charmantier (Centre d'Ecologie Fonctionnelle et Evolutive), Vlieland - Marcel Visser (Netherlands Institute of Ecology), Wytham – Ben Sheldon (Edward Grey Institute, University of Oxford), Ammersee-Starnbergersee - Niels Digemanse (Ludwig-Maximilian University), Sekocin - Marta Szulkin (Museum and Institute of Zoology, Polish Academy of Sciences), Westerholz - Bart Kempenaers (Max Planck Institute for Ornithology)

3. Breeding data

Breeding data on *P. major* and *C. caeruleus* from the population situated in Bergen were collected from 2017 to 2021, under ringing licences issued to A. Mennerat and Arild Breistøl by the Museum in Stavanger. My personal contribution was to collect nest box data at the Bergen site during the breeding season of 2021. Breeding data from the seven other populations were obtained via the Studies of Populations of Individuals Birds network (SPI-birds, see link to webpage in references). For this study we obtained all data on blue tits and great tits breeding at each site from 2011 to 2020. We excluded populations situated in urban habitats or for which there was insufficient data available for the ten-year focal interval. We then further selected study sites based on the amplitude in spring temperature and annual precipitation. The total amount of observations and years with observations vary among locations, due to variation in human resources available for field monitoring and the fact that some study sites were established in more recent time (Table 1). An important aspect of the SPI-birds network is that the data collected by the various research groups is recorded following the same field protocol and formatted using a common pipeline (Culina et al., 2021).

Following standard procedure, nest boxes are visited weekly from mid-April to record the progression of nest building. During the egg-laying phase records include number of eggs and date of clutch initiation, which is either observed or calculated backwards assuming that one egg is laid each day. Species is confirmed during incubation, as well as clutch size (the total number of eggs laid). Incubation lasts on average for 14 days and from mid-May when the first eggs start to hatch, nest boxes are visited more frequently and the number of eggs hatched is recorded. The age of hatchlings is determined based on their development, and used to calculate hatch date for each clutch (the date when the first chick hatched). Nestlings are tagged on the tarsus between 12 to 14 days post-hatching with metal rings displaying unique identification numbers. Adults are captured at the nest 12-15 days post-hatching; untagged individuals are ringed, and all individuals are sexed, weighed, and their tarsus and wing length are measured. Nests are then revisited and checked for dead birds after chicks have fledged to assess fledging success.

TABLE 1. Sample sizes (number of active nests monitored) for each site, year and species. Italic rows represent number of blue tit nests, while bold rows represent number of great tit nests. Note that only years 2017 and 2018 contain data from all sites.

	Total number of nest observations per year, for *blue tits* and **great tits**										
	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Bergen							*10* **11**	*6* **10**	*10* **7**	*16* **10**	*19* **12**
Corsica	*77* **12**	*166* **17**	*149* **34**	*152* **25**	*170* **11**	*169* **14**	*171* **11**	*158* **18**			
Vlieland	*22* **208**	*44* **261**	*46* **127**	*62* **158**	*55* **105**	*53* **164**	*53* **236**	*28* **234**			
Wytham	*205* **100**	*274* **259**	*217* **176**	*310* **233**	*257* **264**	*316* **218**	*247* **222**	*255* **180**			
Ammersee – Starnbergersee	*19* **116**	*45* **233**	*27* **180**	*18* **175**	*40* **215**	*31* **203**	*40* **202**	*22* **166**	*23* **243**		
Rouvière	*6* **3**	*88* **19**	*53* **30**	*93* **45**	*87* **46**	*84* **44**	*79* **48**	*59* **44**			
Westerholz	*14* **16**	*134* **4**	*91* **1**	*74* **10**	*105* **7**	*110* **3**	*119*	*121* **15**			
Sekocin						*13* **14**	*13* **25**	*8* **15**	*7* **27**	*9* **20**	

4. Weather data

To test whether the birds adjust their phenology according to short-term variation in weather, daily meteorological records for average temperature, maximum temperature, minimum temperature, and total precipitation for the period 1st March - 30th June were obtained for years 2011 to 2020, from the weather stations located closest to the study sites. Temperature measurements are recorded 2 meters above ground level. The daily average temperature is calculated from the measurements of maximum and minimum temperature.

For each nest in our dataset, I calculated the mean of average temperature, maximum temperature, minimum temperature, as well as rainfall, for a time window (hereafter W0) spanning from the onset of egg laying until 14 days prior to hatching (assumed start of full incubation). I also averaged the same weather variables over a longer time windows (W6) starting 12 days prior to egg-laying date.

5. Geographical variation in weather

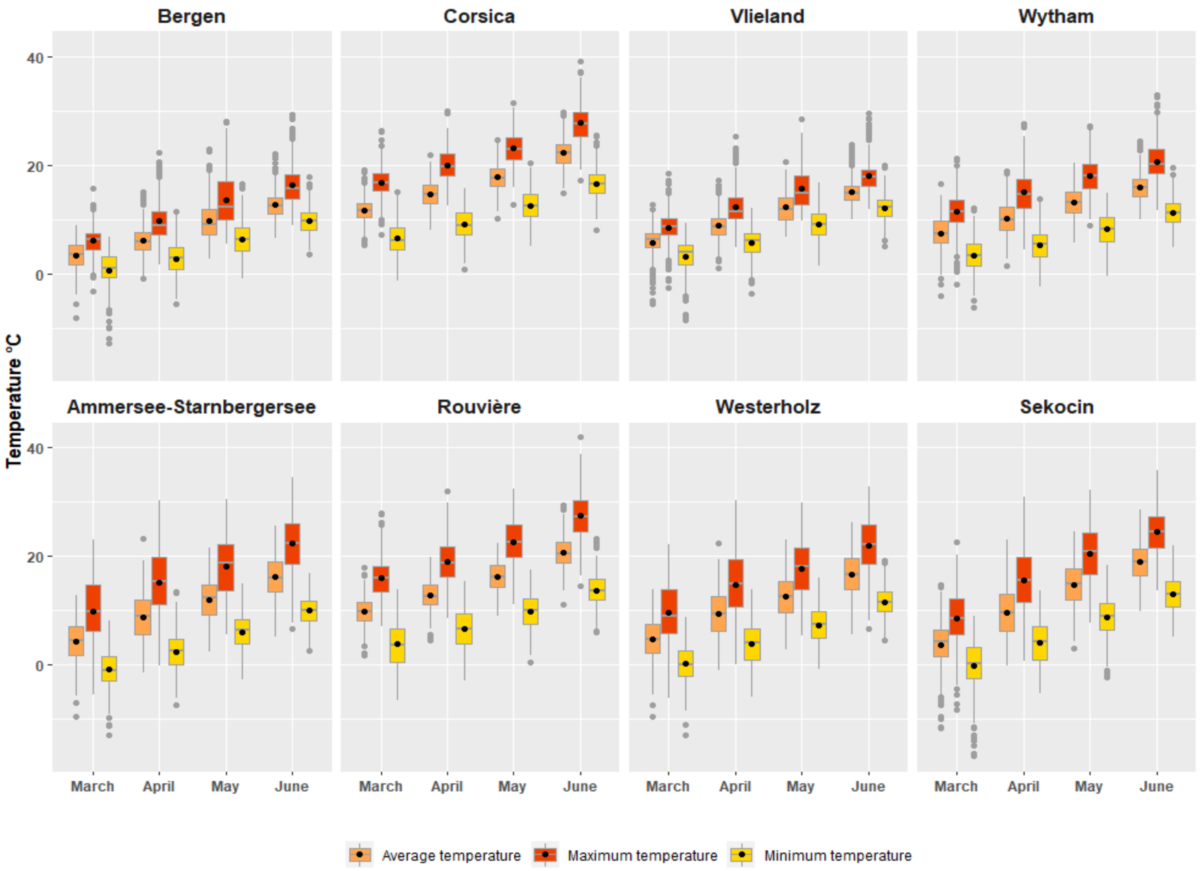

FIGURE 2. Variation in average, maximum, and minimum temperature for the period 2011-2020, for each month and study site. Each boxplot displays the median and interquartile range from 25th to 75th percentile (box), as well as calculated 'minimum' and 'maximum' values (bars) and outliers (grey dots). Black dots show the monthly mean of each temperature metric. Upper row consists of the four sites with the least interannual variation in temperature, while lower row consists of sites the most interannual variation around the monthly means of temperature.

To characterise how the study sites differ in spring climate we explored monthly variation in average, maximum and minimum temperature, as well as rainfall, for all ten years (2011 – 2020) combined (Figure 2). Corsica and Rouvière have a Mediterranean climate and experience the highest maximum temperatures of all the sites. The sites with an oceanic climate, namely

Bergen, Vlieland an Wytham, experience low temperature variation, while the continental sites, Ammersee-Starnbergersee, Westerholz and Sekocin experience high temperature variation, as well as the lowest minimum temperatures.

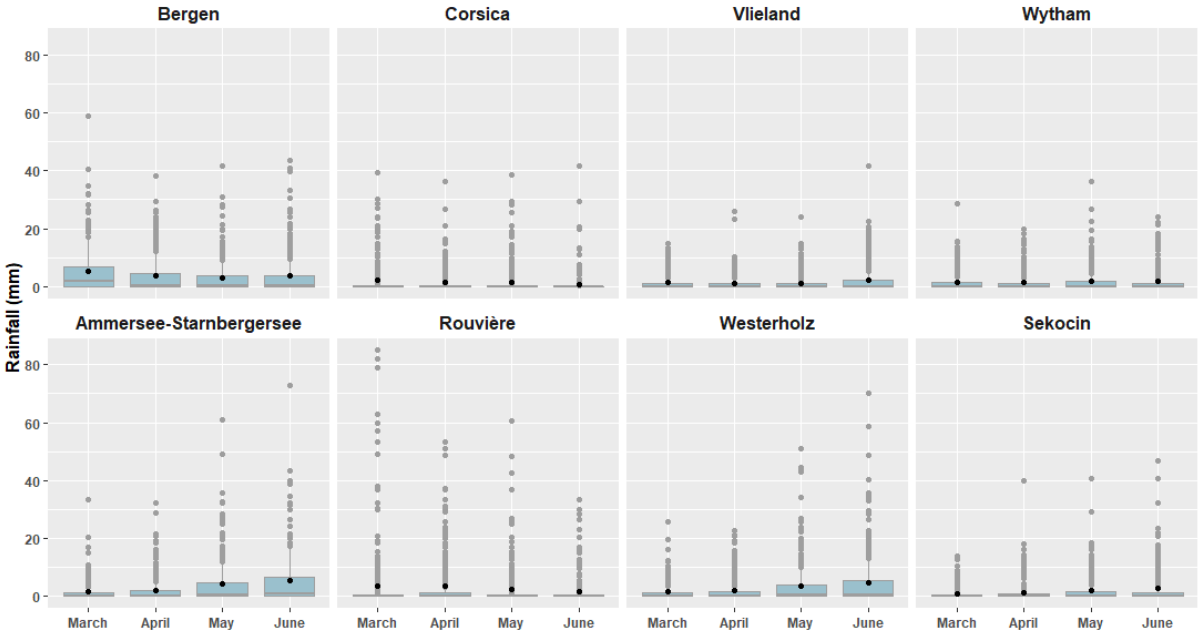

FIGURE 3. Variation in daily rainfall for the period 2011-2020, for each month and study site. Each boxplot displays the median and interquartile range from 25th to 75th percentile (box), as well as calculated ’minimum’ and ’maximum’ values (bars) and outliers (grey dots). Black dots show the monthly mean.

Bergen is the site that experiences the highest amount of rainfall throughout spring, with a higher mean and more variation in March, while Ammersee-Starnbergersee and Westerholz experience increasing variation and amount of rainfall as the spring progresses. Amount of rainfall in Rouvière is highly varied in March, but the mean monthly decreases slightly with spring progression. Sekocin, Corsica and Vlieland experience an even variation in rainfall throughout the season, with monthly means ranging between 0.7 mm and 2.0 mm of rain per day.

6. Statistics

All statistical analyses were conducted using RStudio version 1.4.1106 (RStudio Team (2021). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL: http://www.rstudio.com/). Linear mixed effects models were built using the ‘lme’ function of the ‘nlme’ package *(version 3.1-149),* while generalised linear mixed-effects models were built with the ‘glmmTMB’ function from the ‘glmmTMB’ package (*version 1.1.2.3*). AICc was performed by use of the ‘AICc’ function from the ‘MuMIn’ package (*version 1.43.17*).

1. Using 'hatch gap' as a proxy for flexibility in incubation behaviour

All dates in both the breeding and the weather datasets were converted into Julian dates (1 = March 1st). A key variable in our study is the *hatch gap*, defined as the difference in days between the observed hatch date (day when the first chick hatches), and the predicted hatch date, calculated as follows. By adding the clutch size to the egg-laying date one obtains the date of clutch completion (day when the last egg is laid). Taking an average duration of embryo development under full incubation of 14 days, the predicted hatch date is thus obtained by adding 14 days to the date of clutch completion. This corresponds to the date when chicks would have hatched if females began full incubation upon clutch completion, that is, if the females followed a sequential breeding sequence. *Hatch gap* is defined as *(observed hatch date – predicted hatch date)*, such that a negative hatch gap indicates an earlier hatching than calculated, and a positive hatch gap indicates postponed hatching.

To minimise the risk of large hatching delays reflecting replacement clutches rather than female flexibility, and to account for the fact that advancing incubation is not possible prior to egg-laying date, all observations with hatch gaps outside the [-10 – +11] interval were removed from the dataset. All observations that were experimentally manipulated or categorized as second breeding attempts were further excluded from the dataset. In addition, observations with high outlying values for egg-laying date were assumed to be uncategorized second breeding attempts and were also excluded from analysis.

2. Is hatch gap related to short-term weather variation?

- Overall behavioural response to weather variation:

To test whether the incubation behaviour of female birds is related to weather conditions occurring after the onset of egg laying, Linear Mixed Effects models (LME) were constructed with hatch gap as the response variable, rainfall and temperature during time window W0 as the main explanatory covariates, and year as a random effect. Three models were constructed, each only differing in the temperature metric used as a covariate (average, maximum, or minimum temperature). Clutch size was also included as a covariate because the number of eggs may influence incubation behaviour. Similarly, earlier-breeding females may be higher-quality individuals and differ in their behaviour, and so we therefore also included lay date as a covariate. Lastly, we included species and study site as factors, as well as their interactions with covariates, to account for geographical or interspecific differences in phenological responses.

To test whether the effects of short-term weather variation differed from those of longer-term weather variation we constructed three additional models (one for each temperature metric), this time using weather variables for the longer time window W6. For each of the six models (three models for W0, three models for W6), backwards model selection was carried out based on Akaike's information criterion ((Akaike, 1998), to decide which explanatory variables should be kept in models. All explanatory variables were kept, except the interaction between species and temperature variables. These six general models were then compared by use of second order AICc, Akaike's information criterion corrected for small sample sizes (Akaike, 1998), in order to establish which temperature metric in which time window, W0 or W6, best described the variation in hatch gap (see Appendix for more details and for the results of the models with the longer time window W6).

- Site-specific behavioural response to weather variation:

Because the sensitivity of incubation behaviour to weather may vary among populations, we also constructed single-site models, for each temperature metric, in order to explore which temperature metric is the most influential at each site. These single-site models were constructed in the same manner as the general models. In all models, both general and single-site, the response variable was square root transformed to account for positive skewness of residuals.

TABLE 2. Explanation of variables used in analysis of hatch gap (LME) and reproductive success (GLMM). Models also included several interaction terms involving variables listed, in addition to population and species.

Variable	Explanation
Hatch gap	Difference between expected and observed first day of hatching
Temperature	Mean temperature of interval, either average, maximum or minimum temperature (°C)
Rainfall	Mean amount of rainfall in interval (mm)
Clutch size	Total number of eggs laid in nest
First egg	Date of first egg-laying in nest
Reproductive success	Number of hatchlings fledged / total clutch size

3. Is reproductive success related to hatch gap?

In this study reproductive success is defined for each brood as the number of nestlings alive during tagging (*i.e.*, close to fledging) divided by the original clutch size. To explore the link between adjustments to the time of hatching and reproductive success, we built a Generalized Linear Mixed-effects model (GLMM) with logit link function (logistic regression with proportions) and year as a random effect factor. The 'cbind' function was used to combine clutch size and number of chicks fledged into a response variable representing the ratio of each clutch that successfully fledged. This measure of reproductive success is a combined measure of portion of eggs which end up hatching, as well as the portion of hatchlings which eventually fledge. As we mainly are interested in measuring how many hatchlings eventually fledge, as a proximal measure of synchrony with food peak, we should ideally only have used number of hatchlings which successfully fledged as a measure of reproductive success. There was however, a substantially large portion of observations which missed data on number of hatchlings, and we therefore used clutch size instead. Hatch gap was included as covariate and population and species as factors, as well as interactions between these three. The quadratic term of hatch gap was also included, to test for non-linear relationship between hatch gap and nesting success. For this analysis 299 observations were excluded due to missing data on hatching success, and the data from 2021 breeding season in Bergen were added. An estimated marginal means post hoc test (the 'emmeans' function, from the 'emmeans' package, *version 1.7.2*), was used to compare population estimates against each other.

Results

1. Is hatch gap related to short-term weather variation?

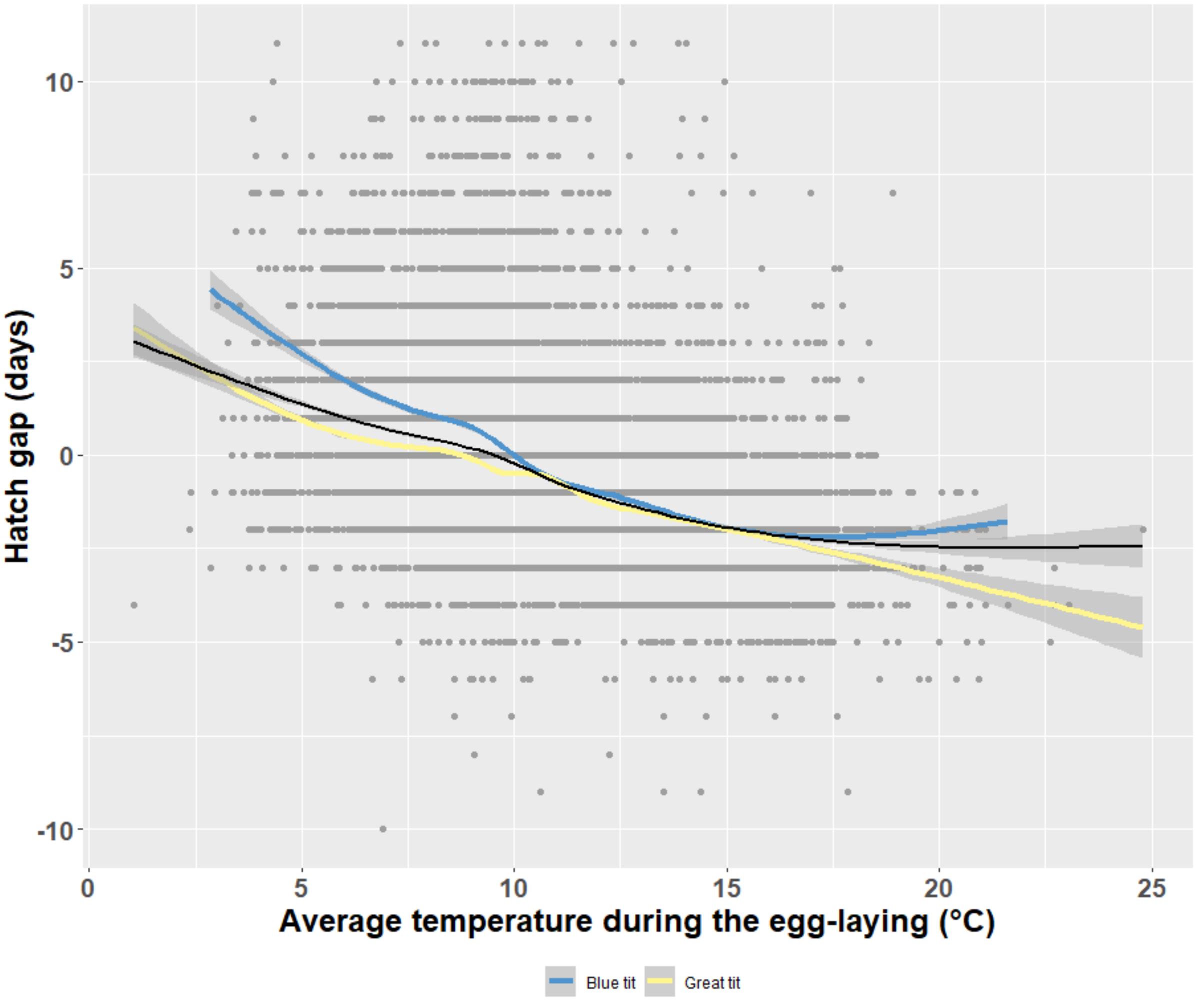

Figure 5. Relation between hatch gap, the difference between expected and observed day of hatching, and mean average temperature during time window W0 (all years combined). The plotted lines are generated from the general linear mixed-effects model (see Materials and Method for details). The black line shows the mean population estimate for both species combined. Shaded areas represent the 95% confidence intervals of model lines.

- Overall pattern for time window W0:

The best general model for all sites combined, includes mean average temperature during time window W0 as an explanatory variable (Table 1 in appendix). In the model, there is an overall significantly negative association of hatch gap with temperature ($F_{1/10766}$ = 1846.70, $p < 10^{-4}$, Figure 5). The interaction between temperature and rainfall is negative ($F_{1/10766}$ = 99.78, $p < 10^{-4}$), and differs significantly among sites ($F_{1/10766}$ = 22.27, $p < 10^{-4}$). Neither clutch size nor first egg has a significant effect on hatch gap, but there is a significantly negative interaction between clutch size and first egg ($F_{1/10766}$ = 39.38, $p < 10^{-4}$). Great tits have a significantly lower value of hatch gap than blue tits ($F_{1/10766}$ = 39.38, $p < 10^{-4}$).

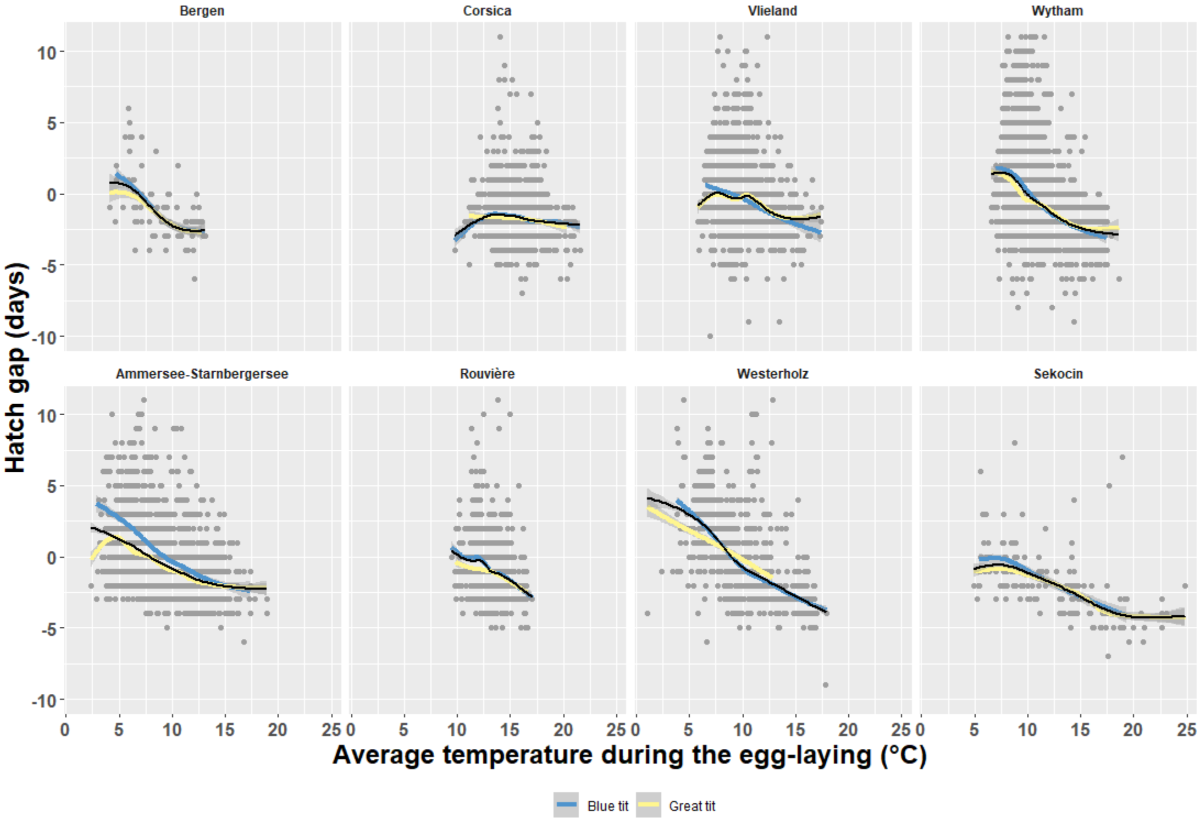

Figure 6. Relation between hatch gap, the difference between expected and observed day of hatching, and mean average temperature during time window W0, for each study site (all years combined). The plotted lines are generated from the general linear mixed-effects model (see Materials and Method for details). The black line shows the mean population estimate for both species combined. Shaded areas represent the 95% confidence intervals of model lines.

- Site-specific patterns for time window W0:

Hatch gap is negatively related to average temperature during time window W0 in all sites except Sekocin where it is not significant. The effect is strongest in Westerholz ($t_{808}{}^{1}$ = -5.36, $p < 10^{-4}$) and Bergen ($t_{69}{}^{1}$ = -2.93, p = 0.005), and weakest in Corsica ($t_{1339}{}^{1}$ = -2.12, p = 0.03) and in Wytham ($t_{3715}{}^{1}$ = -2.83, p = 0.005), (Figure 6). Maximum temperature is significantly negatively related to hatch gap at all sites, including Sekocin. On the contrary, minimum temperature is not significantly related to hatch gap at any site, except Westerholz where the effect is negative (see Appendix for the effects of maximum and minimum temperature).

Hatch gap has a significant association with rainfall during time window W0 in all populations (*all p values < 0.03)*, besides Bergen, Westerholz and Sekocin. The effect is strongest in Vlieland where it is negative ($t_{1837}^1 = -6.30$, $p = 0.019$), and weakest in Rouvière, where it also is negative ($t_{813}^1 = -2.31$, $p = 0.005$). The interaction between rainfall and average temperature is significant in Corsica ($t_{1339}^1 = -2.77$, $p = 0.006$) and Wytham ($t_{3715}^1 = -10.99$, $p < 10^{-4}$) where it is negative, and in Rouvière ($t_{813}^1 = 2.57$, $p = 0.01$) and Vlieland ($t_{1837}^1 = 6.68$, $p = <10^{-4}$), where it is positive (Table 3).

Hatch gap is significantly smaller for great tits than for blue tits, at all sites (*all p values < 0.03*) except Rouvière and Corsica (Figure 7). Egg-laying date and clutch size, as well as their interaction, relate in various ways to hatch gap depending on the study site. The reason they were included in all models was primarily to control for them while focusing on the effects of other variables including weather. For the sake of clarity, I will not to detail these effects here (but, see Table 3 for more details).

TABLE 3. Summary of single-site LME models examining variation in hatch gap and how it is influenced in time window W0 by average temperature and other variables, at the different sites.

AVERAGE TEMPERATURE	Bergen			Corsica			Vlieland			Wytham		
	b ± SE	*t*	*p*	*b ± SE*	*t*	*p*	*b ± SE*	*t*	*p*	*b ± SE*	*t*	*p*
Intercept	3,632± 1,208	3,0	**0,004**	2,469 ± 0,088	28,1	**$<10^{-4}$**	2,918 ± 0,132	22,1	**$<10^{-4}$**	3,198 ± 0,092	34,8	**$<10^{-4}$**
Temperature	-0,046 ± 0,016	-2,9	**0,005**	-0,007 ± 0,003	-2,2	**0,030**	-0,014 ± 0,004	-3,5	**0,001**	-0,007 ± 0,002	-2,8	**0,005**
Rainfall	-0,041 ± 0,064	-0,6	0,531	0,070 ± 0,022	3,2	**0,002**	-0,170 ± 0,027	-6,3	**$<10^{-4}$**	0,104 ± 0,008	13,1	**$<10^{-4}$**
Temperature x Rainfall	0,006 ± 0,007	0,9	0,352	-0,004 ± 0,001	-2,8	**0,006**	0,019 ± 0,003	-6,7	**$<10^{-4}$**	-0,007 ± 0,001	-11,0	**$<10^{-4}$**
Species (Great tit)	-0,153 ± 0,047	-3,2	**0,002**	0,024 ± 0,013	1,8	0,065	-0,102 ± 0,013	-8,0	**$<10^{-4}$**	-0,028 ± 0,006	-4,4	**$<10^{-4}$**
First egg	-0,011 ± 0,018	-0,6	0,562	0,003 ± 0,001	2,1	**0,035**	-0,001 ± 0,002	-0,5	0,588	-0,011 ± 0,002	-6,9	**$<10^{-4}$**
Clutch size	-0,044 ± 0,123	-0,4	0,724	-0,002± 0,010	-0,2	0,818	-0,006 ± 0,014	-0,4	0,697	-0,009 ± 0,008	-1,1	0,282
Clutch size x First egg	$<10^{-4}$ ± 0,002	0,2	0,826	-0,001 ± $<10^{-4}$	-2,6	**0,010**	$<10^{-4}$ ± $<10^{-4}$	-1,2	0,238	$<10^{-4}$ ± $<10^{-4}$	-1,6	0,106

	Ammersee - Starnbergersee			Rouvière			Westerholz			Sekocin		
	b ± SE	*t*	*p*	*b ± SE*	*t*	*p*	*b ± SE*	*t*	*p*	*b ± SE*	*t*	*p*
Intercept	2,647 ± 0,106	24,9	**$<10^{-4}$**	3,052 ± 0,168	18,2	**$<10^{-4}$**	3,444 ± 0,187	18,4	**$<10^{-4}$**	2,706 ± 0,785	3,4	**0,001**
Temperature	-0,008 ± 0,002	-3,3	**0,001**	-0,015 ± 0,007	-2,2	**0,026**	-0,024 ± 0,004	-5,4	**$<10^{-4}$**	-0,015 ± 0,009	-1,6	0,115
Rainfall	0,026 ± 0,007	3,7	**$<10^{-4}$**	-0,053 ± 0,023	-2,3	**0,021**	0,004 ± 0,016	0,3	0,782	-0,017 ± 0,077	-0,2	0,822
Temperature x Rainfall	$<10^{-4}$± 0,001	-0,6	0,519	0,005 ± 0,002	2,6	**0,010**	0,002 ± 0,002	1,2	0,214	0,002 ± 0,008	0,3	0,772
Species (Great tit)	-0,127 ± 0,010	-12,3	**$<10^{-4}$**	-0,018 ± 0,013	-1,4	0,170	-0,337 ± 0,032	-10,6	**$<10^{-4}$**	-0,071 ± 0,030	-2,3	**0,021**
First egg	0,003 ± 0,002	1,4	0,173	-0,006 ± 0,003	-1,7	0,095	-0,008 ± 0,003	-2,3	**0,020**	0,005 ± 0,016	0,3	0,742
Clutch size	0,029 ± 0,012	2,4	**0,015**	-0,020 ± 0,015	-1,3	0,180	0,015 ± 0,019	0,8	0,444	0,030 ± 0,078	0,4	0,702
Clutch size x First egg	-0,001 ± $<10^{-4}$	-4,5	**$<10^{-4}$**	$<10^{-4}$ ± $<10^{-4}$	-0,4	0,697	-0,001 ± $<10^{-4}$	-3,0	**0,003**	-0,001 ± 0,002	-1,0	0,338

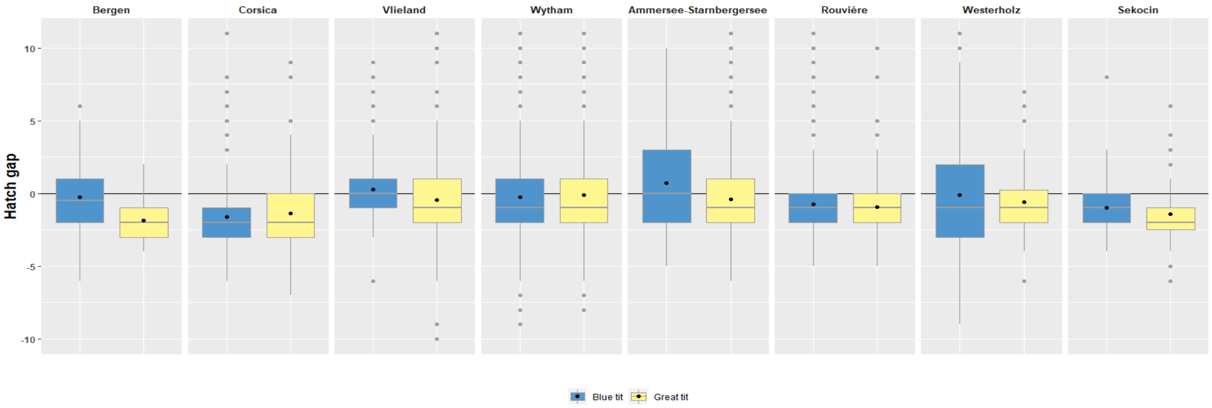

FIGURE 7. Boxplot with distribution of hatch gap between species, for each population and all years combined. Black dots show mean hatch gap across years.

2. Is reproductive success related to hatch gap?

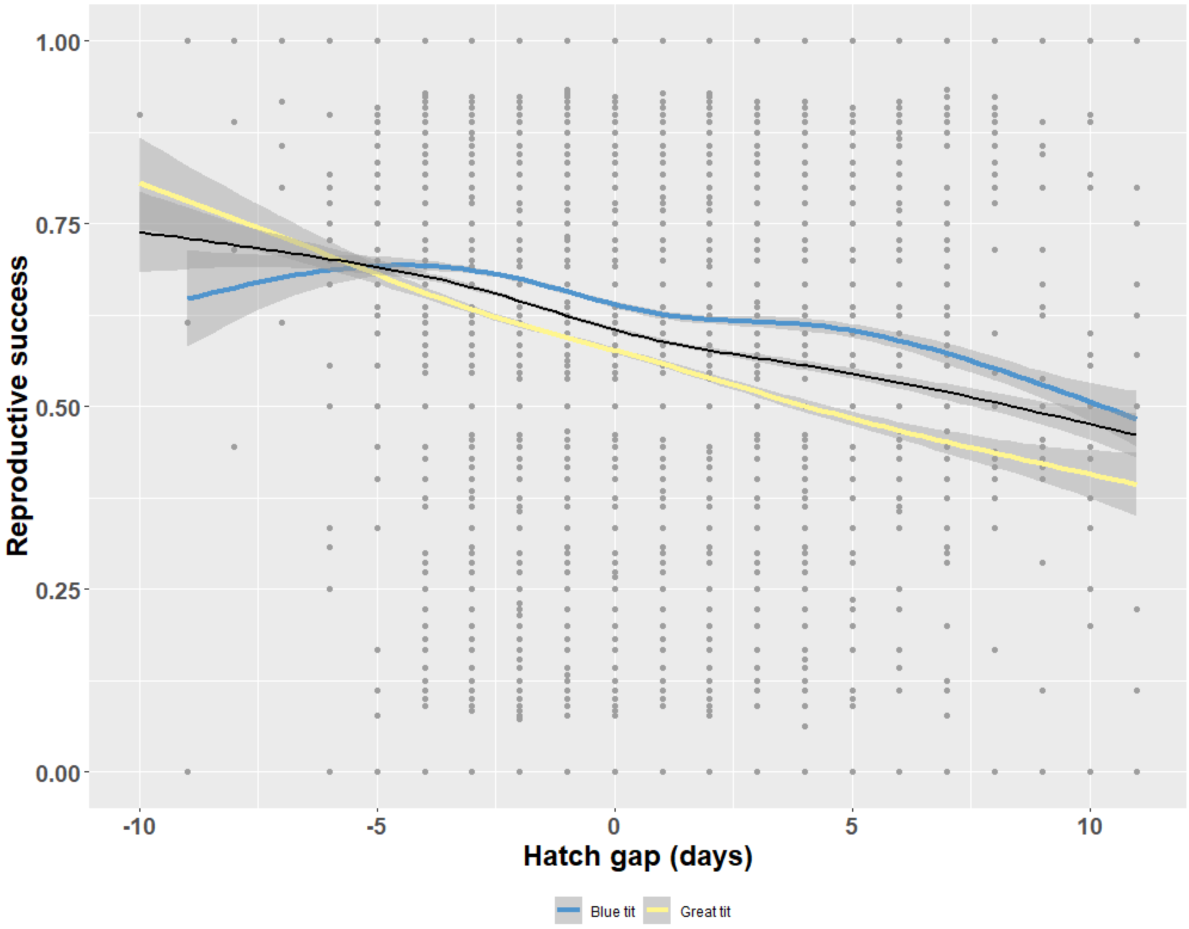

Figure 8. Relation between reproductive success (proportion of chicks per clutch that successfully fledged) and hatch gap, for all years and sites combined. The lines are generated from a binomial GLMM with hatch gap (both linear and quadratic terms), population, species, and interactions as fixed effects, and year as a random effect. The black line is overall estimate for both species. The shaded areas represent the 95% confidence interval of model lines.

Overall, reproductive success decreases with increasing hatch gap (Figure 8). The negative relationship is significant not only for the linear, but also for the quadratic term (*p* <0.005 and *p* <0.05 respectively). Strikingly, this relationship is stronger for great tits than for blue tits, both overall (Figure 8) and for most sites separately (Figure 9). In most sites the reproductive success of the two species relate to hatch gap in markedly different ways, and sometimes opposite directions (Figure 9). Two sites stand out, namely Bergen and Ammersee-Starnbergersee, in terms of the difference between blue tits and great tits. In Bergen reproductive success relates to hatch gap negatively in blue tits, but positively in great tits. The opposite is found for Ammersee-Starnbergersee. The full output of analysis of reproductive success is given in appendix.

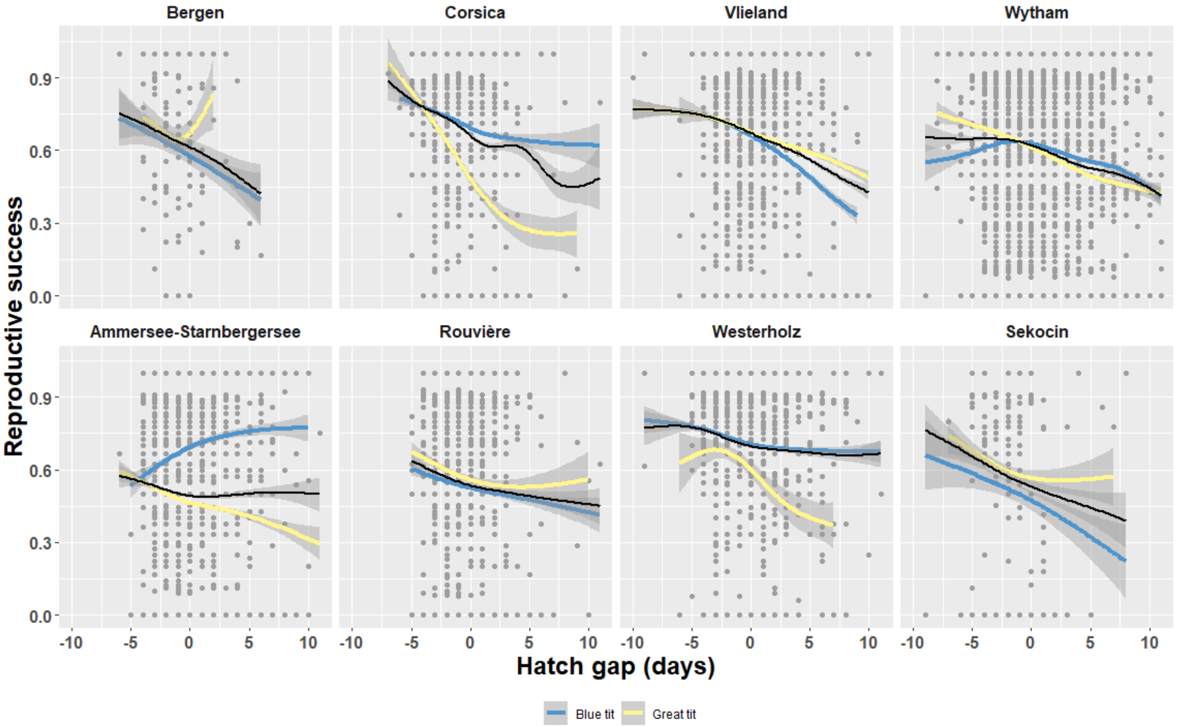

Figure 9. Relation between reproductive success (proportion of chicks per clutch that successfully fledged) and hatch gap, for all years combined. The lines are generated from a binomial GLMM with hatch gap (both linear and quadratic terms), species, and interactions as fixed effects, and year as a random effect. The black line is overall estimate for both species. The shaded areas represent the 95% confidence interval of model lines.

Discussion

The aim of this thesis has been to examine the variation and flexibility in incubation behaviour in several European populations of two small forest passerines, the blue tit and the great tit, and to investigated whether these behavioural adjustments are influenced by weather occurring during the incubation phase, and if such differences can be linked variability in the spring conditions experienced by each of these populations. We additionally examined if the presence of flexibility in incubation behaviour showed any clear correlation with reproductive success, indicating whether adjustments have a direct effect on reproductive output. In order to address these questions, we quantified the difference between the observed and the expected time of hatching, as a proximate measure of incubation behaviour. And, by using all available nest box data for years 2011 – 2021 from eight populations of wild blue tits and great tits around Europe, we show that hatch gaps are negatively associated with temperature occurring in the time-window between clutch initiation and estimated onset of incubation. This association between temperature and hatch gap was consistent for both species across all sites, and for all temperature metrics. Moreover, reproductive success generally correlated with advanced hatching.

The finding that hatch gap is negatively associated with temperature, is both in line with our initial predictions and the results of other studies on incubation behaviour (Schaper et al., 2012; Simmonds et al., 2017). According to our results, hatching is postponed when the ambient temperature occurring in period after clutch initiation decreases, and advanced when it increases. One important question regarding this observed correlation is whether postponed or advanced hatching reflect adaptive responses that improve time of hatching, or simply reflect that the females are energetically constrained by suboptimal conditions during the egg-laying phase. Comparisons of annual shifts in caterpillar abundance, clutch initiation dates and the observed and predicted hatching dates show that overall, observed hatching date coincided more with time of caterpillar peak abundance than the predicted hatch date (García-Navas & Sanz, 2011; Simmonds et al., 2017; van Noordwijk, McCleery, & Perrins, 1995). These findings strongly support the idea that behaviour adjustments reflect strategic decisions which improve synchrony with peak caterpillar abundance (Naef-Daenzer, Nager, Keller, & Naef-Daenzer, 2004). There is, however, also ample evidence that energetic constraints can have a lot of influence on incubation behaviour, and that the two explanations are not mutually exclusive, but rather interact (Naef-Daenzer et al., 2004). Cold spells occurring after clutch initiation could incur energy demands adding up to the already costly process of egg production, and thereby force the female to prioritize self-maintenance by postponing incubation after clutch completion (Kluen, de Heij, & Brommer, 2011), and/or by introducing laying gaps which prolong the period of egg laying (Glądalski et al., 2020). Meanwhile, advanced hatching can be a reflection of relaxed constraints related to egg production and incubation effort (Álvarez & Barba, 2014; Coe, Beck, Chin, Jachowski, & Hopkins, 2015; Wang & Beissinger, 2009). We have hypothesized that flexibility in incubation behaviour is an adaptive response to weather fluctuations occurring after the onset of reproduction.

Based on the finding that incubation behaviours have been linked to increased reproductive success through improved synchrony with the food source, we might wonder whether there exists a heritable component for this plasticity for which selection can work on. Whether or not phenotypic flexibility is adaptive, depends on the environment in which it is expressed (Ghalambor, McKay, Carroll, & Reznick, 2007). In general, phenotypic flexibility is thought to be important for fitness in environments that are variable (Snell-Rood, 2013). As our results indicate that there is a significant correlation between temperature and hatch gap, it is reasonable to assume that the range of variation in ambient temperature during the breeding season is likely to influence the degree of selection on plasticity. And, because the occurrence of extreme thermal conditions, both warm and cold, have the most extensive fitness consequences (Glądalski et al., 2020), it is presumably in environments where such conditions are frequent that flexibility in incubation behaviour will be most adaptive (Chevin & Hoffmann, 2017). Regular frequency of extreme thermal conditions is a prerequisite for behavioural adaptation in extreme environments, as there needs to be a stable selection pressure for there to be directional selection on increased flexibility (Reed, Waples, Schindler, Hard, & Kinnison, 2010). Looking at the variation in weather at the different sites, Rouvière, Ammersee-Starnbergersee, Westerholz and Sekocin show a high degree of variation in both maximum and minimum temperature. The latter three frequently experiencing considerably low minimum temperatures during March, April and May, while Rouvière regularly experience more extreme maximum temperatures. Based on this reasoning, we would therefore expect these four sites to have experienced more selection for phenological flexibility in incubation behaviour.

The most extreme postponements of hatching were observed within three of the populations with the least variation in thermal conditions; Vlieland, Wytham and Bergen, are all linked to low mean ambient temperature, with mean average temperatures of less than 12.5 °C (Figure 6). These observed postponements are likely caused by energetic constraints posed by the harsh thermal conditions experienced in interval after clutch initiation. The birds in Corsica and Rouvière, the two sites located on the southern limit of distribution, have the highest mean ambient temperatures observed in interval after clutch initiation. The birds here are likely not as restricted by low temperatures as at the other sites, but perhaps limited by conditions becoming too warm and dry. Overall, it is plausible that many of the most extreme postponements, across all populations, are the result of sudden cold spells after clutch initiation, and therefore mostly reflect energetic constraints. A possible explanation for why we find higher reproductive success to be associated with advanced hatching, while postponement appear to lower success could be that delaying of hatching comes with the price of decreased egg viability (Monros, Belda, & Barba, 1998), and reduced nestling growth in chicks that survive until hatching (Kluen et al., 2011)

The geographical variation in the increase of spring temperature caused by asymmetric climate change, where the level of increase in temperature development during early spring; the pre-laying period, and late spring; the nesting-period differ (Bernstein et al., 2008), could restrict plasticity in clutch initiation (Marcel E. Visser et al., 2003), and is therefore a possible source of altered selection pressure on phenotypic plasticity in incubation behaviour. In populations where there is an increase in ambient temperature during nesting period, but not during pre-laying period, the birds might be restricted from starting to laying eggs sufficiently early to establish synchrony with food peak in most years, without additionally adjusting their incubation regime (Matthysen, Adriaensen, & Dhondt, 2011; Marcel E. Visser et al., 2003).

Indeed, there are also indications that the food peak not only has shifted forward in time, but additionally narrowed in length (Matthysen et al., 2011). Therefore, the marked association between reproductive success and advanced hatching in our findings could also reflect that the birds more often have to advance hatching than delay it, in order to synchronize with the early caterpillar peak, and that the fitness consequences of failing to do so increases with the shortening of the time of peak caterpillar abundance. This could perhaps have induced selection for flexibility in advancement of hatching, even in Bergen, Corsica, Vlieland and Wytham, and may even explain why, in our findings, all populations largely display an equal ability to advance hatching, and why all populations have negatively skewed distributions of hatch gaps across species (Figure 7).

We have so far only presented mechanisms that are likely to shape the role and extent of flexibility of incubation behaviour at the populational level, based on climatic constraints. And, although we have detected significant overall directional effects related to hatch gap, temperature and the influence it has on reproductive success, both the high standard errors of our estimates as well as the data reveal that there is great variation in incubation behaviour and reproductive success. This could indicate other influential factors, such as the condition, age and experience of the breeding female, and habitat quality. There is environmental heterogeneity among territories within a population, most importantly in terms of vegetation, which largely determines prey availability (Blondel, Paula Cristina, Maistre, & Perret, 1993). There is generally more caterpillar prey in habitats dominated by deciduous trees than in mixed or evergreen-dominated areas (Blondel et al., 1993), and there can be great variation in the annual phenology of trees, and therefore also the caterpillars, within a population (Porlier et al., 2012). A study based on long term data from the Wytham population of great tits found that, in addition to the effect of local weather conditions, the birds displayed breeding phenology which correlated significantly to the small-scale spatial variation of their territories (Hinks et al., 2015). We have not investigated the effect of spatial variation within populations, but believe that it could account for a portion of the variation in incubation behaviour and reproductive success observed.

We found that great tits advanced hatching in response to higher temperatures more than blue tits at all sites except Rouvière and Corsica. It should be noted that the sites where there are markedly different patterns in association between reproductive success and hatch gap, between species, are the sites with either few observations in all; Bergen and Sekocin, or with few observations for one species, as is the case for Ammersee-Starnbergersee and Westerholz.

One weakness of using a proximal measure of incubation behaviour is that we are unable to assign causality, in that we cannot distinguish which between the different mechanism of advancing or postponing hatching, we can only quantify the net result of these actions. Neither can we detangle when the observed incubation behaviour reflects energetic constraints and/or strategic decisions, and whether the birds are able to sufficiently track the phenology of caterpillar prey. Because there is large interannual variation in weather, which give rise to interannual variation in hatch gaps, the lack of a completely overlapping time series of breeding data, particularly for Sekocin and Bergen where we only have data from more recent years, for which there are few other populations we have data on, could be a possible source of bias. (Glądalski et al., 2020) have, for a population of great tits in central Poland, reported on the effects of spring temperature on patterns of incubation behaviour from two consecutive years where one breeding season was extremely cold and the other extremely warm; 2017 and 2018. These extreme conditions were noticeable in all of Europe, so extending this study to include several different populations across the continent and correlating the variation in behavioural response and resulting fitness to local characteristics could reveal valuable insights into extent and role of flexibility at the population-level, without the need of long time-series of data. Another interesting approach for future studies would be to investigate the heritable component of flexibility, by quantifying and comparing the individual reaction norms of related female birds across multiple years, such as was done by (Husby et al., 2010). This type of study could reveal more about the genetic variation in flexibility and whether it can evolve under selection, within a population. It could also be useful for comparing genetic variation between adjacent populations whom are subject to different local conditions, to establish where birds are exposed to genetic flow, which might hinder consistent selection on flexibility in incubation behaviour. A simple improvement of our study design would be to include data on caterpillar phenology, to see whether behavioural adjustments to time of hatching improve synchrony, or quantify spatial differences in the forage grounds surrounding nests, to get a better understanding of how much small-scale spatial variation contributes to the individual-level diversity of incubation behaviour

In conclusion, our study has found significant overall directional effects related to hatch gap, temperature and the influence it has on reproductive success, across Europe. This leads us to the assumption that although the overall incubation behavioural response follows the same pattern across the continent, other important aspects such as pattern of climate change, small-scale habitat variation and genetic flow differing between populations are influencing the way birds are able to alter their breeding phenology and is the source of variation at both the populational level, as well as individual level.

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