Spatial, social and environmental drivers of the timing of reproduction in the wild

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Declaration

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated. The work has not been submitted for any degree or professional qualification except as specified.

Carys Jones, Michaelmas Term 2024

Acknowledgments

I can't quite believe that I am writing this, there have been many points along the way of this PhD where I thought I would not get to this point, it is almost surreal, yet here I am at 4am a couple of days before my deadline writing my acknowledgments, maybe I am actually just asleep and dreaming?! These past 4 years have been some of the most challenging but also rewarding of my life. I have learnt many things: about science, about making friends and community, about great tits, about working hard, about how both simultaneously long and short 4 years can feel, and probably much more.

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Free Palestine.

Abstract

Phenotypic variation provides the raw material needed for natural selection, and therefore identifying what causes and maintains this variation is important for understanding ecological and evolutionary processes. Behavioural timing traits, such as when an individual begins breeding during the reproductive season (often referred to as phenology), often show continuous variation between individuals within populations. Like any quantitative trait, this variation is influenced by both genetic and environmental factors, but disentangling their respective contributions can be challenging. Estimating the genetic contribution requires careful consideration of environmental effects across suitable scales. The environment experienced by individuals will encompass both physical and social factors, and will often vary over small scales. The study of small-scale environmental (both physical and social) effects on phenotypic variation is becoming a growing area of interest and is widely recognised as important for determining the causes and consequences of phenotypic variation between individuals. To explain the phenotypic variation observed in phenological traits there must be consideration of 1) environmental factors at the appropriate spatial scale and 2) the social dependence of these responses, both of which I address in this thesis.

Our study system, a long-term monitored population of great tits in Wytham Woods, Oxford, UK, provides a robust dataset for investigating these questions. This population has been monitored extensively for over 60 years, with detailed data collected on individual birds' breeding attempts every spring, offering unique insights into the drivers of variation in a seasonal timing trait. First, in Chapter 2, I used multi-matrix quantitative genetic animal models to quantify the relative contributions of additive genetic and environmental factors to phenotypic variation, accounting for similarities between the local environment of individuals by modelling spatial proximity and breeding environment similarity. I found that the environment experienced by individuals explains around a fifth of the variation seen in reproductive timing, and accounting for this leads to decreased estimates of heritability. In Chapter 3, I considered the social influence on breeding timing and explored how the age of neighbouring individuals in the population affects the variation seen in timing, drawing conclusions on the possible effect of neighbouring birds on a focal bird's timing decisions. I found that adults breed relatively later when their neighbours are also adults, but no evidence that local age structure affects juvenile timing. This may indicate that juveniles do not use social cues from older more experienced birds to time breeding, potentially due to limited phenotypic plasticity. In Chapter 4, I look at the influence of familiarity with breeding partners and breeding sites on breeding timing. I find that birds with either familiar partners, or birds nesting in a familiar nest box, lay earlier relative to a population level measure of laying date. The same pattern was found when considering laying date as mismatch to a local laying average. Interestingly, I found there is however no evidence of an additive effect of having both a familiar partner and nest box, but instead it appears that familiarity with either advances laying similarly. Finally, in Chapter 5, I explore the ecological and individual drivers of multiple breeding attempts within seasons, and discuss how this might be important as a reproductive strategy. I found the occurrence of second breeding attempts in this population is non-random in regards to when individuals are initiating them, and appears to be shaped by individual factors, including age and timing of first-brood failure. I then bring all these areas together in Chapter 6 and discuss how this thesis impacts our knowledge about the causes of intraspecific variation in this population, and what this might mean for other phenological traits more broadly too.

Author Contributions

Chapter 2. **Jones, C.V.**, Regan, C.E., Firth, J.A., Cole, E.F., Sheldon, B.C. (2024). Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits. ***Evolution***, qpae155. https://doi.org/10.1093/evolut/qpae155

> All authors conceptualised the idea. All authors have participated in data collection. CVJ conducted data analysis with input from CER. CVJ produced first draft of the manuscript. CER, EFC, JAF, and BCS provided detailed feedback on methodology, and contributed critically to drafts.

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> JPW and CVJ conceptualised the idea, conducted data analysis and produced first draft of the manuscript. JAF and BCS provided feedback on methodology and the manuscript.This chapter is also submitted as part of joint first author JPW's DPhil Thesis in Trinity Term 2024.

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> CVJ conceptualised the idea, conducted data analysis and produced first draft of the manuscript. CER, JAF and BCS provided feedback on methodology and the manuscript

Chapter 5. **Jones, C.V.**, Regan, C.E., Firth, J.A., Sheldon, B.C. (2025). Predictors of second breeding attempts in a predominantly single brooded bird population *In preparation*

> CVJ conceptualised the idea, conducted data analysis and produced first draft of the manuscript. CER, JAF and BCS provided feedback on methodology and the manuscript

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General Introduction

General Introduction

Intraspecific phenotypic variation

Explaining the diversity we see in phenotypes between individuals is one of the key questions of biology, and has fascinated scientists for hundreds of years (Darwin 1859). Phenotypic variation provides the raw material needed for natural selection (Wilson 1998), and therefore identifying what drives and maintains it is important for understanding ecological and evolutionary processes (Mayr 1961). A phenotype is any observable characteristic of an organism, including but not limited to morphological, behavioural, and physiological traits. Some traits will show no variation between individuals, for example all mammals have the same number of cervical vertebrae. Whereas other traits will show a large amount of continuous variation: these are quantitative traits. Quantitative traits can appear vastly different between individuals within a species or population, for example, the height and weight of people, or the milk yield of cows. Variation in quantitative traits is of particular interest as it is substantial in most populations (Herz et al. 2017; Messier, McGill, and Lechowicz 2010; Violle et al. 2012), and it is in these traits where most microevolutionary change occurs (Falconer and Mackay 1996).

Observing the variation seen in phenotypes between individuals raises many key questions: Why do some traits show so much variation and others do not? What causes the variation we see between individuals? How is this variation maintained in the presence of natural selection? These questions make up a major component of the study of ecology and evolution. Understanding which traits show continuous variation across individuals and why can help us understand how natural selection operates and how species might evolve going forward and in response to change (Houle 1992).

Phenotypic variation is determined by the contribution of genetic and environmental effects, as well as the interaction between the two (genotype x environment interactions) (Boag and van Noordwijk 1987; Falconer and Mackay 1996). This is a simplified interpretation of what is actually a complex combination of many factors, but it can be very useful for understanding the major contributions to phenotypic variation. The proportional contribution of additive genetic variation to phenotypic variation of a trait is the narrow sense heritability (Falconer and Mackay 1996; Lynch and Walsh 1998). The ability to estimate the heritability of a trait can give us the possibility to estimate a population's ability to respond to selection (Houle 1992). As evolution can only occur if a trait is heritable, the genetic aspect of traits was originally the main focus of much research, but to accurately separate out the effect of genotypes on phenotypic variation requires consideration of how phenotypes are influenced by the environment (Boag and van Noordwijk 1987; Falconer and Mackay 1996).

Environmental factors encompass the contribution of any non-genetic effects, including effects of the physical environment, biotic influences of other organisms, and effects of an individual's social environment, and are now understood to make up a large proportion of the phenotypic variation in most quantitative traits (Price and Schluter 1991). These factors can cause changes in the phenotype of individuals during growth and development, and by phenotypic plasticity, when a single genotype can give rise to a range of different phenotypes depending on the conditions that an individual is exposed to (Pigliucci 2005; Schlichting 1986; Via et al. 1995).

Individuals within a population will experience varying physical and social environments; important environmental factors like habitat quality and weather conditions can vary over very small spatial scales (Cole, Regan, and Sheldon 2021; Cole and Sheldon 2017; Matthysen et al. 2021), and social information is most often gathered from individuals in close proximity. This small-scale variation in environments may lead to the expression of different phenotypes, as well as variation in the way selection is imposed across individuals within a population (Visser et al. 2015). The study of small-scale environmental (both physical and social) effects on phenotypic variation is becoming a growing area of interest and is important for determining the causes and consequences of phenotypic variation between individuals.

Phenological traits

Behavioural timing traits, often referred to as phenology, show continuous variation between individuals within the population (Cole and Sheldon 2017; Germain et al. 2016; Matthysen et al. 2021). A wide variety of phenological traits have been studied, including timing of parturition or hibernation in mammals (Maldonado-chaparro et al., 2015; Moyes et al., 2011; Plard et al., 2014), first egg and hatching date in birds (Both et al., 2004; Crick et al., 1997), migration in many species (Crozier et al., 2011; Sirot & Touzalin, 2014; Sokolov et al., 1998), eclosion or hatching date in insects (Ouyang et al., 2016; Yocum et al., 1994), spawning date in fish, reptiles and amphibians (Cushing, 1969; Prodon et al., 2020), and flowering or green up date in plants (Fitter et al., 1995).

Phenology has evolved under the influence of annual and seasonal cycles and the timing of abiotic events, and has far reaching impacts on many aspects of ecology and evolution. Understanding individual level patterns in phenology is vital for understanding the population level patterns we see (Forrest and Miller-Rushing 2010). We interpret the decisions individuals take as having been moulded by selection, such that it results in individuals timing their arrival at a certain development stage with a particular component of its environment, and mistiming can have consequences at the individual level which can also scale to the population level (Visser et al. 2010). For example, individual birds aiming to time breeding with a peak in prey abundance (Visser et al. 1998; Visser, Both, and Lambrechts 2004), or migrating to arrive at a breeding site when there are weather conditions suitable for breeding (Emmenegger et al. 2016), where mistiming of these events will have consequences for breeding success and survival, and thus can scale to changes in population size (Brook et al. 2015; Simmonds et al. 2020; Thomas et al. 2001).

Effect of the environment on variation in a phenological trait

Various aspects of the physical environment experienced by individuals can influence their phenology (Forrest and Miller-Rushing 2010; Pau et al. 2011). This includes abiotic factors such as local habitat composition, food availability, light availability, climatic conditions, altitude or latitude. There are many studies showing changes in timing of phenological traits in response to a changing environment, as climate change is causing shifts in seasons and seasonally variable resources (Cleland et al. 2007; Crick et al. 1997; Hetem et al. 2014). Very often this has been observed as an average change at the population level, using population mean trait values, and in relation to a single measure of the physical environment. For example increasing temperatures have been related to advancement in the mean first flowering date of a range of plant species in southern England (Fitter et al. 1995), earlier mean migration arrival dates of passerine species (Sokolov et al. 1998), and advancement of mean laying date in a wide range of birds (Both et al. 2004). Using population mean values treats the environment as equivalent for all individuals, but in wild systems this is almost never the case. We know that many of these environmental factors will vary on small-scales, and therefore individuals within populations will experience different conditions. For example, the local tree species composition and quality influences the breeding timing of individual blue tits and great tits through affecting the timing of food availability (Matthysen et al. 2021; Wilkin, Perrins, and Sheldon 2007).

Individuals within populations will also be influenced to varying degrees by biotic factors; the effect of other organisms or individuals on a focal individual's phenotype. One important factor are maternal environment effects, these occur when a mother influences her offspring's phenotype in ways other than via direct inheritance of genes (e.g. by prenatal or postnatal effects) (Charmantier, Garant, and Kruuk 2014; Falconer and Mackay 1996). Additionally, phenotypes can be shaped indirectly by social interactions with other individuals, where one individual's behaviour influences the phenotype of another. For example, an individual may experience varying levels of competition from its neighbours over resources, and this can in turn influence their ability to establish a territory and therefore their breeding timing (Minot, 1981; Sirot & Touzalin, 2014). Social interactions might also be governed by the genetics of those they interact with, known as indirect genetic effects (Charmantier et al., 2014). These interactions highlight the complex ways in which biotic factors can contribute to phenotypic variation in populations.

Within this thesis we are interested in understanding how different genetic and environmental factors contribute towards the variation we see in breeding timing within a population. A natural next question is exploring the fitness implications of this variation in breeding timing, for example on within season or overall lifetime breeding success. This further analysis is not within the scope of this thesis, however the following chapters lay the important groundwork for these interesting next steps.

Separating environment and genetic contributions to phenological variation

We know the environment varies spatially, and consideration of this small-scale environmental variation and its effects on individuals' phenotypes may be more biologically realistic. However, there has been limited consideration of how small-scale environmental factors that individuals experience influences their phenology both directly and indirectly.

Quantitative genetics methods have made it possible to separate additive genetic and environmental causes of phenotypic variation using indirect statistical inference techniques (Boag and van Noordwijk 1987; Charmantier et al. 2014; Falconer and Mackay 1996). Built on basic concepts laid down since the early 1900s (Fisher, 1918), quantitative genetic methods rely on the assumption that the inheritance of shared genetic information results in some degree of phenotypic similarity, and that with careful consideration of causal effects the heritability of traits can be estimated (Falconer and Mackay 1996).

The application of quantitative genetic methods to wild populations of animals began in the 1970s (Boag and Grant 1978; Noordwijk and Scharloo 1981; van Noordwijk, van Balen, and Scharloo 1981; Perrins and Jones 1974). Since, they have been used extensively across a range of long-term studies in wild populations, and the genetic contribution to phenotypic variation has been estimated for a number of different phenological traits (e.g. van Noordwijk et al. 1981; Merilä and Sheldon 2000; Van Der Jeugd and McCleery 2002; Teplitsky et al. 2010; Liedvogel et al. 2012; Regan et al. 2017; Lane et al. 2018; Edic et al. 2020; Evans et al. 2020).

In many phenological traits genetic heritability is estimated to be relatively low, but the variation seen in these traits is often large. A substantial proportion of this variation can be explained by phenotypic plasticity driven by the environment (Merilä and Hendry 2014). Untangling these genetic and plastic effects requires the consideration of confounding factors that will upwardly bias the apparent similarity between individuals. Common environment effects occur when the environment has an influence on the phenotype, and related individuals who share genes, also share an environment, potentially leading to overestimation of the direct genetic contribution to phenotypic variation (Germain et al. 2016; Van Der Jeugd and McCleery 2002; Kruuk and Hadfield 2007).

Some studies have attempted to address the non-independence between shared genes and shared environments by incorporating spatial autocorrelation (Kruuk & Hadfield, 2007; Van Der Jeugd & McCleery, 2002), on the assumption that being closer in space is equivalent to sharing a more similar environment. However, this might not always hold true. In many ecological systems the expectation is that places closer together will be more similar, but environments are often complex in their spatial structure. This is particularly important when variation occurs over distances that are relevant to the scales that individual organisms operate. This can lead to instances where individuals that are far apart in space may experience a more similar environment, and individuals close together experiencing a more different environment. By considering solely spatial proximity as a cover all measure for the similarity in environments experienced by individuals this may not capture all that is relevant to determining an individual's phenotype.

The 'animal model', a mixed effects modelling approach, has been used to account for the influence of common environments between individuals, whilst estimating the proportional contribution of additive genetic variation (Kruuk 2004; Wilson et al. 2010). These methods allow the inclusion of individual by individual matrices, used to denote the similarity of various factors between all individuals as pairwise similarities. For example this could be genetic or social relatedness, or some measure of the environment. Specifically, multi-matrix animal models can account for common environment effects by fitting random effects with associated covariance matrices (Thomson et al. 2018). With the development of these methods, there are more studies of wild populations that are now addressing the assumption that spatial proximity is the key factor, or a reliable proxy for environmental similarity, and accounting for space sharing between relatives, using similarity matrices, for example to consider home-range overlap and space sharing between individuals (Germain et al., 2016; Regan et al., 2017; Rutschmann et al., 2020; Stopher et al., 2012).

This approach still overlooks the potential for individuals that share similar environments not being close to one another in space or individuals that are close in space but subject to different environmental conditions. Therefore, to accurately estimate the additive genetic contribution to phenotypic variation, there must be consideration of how phenotypes are influenced by similarities in the environment (both biotic and abiotic) experienced by individuals at an appropriate scale, regardless of their spatial proximity (Jones et al. 2024). Recent approaches using multi-matrix animal models, including a matrix of environmental similarity alongside the matrix of genetic relatedness have begun addressing this issue (Thomson et al. 2018; Gervais et al. 2022). Accounting for common environment effects will be important for understanding how and when heritability estimates may be biased.

Social contribution to variation in a phenological trait

The influence of social interactions has gained increasing attention as a driver of phenotypic variation. Social environments, consisting of interactions with conspecifics and heterospecifics, neighbours, and breeding partners, can significantly affect individual behaviour, often through phenotypic plasticity or indirect genetic effects (Charmantier et al., 2014). Seasonal activities take place in social contexts; for example avian seasonal behaviours are transmitted both actively and inadvertently, via cooperation and competition (Helm, Piersma, and van der Jeugd 2006).

In birds, individuals may use social information from conspecifics to make decisions in relation to breeding timing; male song can enhance the reproductive activity of females, shown in playback experiments both in captivity and in the wild (Bentley et al. 2000; Mota and Depraz 2004), the familiarity of partners can influence laying date (Culina, Firth, and Hinde 2020), and there are various examples of birds using cues for breeding from watching and hearing others (Danchin et al. 2004; Slagsvold 1977; West, King, and White 2003). There is evidence of birds breeding in nestboxes making visits to neighbouring boxes during the breeding season, with females showing a reduction in the number of visits in the lead up to laying (Firth et al., 2018; Santema & Kempenaers, 2023). These visits could provide a possible mechanism for gaining social information from neighbours on the timing of breeding.

Age is a particularly important factor; older individuals often exhibit greater breeding performance, which includes earlier phenological timing, due to accumulated experience. Breeding performance typically improves with age before declining due to senescence. Notably, in many bird species, older individuals tend to breed earlier, as demonstrated in multiple studies (Forslund & Pärt, 1995; Martin, 1995; Mills & Shaw, 1980; Newton, 1989; Nol & Smith, 1987; Sæther, 1990). Despite these findings, there is a limited understanding of how local timing is related to the ages of individuals in their local neighborhood, and the role of age related social mechanisms in mediating this, such as competition effects and social learning.

Social familiarity with individuals and environment

Experience and familiarity with partners, neighbours or environments can also influence an individual's breeding timing. Long term pair bonds can confer a number of benefits, such as improved coordination, reduced conflict, and more efficient resource provisioning (Martin & Shepherdson, 2012; Sánchez-Macouzet et al., 2014). These effects have been shown to sometimes extend to reproductive success, for instance, pair fidelity is linked to higher reproductive success in a number of species, with unfamiliar pairs having reduced breeding success (Leach et al. 2020). However, pair fidelity does not always guarantee better outcomes; in some cases, forming new pair bonds, or "divorce," may enhance reproductive success (Pampus et al., 2004; Culina et al., 2014).

Familiarity extends beyond partners to breeding sites and the surrounding environment. Site fidelity, for example, is a widespread behaviour in birds, with individuals returning to familiar breeding locations year after year (Harvey et al., 1979). Such fidelity may allow individuals to optimise their timing and increase reproductive success. Experience with a specific environment or breeding location can confer significant advantages, where familiarity with local resources and conditions can enhance decision-making and reduce the costs of maladaptive timing (Harvey et al., 1979; Vergara et al., 2006).

Given that climate change is altering phenology across trophic levels, understanding how factors like age, experience, and familiarity shape breeding timing is essential for identifying the drivers of phenotypic plasticity in wild populations.

Age-related variations in breeding timing at both individual and neighborhood levels, along with the potential benefits of familiarity with partners and breeding sites, may play a crucial role in determining an individuals reproductive timing. Investigating these interconnected factors will provide insights into how populations adapt to changing environments and maintain reproductive success.

Multiple reproductive attempts within a season

Many species adopt flexible reproductive strategies, showing variation in the frequency and timing of breeding attempts, with this variation shaped by environmental conditions and individual factors (Stearns, 1992). How can we consider breeding phenology in systems where individuals have multiple breeding attempts? What could the consequences be of only considering an individual's first breeding attempt? Very often breeding timing is assessed as a single measure, such as the timing of an individual's first reproductive attempt in a year. However, this approach may oversimplify the complexity of reproductive behaviour, particularly in species capable of multiple breeding attempts within a single season.

Second breeding attempts can be categorised into "true" and "replacement" second attempts. True second attempts occur following a successful first breeding attempt (from here on referred to as "successive breeding attempts"). These are more common in populations with extended breeding seasons and abundant resources, giving individuals the opportunity to maximize reproductive output within a year (Rowley et al., 1991). Replacement attempts on the other hand are breeding attempts that occur after the failure of a first attempt. These may be particularly important in species that synchronise breeding with resource availability, as they could enable individuals to compensate for a failed first attempt before the season concludes (Yasué & Dearden, 2008). Both successive and replacement breeding attempts are widespread across taxa and may have significant implications for understanding reproductive strategies. For short-lived species with constrained breeding windows, the ability to have a second breeding attempt, both successive and replacement, will be important for maximising lifetime reproductive success (Husby et al., 2009).

The timing and occurrence of second breeding attempts are influenced by a range of individual-level predictors, including age, experience, resource access, and local environmental conditions (Rowley et al., 1991; Stearns, 1976; Yasué & Dearden, 2008). These predictors are rarely random; for example, older or more experienced individuals may be better equipped to initiate second attempts due to improved resource acquisition or previously established pair bonds (Hoffmann et al., 2015). Conversely, environmental factors, such as resource abundance and weather conditions, may constrain or enable second breeding attempts. While studies often focus on first breeding attempts due to the better availability of data, understanding the drivers of second attempts is essential for a comprehensive view of reproductive strategies across species.

Summary

Explaining the phenotypic variation observed between individuals in phenological traits is clearly complex. With the contribution of both genetic and environmental effects and their interactions providing important information about the evolutionary potential of traits, and the causes and consequences of how organisms can respond to environmental change. Considering the scale of environmental effects, the similarity in environments experienced by individuals, and the impacts of social information use is important for determining the causes and consequences of phenotypic variation between individuals. To do this requires detailed data collected over time and space, with unique individuals identified and detailed information gathered on their breeding attempts.

Study system

The extensively studied great tit *(Parus major)* population in Wytham Woods, Oxfordshire, provides a useful system in which to study the genetic and environmental drivers of phenological variation as there are data on timing of breeding of individuals over many generations, as well as individual level environmental and social data.

The great tits are part of a tri-trophic system, where they rely on timing their breeding with both a primary producer and a primary consumer. The emergence of new leaves on deciduous trees (primary producer) within the woodland is followed by a peak in phytophagous insects (primary consumer), which are relied on by the tits to feed their growing chicks in the nest. In this system one of the main insects is the winter moth caterpillar *(Opheroptera brumata)*, and the main tree is oak *(Quercus robur)*. It is advantageous for the birds to coincide their peak energy requirements, when chicks are approximately 8-10 days old, with the peak in caterpillar abundance. If they are too early or too late, there is not enough food to successfully raise chicks to fledging (Gienapp et al., 2013; Visser et al., 2004, 2006).

The timing of breeding has been found to be heritable in this population (Evans et al., 2020; Garant et al., 2008; Liedvogel et al., 2012; Van Der Jeugd & McCleery, 2002). It is also highly plastic, with phenotypic plasticity playing a key role in the adjustment of great tit breeding timing to track environmental change (Charmantier et al., 2008; Vedder et al., 2013). There are multiple examples of the environment at small spatial scales having important effects on phenology, including effects of altitude, aspect and proximity to oak trees (Wilkin et al., 2006, 2007), and the rate of change in laying date can be linked to local oak tree health (Cole et al., 2021). Furthermore, great tit breeding timing has been correlated with local variation in trees, including in timing of green up (Cole et al., 2015; Cole & Sheldon, 2017), and composition of species (Matthysen et al., 2021).

Great tits live in a complex social system with social monogamy and territoriality (Aplin et al., 2012; Krebs, 1982; Slagsvold, 1993). Individuals interact with one another and influence each other's behaviour. Great tit pairs meeting earlier before the breeding season have been shown to breed significantly earlier (Culina et al., 2020). Furthermore, familiarity with neighbours during the breeding season also has benefits for fledgling's success (Grabowska-Zhang et al., 2012).

Long-term breeding data

Great tits are secondary cavity nesters; in this population they preferentially choose to breed in the nest boxes placed throughout the woods. There are 1019 nest boxes (shown in Figure 1) which can be used by great tits, and have been monitored for over 60 years, with life history traits recorded following a standardised protocol (Perrins, 1965). Each year about 60% of the nest boxes are occupied and monitored over the breeding season (March-May). Data collected include laying date of first egg, hatching date, and breeding location; an overview of when and how these data are collected is show in Table 1.

Table 1 – Breeding Season Data Collection Summary: An overview of when, what and how data are collected at nest boxes over the breeding season.

Timeline	What recorded?	How?
1st egg	Date of 1st egg as April Days (April 1st = 1)	If multiple eggs laid count back assuming 1 egg laid each day
Onset of incubation	Date female starts incubating eggs Female ID if PIT tagged	Visit eggs regularly until they are found to be incubated by female or are warm to the touch. If female sits tight on nest her PIT tag can be recorded.
Hatching date = Chicks day 1	Date of first egg hatching	Visit approx. 12 days after incubation began, if not yet hatched visit again the next day. If eggs are all hatched weigh chicks to estimate when they hatched.
Chicks day 5	ID of parents if PIT tagged	Use RFID readers around nest box entrance to record visits of adults, if they are PIT tagged their ID will be recorded.
Chicks days 11-14	ID of parents who were not PIT tagged	Use traps or rushing to catch parents whilst feeding chicks, to ring (BTO ring and PIT tag), age and sex them
Chicks day 15	Ring chicks with BTO ring and PIT tag. Weigh all chicks	Ring chicks at nest

Timeline	What recorded?	How?
Chicks day 23+	Number of chicks fledged	Check boxes to see if they are empty. If any dead chicks left inside record their ring numbers.

Great tits *(Parus major)* are facultative multibrooders; multibrooding is common in mainland Europe, and less frequent in the UK (Bukor et al., 2021). Laying date is defined as the day the first egg was laid, assuming that females lay one egg a day early in the morning. Nest boxes are visited at least once a week until a first egg is found, if there is more than one egg the date of first egg is inferred by counting back one egg per day. Hatching date is defined as the day the first egg was hatched. After the onset of incubation, the nests are not visited until the estimated hatching date, 12 days after. As incubation duration can vary, this may not always be accurate, so if no eggs are hatched yet nests are visited every other day until there are chicks or the nest is declared abandoned. If the chicks are not obviously freshly hatched their weight is used to estimate their hatching date, against data known about the species. Sometimes there can be asynchronous hatching, meaning some chicks hatch over a few days, so this adds a slight uncertainty to the estimates. Dates are recorded in April Days (1st April = 1).

Birds are uniquely identified with metal BTO (British Trust for Ornithology) rings and since 2007 all birds are also fitted with plastic rings which contain a passive integrated transponder (PIT tag). When these rings come within a short distance of Radio Frequency Identification (RFID) antennae they transmit a code unique to that bird. These RFID antennae can be placed on bird feeders, or around nest box entrance holes, allowing identification of individuals without the need to catch them. All nestlings are ringed before they leave the nest, and parents are identified (either remotely, using RFID tag readers or via trapping) during the nestling phase. For nests that are failed or abandoned before fledging often only mother ID is recorded. Mist netting is carried out over the winter to catch and ring as many immigrant birds as possible, so there is more chance of breeding birds being ringed already and therefore easier to identify.

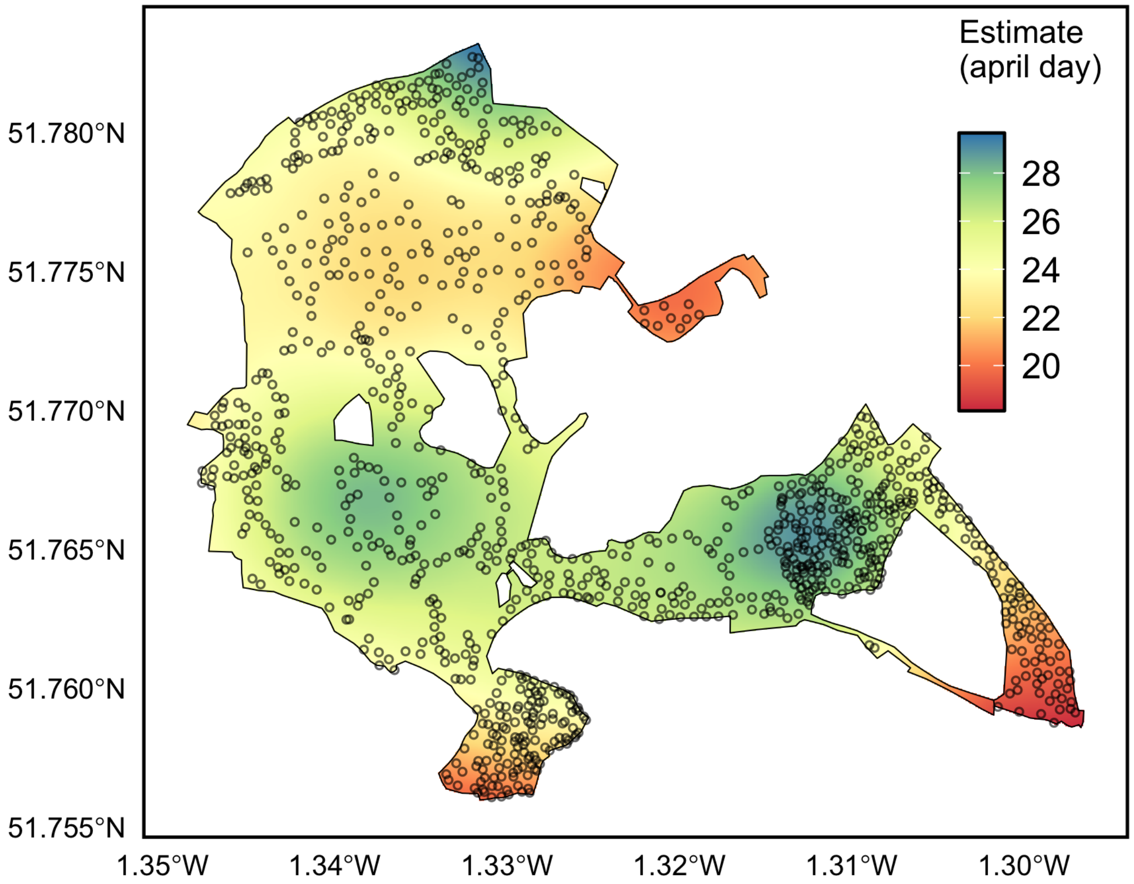

Figure 1: Estimation of first egg date across Wytham Woods - posterior conditional effects of spatial predictor across 3 years of data (2014-2016), this represents well the variation in timing seen across the woods as local timing is repeatable over years. April day: 1st April = 1. Each circle represents a nest box.

Overall there are 17,996 recorded breeding attempts over 63 years (1960-2022). 15,279 attempts have a recorded laying date, and 11,658 of those have a mother identified. Identification of individuals at the nest box has allowed the creation of a pedigree across many years. It is assumed that the adult birds seen incubating or feeding chicks at a nest are the biological parents. There are low levels of extra-pair paternity recorded in this population and it is not thought to have significant influence on quantitative genetic methods and estimates of heritability (Firth et al., 2015; Patrick et al., 2012). The full pedigree is made up of 99,239 individuals. This cut down to an informative pedigree (only including those birds that have a laying date recorded and their relatives who would contribute to the estimation of quantitative genetic parameters) includes 15,744 individuals and spans 37 generations, with 7,791 maternities and 7,078 paternities, 4,411 full siblings, 3,221 maternal half siblings and 2,318 paternal half siblings. This translates to 79% of records with a known mother recorded, and 59% with both a known mother and father.

Environmental data

Wytham Woods is a 385ha mixed deciduous woodland, surrounded by farmlands. The location of all boxes throughout the woods are shown in Figure 1. For each box we know their coordinates, aspect, northness, altitude, edgeness (proximity to edge of woodland), and data on the surrounding habitat type and local oak tree density. Boxes remain in the same location unless a tree falls down, in which case they are placed back up on the nearest suitable tree. There is a known altitudinal effect on breeding timing (Wilkin et al., 2006, 2007). Across the woods there is a 102.5m range in altitude, and a linear regression of altitude on laying date shows that laying date gets later by 0.031 days per metre (which translates to a 3-day difference between the birds at highest and lowest altitudes). However, when potentially confounding factors, like spring temperature and aspect are controlled for, this estimate decreases, leaving about 1 day attributable to altitude, and the rest to other environmental factors that vary within the landscape (Wilkin et al., 2007). These other environmental effects that have been shown in the Wytham great tits include: birds that breed in boxes with a northerly aspect and Oak-rich areas tend to on average breeding earlier (Wilkin et al., 2007), and birds with smaller territories have on average a later laying date (Wilkin et al., 2006). Within the woods there is local variation in the green up of trees, with individual trees showing repeatable variation between years (Cole & Sheldon, 2017). Individual differences in breeding time are significantly explained by the local vegetation green-up and health, suggesting birds time their breeding specifically with local tree phenology (Cole et al., 2015, 2021).

Variation in breeding timing in this population

In Wytham, first egg laying date has advanced almost 2 weeks over 60 years (Cole et al., 2021). In addition to this long-term trend, great tit breeding timing in the Wytham population varies greatly between years, and between individuals within years, as shown in Figure 2. For example, the years highlighted in red boxes, 1984 and 1987, show a contrast in amplitude at the mode. In 1984 the breeding season showed a greater variation in laying. Whereas in 1987 there was a very steep peak around the mean, and less variation between individuals. The years highlighted in orange, 2013 and 2014, show a contrast in the timings, 2013 was a late year, with the peak in laying coming after the overall mean date, whereas 2014 was a particularly early year, with the peaks sitting to the left of the mean lines. There is also variation across space within the woods, with some areas more often being relatively early or later, Figure 1 shows the variation in first egg laying date across the woods over a subset of 3 years, but this pattern is reflected similarly across most study years. This very clearly demonstrates the variation that occurs in timing of breeding between years but also between individuals within years.

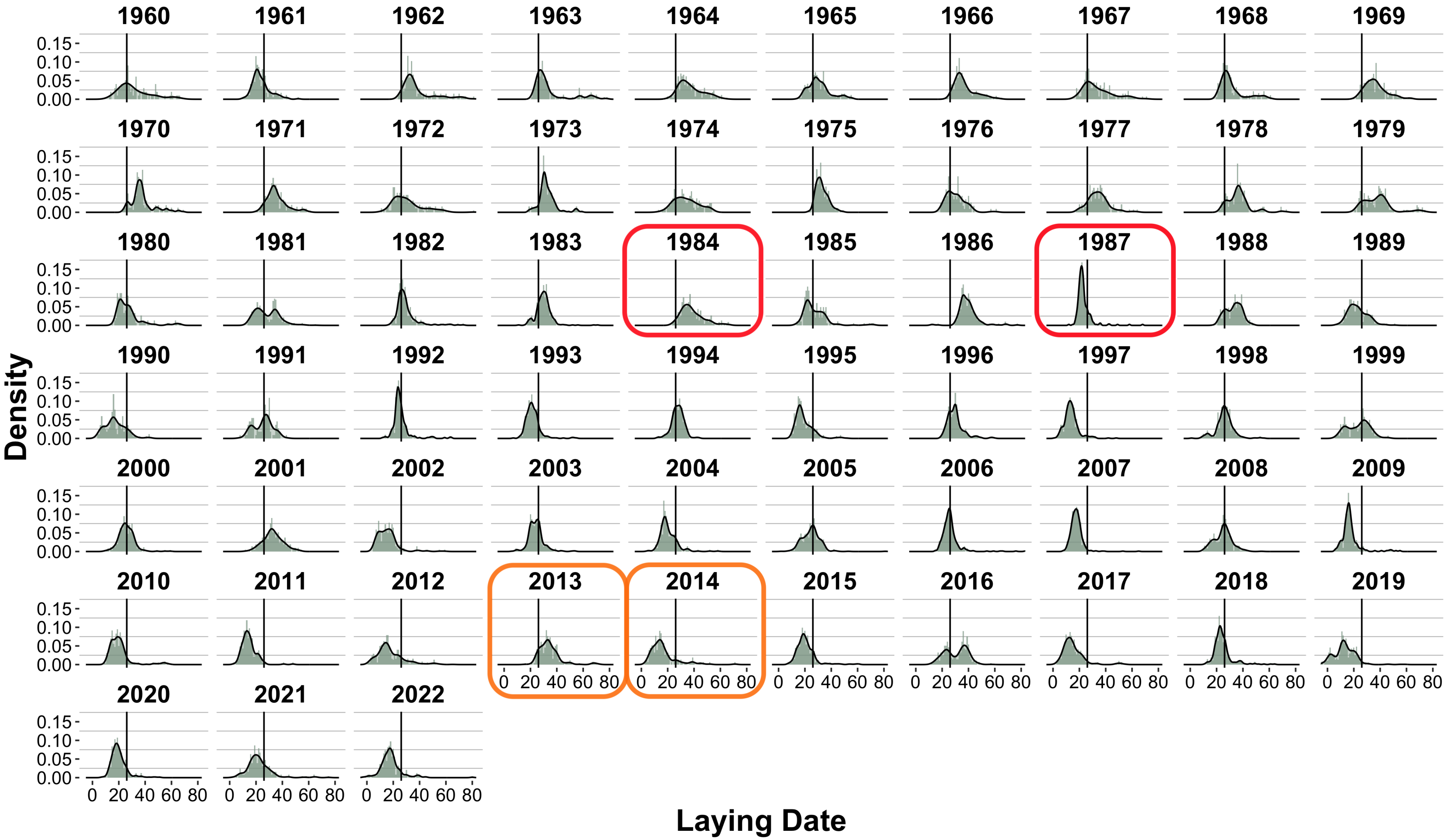

Figure 2: Distributions of first egg laying date and hatching dates of great tits over 63 years in Wytham Woods, plotted as April dates (1st April = 1). The red and orange boxes highlight some particularly interesting years in terms of variation in the distribution, described further in the text. Each vertical line shows the overall mean over all study years of laying date, to make it easier to visualise how the annual mean varies over time. N = 15,279 first breeding attempts.

Thesis aims

The overarching aim of this body of work was to investigate the genetic, environmental and social drivers of breeding timing in a population of wild birds. In **Chapter 2** to estimate the genetic contribution to breeding timing we used quantitative genetic methods to assess heritability of timing of breeding in the Wytham great tit population. I used animal models, which can account for the relatedness between all individuals and consider fixed and random effects to quantify the relative contributions of additive genetic and environmental factors to phenotypic variation. I account for similarities between the local environment of individuals by modelling spatial proximity and habitat similarity. In **Chapter 3**, to consider the social influence on breeding timing, I explored how age assortment in the population affects the variation seen in timing, and try to draw conclusions of the possible effect of neighbouring birds on a focal bird's timing. Furthermore, in **Chapter 4** I investigate the influence of familiarity with breeding partners and breeding sites on breeding timing. The chapters so far focus on an individual's first reproductive attempt in a season, however some individuals will have multiple reproductive attempts a year, so in **Chapter 5** I explore how common this is in this population, and the individual and ecological factors that explain the variation we see in its occurrence. I will then bring all these areas together in **Chapter 6** and discuss how this impacts our knowledge about causes of intraspecific variation in this population and in phenological traits in general, and point to avenues for future research building on the work in this thesis.

References

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society B: Biological Sciences, 279(1745), 4199–4205. https://doi.org/10.1098/rspb.2012.1591

Bentley, G. E., Wingfield, J. C., Morton, M. L., & Ball, G. F. (2000). Stimulatory effects on the reproductive axis in female songbirds by conspecific and heterospecific male song. Hormones and Behavior, 37(3), 179–189. https://doi.org/10.1006/hbeh.2000.1573

Boag, P. T., & Grant, P. R. (1978). Heritability of external morphology in Darwin ' s finches Photoreceptor shedding can be initiated within the eye. 274(August), 793–794.

Boag, P. T., & van Noordwijk, A. J. (1987). Quantitative Genetics. In Avian Genetics. https://doi.org/10.1016/b978-0-12-187571-8.50009-5

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Järvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P. A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Török, J., . . . Visser, M. E. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society B: Biological Sciences, 271(1549), 1657–1662. https://doi.org/10.1098/rspb.2004.2770

Brook, R. W., Leafloor, J. O., Abraham, K. F., & Douglas, D. C. (2015). Density dependence and phenological mismatch: Consequences for growth and survival of sub-arctic nesting Canada Geese. 10(1). https://doi.org/10.5751/ACE-00708-100101

Bukor, B., Seress, G., Pipoly, I., Sándor, K., Sinkovics, C., Vincze, E., & Liker, A. (2021). Double-brooding and annual breeding success of great tits in urban and forest habitats. Current Zoology, 68(5), 517–525. https://doi.org/10.1093/cz/zoab096

Charmantier, A., Garant, D., & Kruuk, L. E. B. (2014). Quantitative Genetics In The Wild. Oxford University Press.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science, 320(5877), 800–803. https://doi.org/10.1126/science.1157174

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. Trends in Ecology and Evolution, 22(7), 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Cole, E. F., Long, P. R., Zelazowski, P., Szulkin, M., & Sheldon, B. C. (2015). Predicting bird phenology from space: Satellite-derived vegetation green-up signal uncovers spatial variation in phenological synchrony between birds and their environment. Ecology and Evolution, 5(21), 5057–5074. https://doi.org/10.1002/ece3.1745

Cole, E. F., Regan, C. E., & Sheldon, B. C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. Nature Climate Change, 11(10), 872–878. https://doi.org/10.1038/s41558-021-01140-4

Cole, E. F., & Sheldon, B. C. (2017). The shifting phenological landscape: Within- and between-species variation in leaf emergence in a mixed-deciduous woodland. Ecology and Evolution, 7(4), 1135–1147. https://doi.org/10.1002/ece3.2718

Crick, H. Q. P., Dudley, C., Glue, D. E., & Thomson, D. L. (1997). UK birds are laying eggs earlier. Nature, 388, 526–527.

Crozier, L. G., Scheuerell, M. D., & Zabel, R. W. (2011). Using time series analysis to characterize evolutionary and plastic responses to environmental change: A case study of a shift toward earlier migration date in sockeye salmon. American Naturalist, 178(6), 755–773. https://doi.org/10.1086/662669

Culina, A., Firth, J. A., & Hinde, C. A. (2020). Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population: Pairs that meet earlier do better. Proceedings of the Royal Society B: Biological Sciences, 287(1941). https://doi.org/10.1098/rspb.2020.1554rspb20201554

Culina, A., Radersma, R., & Sheldon, B. C. (2015). Trading up: The fitness consequences of divorce in monogamous birds. Biological Reviews, 90(4), 1015–1034. https://doi.org/10.1111/brv.12143

Cushing, D. H. (1969). The Regularity of the Spawning Season of Some Fishes. ICES Journal of Marine Science, 33(1), 81–92. https://doi.org/10.1093/icesjms/33.1.81

Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). From Nosy Neighbors to Cultural Evolution. Science, 305(5683), 487–491.

Edic, M. N., Martin, J. G. A., & Blumstein, D. T. (2020). Heritable variation in the timing of emergence from hibernation. Evolutionary Ecology, 34(5), 763–776. https://doi.org/10.1007/s10682-020-10060-2

Emmenegger, T., Hahn, S., Arlettaz, R., Amrhein, V., Zehtindjiev, P., & Bauer, S. (2016). Shifts in vegetation phenology along flyways entail varying risks of mistiming in a migratory songbird. Ecosphere, 7(6), 1–9. https://doi.org/10.1002/ecs2.1385

Evans, S. R., Postma, E., & Sheldon, B. C. (2020). It takes two: Heritable male effects on reproductive timing but not clutch size in a wild bird population*. Evolution, 74(10), 2320–2331. https://doi.org/10.1111/evo.13980

Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to Quantitative Genetics. Longman Group Ltd.

Firth, J. A., Hadfield, J. D., Santure, A. W., Slate, J., & Sheldon, B. C. (2015). The influence of nonrandom extra-pair paternity on heritability estimates derived from wild pedigrees. Evolution, 69(5), 1336–1344. https://doi.org/10.1111/evo.12649

Firth, J. A., Verhelst, B. L., Crates, R. A., Garroway, C. J., & Sheldon, B. C. (2018). Spatial, temporal and individual-based differences in nest-site visits and subsequent reproductive success in wild great tits. Journal of Avian Biology, 49(10), e01740. https://doi.org/10.1111/jav.01740

Fitter, A. H., Fitter, R. S. R., Harris, I. T. B., & Williamson, M. H. (1995). Relationships between first flowering date and temperature in the flora of a locality in Central England. Functional Ecology, 9(1), 55–60.

Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1555), 3101–3112. https://doi.org/10.1098/rstb.2010.0145

Forslund, P., & Pärt, T. (1995). Age and reproduction in birds—Hypotheses and tests. Trends in Ecology & Evolution, 10(9), 374–378. https://doi.org/10.1016/S0169-5347(00)89141-7

Garant, D., Hadfield, J. D., Kruuk, L. E. B., & Sheldon, B. C. (2008). Stability of genetic variance and covariance for reproductive characters in the face of climate change in a wild bird population. Molecular Ecology, 17(1), 179–188. https://doi.org/10.1111/j.1365-294X.2007.03436.x

Germain, R. R., Wolak, M. E., Arcese, P., Losdat, S., & Reid, J. M. (2016). Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows. Journal of Animal Ecology, 85(6), 1613–1624. https://doi.org/10.1111/1365-2656.12575

Gervais, L., Morellet, N., David, I., Hewison, A. J. M., Réale, D., Goulard, M., Chaval, Y., Lourtet, B., Cargnelutti, B., Merlet, J., Quéméré, E., & Pujol, B. (2022). Quantifying heritability and estimating evolutionary potential in the wild when individuals that share genes also share environments. Journal of Animal Ecology, 0–2. https://doi.org/10.1111/1365-2656.13677

Gienapp, P., Lof, M., Reed, T. E., McNamara, J., Verhulst, S., & Visser, M. E. (2013). Predicting demographically sustainable rates of adaptation: Can great tit breeding time keep pace with climate change? Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1610). https://doi.org/10.1098/rstb.2012.0289

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2008). Climate change and evolution: Disentangling environmental and genetic responses. Molecular Ecology, 17, 167–178. https://doi.org/10.1111/j.1365-294X.2007.03413.x

Grabowska-Zhang, A. M., Wilkin, T. A., & Sheldon, B. C. (2012). Effects of neighbor familiarity on reproductive success in the great tit *(Parus major)*. Behavioral Ecology, 23(2), 322–333. https://doi.org/10.1093/beheco/arr189

Harvey, P. H., Greenwood, P. T., & Perrins, C. M. (1979). The Role of Dispersal in the Great Tit *(Parus major)*. Journal of Animal Ecology, 48, 305–313.

Helm, B., Piersma, T., & van der Jeugd, H. (2006). Sociable schedules: Interplay between avian seasonal and social behaviour. Animal Behaviour, 72(2), 245–262. https://doi.org/10.1016/j.anbehav.2005.12.007

Herz, K., Dietz, S., Haider, S., Jandt, U., Scheel, D., & Bruelheide, H. (2017). Drivers of intraspecific trait variation of grass and forb species in German meadows and pastures. Journal of Vegetation Science, 28(4), 705–716. https://doi.org/10.1111/jvs.12534

Hetem, R. S., Fuller, A., Maloney, S. K., & Mitchell, D. (2014). Responses of large mammals to climate change. Temperature, 1(2), 115–127. https://doi.org/10.4161/temp.29651

Hoffmann, J., Postma, E., & Schaub, M. (2015). Factors influencing double brooding in Eurasian Hoopoes Upupa epops. Ibis, 157(1), 17–30. https://doi.org/10.1111/ibi.12188

Houle, D. (1992). Comparing evolvability and variability. Genetics, 130(1), 195–204.

Husby, A., Kruuk, L. E. B., & Visser, M. E. (2009). Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. Proceedings of the Royal Society B: Biological Sciences, 276(1663), 1845–1854. https://doi.org/10.1098/rspb.2008.1937

Jones, C. V., Regan, C. E., Cole, E. F., Firth, J. A., & Sheldon, B. C. (2024). Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits. Evolution, qpae155. https://doi.org/10.1093/evolut/qpae155

Krebs, J. R. (1982). Territorial defence in the great tit *(Parus major)*: Do residents always win? Behavioral Ecology and Sociobiology, 11(3), 185–194. https://doi.org/10.1007/BF00300061

Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the 'animal model'. Philosophical Transactions of the Royal Society B: Biological Sciences, 359(1446), 873–890. https://doi.org/10.1098/rstb.2003.1437

Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. Journal of Evolutionary Biology, 20(5), 1890–1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Lane, J. E., McAdam, A. G., McFarlane, S. E., Williams, C. T., Humphries, M. M., Coltman, D. W., Gorrell, J. C., & Boutin, S. (2018). Phenological shifts in North American red squirrels: Disentangling the roles of phenotypic plasticity and microevolution. Journal of Evolutionary Biology, 31(6), 810–821. https://doi.org/10.1111/jeb.13263

Leach, A. G., Riecke, T. V., Sedinger, J. S., Ward, D. H., & Boyd, S. (2020). Mate fidelity improves survival and breeding propensity of a long-lived bird. Journal of Animal Ecology, 89(10), 2290–2299. https://doi.org/10.1111/1365-2656.13286

Liedvogel, M., Cornwallis, C. K., & Sheldon, B. C. (2012). Integrating candidate gene and quantitative genetic approaches to understand variation in timing of breeding in wild tit populations. Journal of Evolutionary Biology, 25(5), 813–823. https://doi.org/10.1111/j.1420-9101.2012.02480.x

Lynch, M., & Walsh, B. (1998). Genetics and Analysis of Quantitative Traits. Sinauer Associates, Inc.

Maldonado-chaparro, A. A., Martin, J. G. A., Armitage, K. B., Oli, M. K., & Blumstein, D. T. (2015). Environmentally induced phenotypic variation in wild yellow-bellied marmots. 96(2), 269–278. https://doi.org/10.1093/jmammal/gyu006

Martin, M. S., & Shepherdson, D. J. (2012). Role of Familiarity and Preference in Reproductive Success in Ex Situ Breeding Programs. Conservation Biology, 26(4), 649–656. https://doi.org/10.1111/j.1523-1739.2012.01880.x

Matthysen, E., Adriaensen, F., Van de Kerckhove, P., & Vandekerkhove, K. (2021). Great and blue tit laying dates vary with fine-scale variation in local tree composition but not tree budburst. Journal of Ornithology, 162(3), 709–722. https://doi.org/10.1007/s10336-021-01872-2

Mayr, E. (1961). Causes and Effect in Biology. Science, 134, 1501–1506.

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. Evolutionary Applications, 7(1), 1–14. https://doi.org/10.1111/eva.12137

Merilä, J., & Sheldon, B. C. (2000). Lifetime reproductive success and heritability in nature. American Naturalist, 155(3), 307–310. https://doi.org/10.1086/303330

Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. Ecology Letters, 13(7), 838–848. https://doi.org/10.1111/j.1461-0248.2010.01476.x

Mills, J. A., & Shaw, P. W. (1980). The influence of age on laying date, clutch size, and egg size of the white-fronted tern, Sterna striata. New Zealand Journal of Zoology, 7(1), 147–153. https://doi.org/10.1080/03014223.1980.10423772

Minot, E. O. (1981). Effects of Interspecific Competition for Food in Breeding Blue and Great Tits. Journal of Animal Ecology, 50(2), 375–385. https://doi.org/10.2307/4061

Mota, P. G., & Depraz, V. (2004). A Test of the Effect of Male Song on Female Nesting Behaviour in the Serin (Serinus serinus): A Field Playback Experiment. Ethology, 110, 841–850.

Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., Morris, S., Pemberton, J. M., Kruuk, L. E. B., & Clutton-Brock, T. H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. Global Change Biology, 17(7), 2455–2469. https://doi.org/10.1111/j.1365-2486.2010.02382.x

Nol, E., & Smith, J. N. M. (1987). Effects of Age and Breeding Experience on Seasonal Reproductive Success in the Song Sparrow. Journal of Animal Ecology, 56(1), 301–313. https://doi.org/10.2307/4816

Noordwijk, A. J. V., & Scharloo, W. (1981). Inbreeding in an Island Population of the Great Tit. Evolution, 35(4), 674. https://doi.org/10.2307/2408240

Ouyang, F., Hui, C., Men, X., Zhang, Y., Fan, L., Shi, P., Zhao, Z., & Ge, F. (2016). Early eclosion of overwintering cotton bollworm moths from warming temperatures accentuates yield loss in wheat. Agriculture, Ecosystems & Environment, 217, 89–98. https://doi.org/10.1016/j.agee.2015.11.010

Pampus, M., Schmidt, K.-H., & Wiltschko, W. (2005). Pair bond and breeding success in Blue Tits *(Parus caeruleus)* and Great Tits *(Parus major)*. Ibis, 147(1), 92–108. https://doi.org/10.1111/j.1474-919x.2004.00376.x

Patrick, S. C., Chapman, J. R., Dugdale, H. L., Quinn, J. L., & Sheldon, B. C. (2012). Promiscuity, paternity and personality in the great tit. Proceedings of the Royal Society B: Biological Sciences, 279(1734), 1724–1730. https://doi.org/10.1098/rspb.2011.1820

Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., Betancourt, J. L., & Cleland, E. E. (2011). Predicting phenology by integrating ecology, evolution and climate science. Global Change Biology, 17(12), 3633–3643. https://doi.org/10.1111/j.1365-2486.2011.02515.x

Perrins, C. M. (1965). Population Fluctuations and Clutch-Size in the Great Tit. Journal of Animal Ecology, 34(3), 601–647.

Perrins, C. M., & Jones, P. J. (1974). The Inheritance of Clutch Size in the Great Tit *(Parus major L .)*. The Condor, 76(2), 225–229.

Pigliucci, M. (2005). Evolution of phenotypic plasticity: Where are we going now? Trends in Ecology and Evolution, 20(9), 481–486. https://doi.org/10.1016/j.tree.2005.06.001

Plard, F., Gaillard, J. M., Coulson, T., Hewison, A. J. M., Delorme, D., Warnant, C., & Bonenfant, C. (2014). Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. PLoS Biology, 12(4), 1–8. https://doi.org/10.1371/journal.pbio.1001828

Price, T., & Schluter, D. (1991). On the low heritability of life-history traits. Evolution, 45(4), 853–861. https://doi.org/10.1111/j.1558-5646.1991.tb04354.x

Prodon, R., Geniez, P., Cheylan, M., & Besnard, A. (2020). Amphibian and reptile phenology: The end of the warming hiatus and the influence of the NAO in the North Mediterranean. International Journal of Biometeorology, 64(3), 423–432. https://doi.org/10.1007/s00484-019-01827-6

Regan, C. E., Pilkington, J. G., Bérénos, C., Pemberton, J. M., Smiseth, P. T., & Wilson, A. J. (2017). Accounting for female space sharing in St. Kilda Soay sheep (Ovis aries) results in little change in heritability estimates. Journal of Evolutionary Biology, 30(1), 96–111. https://doi.org/10.1111/jeb.12990

Rowley, I., Brooker, M., & Russell, E. (1991). The Breeding Biology of the Splendid Fairy-wren Malurus splendens: The Significance of Multiple Broods. Emu, 91(4), 197–221. https://doi.org/10.1071/mu9910197

Rutschmann, A., de Villemereuil, P., Brekke, P., Ewen, J. G., Anderson, N., & Santure, A. W. (2020). Consequences of space sharing on individual phenotypes in the New Zealand hihi. Evolutionary Ecology, 34(5), 821–839. https://doi.org/10.1007/s10682-020-10063-z

Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: Pair bond duration increases individual fitness independent of age-related variation. 281. https://doi.org/10.1098/rspb.2013.2843

Santema, P., & Kempenaers, B. (2023). Patterns of extra-territorial nest-box visits in a songbird suggest a role in extrapair mating. Behavioral Ecology, 34(1), 150–159. https://doi.org/10.1093/beheco/arac111

Schlichting, C. D. (1986). The Evolution Of Phenotypic Plasticity In Plants. Annual Review of Ecology and Systematics, 17, 667–693. https://doi.org/10.1093/cz/zow084

Simmonds, E. G., Cole, E. F., Sheldon, B. C., & Coulson, T. (2020). Testing the effect of quantitative genetic inheritance in structured models on projections of population dynamics. Oikos, 129(4), 559–571. https://doi.org/10.1111/oik.06985

Sirot, E., & Touzalin, F. (2014). Temporal patterns of arrival from migration as a response to competition for breeding space. Journal of Avian Biology, 45(1), 109–112. https://doi.org/10.1111/j.1600-048X.2013.00184.x

Slagsvold, T. (1977). Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. Ornis Scandinavica, 8(2), 197–222.

Slagsvold, T. (1993). Female-Female Aggression and Monogamy in Great Tits *(Parus major.)* Ornis Scandinavica (Scandinavian Journal of Ornithology), 24(2), 155–158. https://doi.org/10.2307/3676366

Sokolov, L. V., Markovets, M. Y., Shapoval, A. P., & Morozov, Y. G. (1998). Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. Avian Ecology and Behaviour, 1, 1–21.

Stearns, S. C. (1976). Life-History Tactics: A Review of the Ideas. The Quarterly Review of Biology. https://doi.org/10.1086/409052

Stearns, S. C. (1992). The Evolution of Life Histories. Oxford University Press. https://doi.org/10.1046/j.1420-9101.1993.6020304.x

Stopher, K. V., Walling, C. A., Morris, A., Guinness, F. E., Clutton-Brock, T. H., Pemberton, J. M., & Nussey, D. H. (2012). Shared spatial effects on quantitative genetic parameters: Accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. Evolution, 66(8), 2411–2426. https://doi.org/10.1111/j.1558-5646.2012.01620.x

Teplitsky, C., Mills, J. A., Yarrall, J. W., & Merilä, J. (2010). Indirect genetic effects in a sex-limited trait: The case of breeding time in red-billed gulls. Journal of Evolutionary Biology, 23(5), 935–944. https://doi.org/10.1111/j.1420-9101.2010.01959.x

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M., & Speakman, J. R. (2001). Energetic and Fitness Costs of Mismatching Resource Supply and Demand in Seasonally Breeding Birds. Science, 291(5513), 2598–2600. https://doi.org/10.1126/science.1057487

Thomson, C. E., Winney, I. S., Salles, O. C., & Pujol, B. (2018). A guide to using a multiple-matrix animal model to disentangle genetic and nongenetic causes of phenotypic variance. PLOS ONE, 13(10), e0197720. https://doi.org/10.1371/journal.pone.0197720

Van Der Jeugd, H. P., & McCleery, R. (2002). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. Journal of Evolutionary Biology, 15(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

van Noordwijk, A. J., van Balen, J. H., & Scharloo, W. (1981). Genetic variation in the timing of reproduction in the Great Tit. Oecologia, 49(2), 158–166. https://doi.org/10.1007/BF00349183

Vedder, O., Bouwhuis, S., & Sheldon, B. C. (2013). Quantitative Assessment of the Importance of Phenotypic Plasticity in Adaptation to Climate Change in Wild Bird Populations. PLoS Biology, 11(7), 1–10. https://doi.org/10.1371/journal.pbio.1001605

Vergara, P., Aguirre, J. I., Fargallo, J. A., & Dávila, J. A. (2006). Nest-site fidelity and breeding success in White Stork Ciconia ciconia. Ibis, 148(4), 672–677. https://doi.org/10.1111/j.1474-919X.2006.00565.x

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., & Van Tienderen, P. H. (1995). Adaptive phenotypic plasticity: Consensus and controversy. Trends in Ecology & Evolution, 10(5), 212–217. https://doi.org/10.1016/S0169-5347(00)89061-8

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. Trends in Ecology and Evolution, 27(4), 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Visser, M. E., Both, C., & Lambrechts, M. M. (2004). Global Climate Change Leads to Mistimed Avian Reproduction. Advances in Ecological Research, 35, 89–110. https://doi.org/10.1016/S0065-2504(04)35005-1

Visser, M. E., Caro, S. P., Oers, K. V., Schaper, S. V., & Helm, B. (2010). Phenology, seasonal timing and circannual rhythms: Towards a unified framework. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1555), 3113–3127. https://doi.org/10.1098/rstb.2010.0111

Visser, M. E., Gienapp, P., Husby, A., Morrisey, M., de la Hera, I., Pulido, F., & Both, C. (2015). Effects of Spring Temperatures on the Strength of Selection on Timing of Reproduction in a Long-Distance Migratory Bird. PLoS Biology, 13(4), 1–17. https://doi.org/10.1371/journal.pbio.1002120

Visser, M. E., Holleman, L. J. M., & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia, 147(1), 164–172. https://doi.org/10.1007/s00442-005-0299-6

Visser, M. E., Van Noordwijk, A. J., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits *(Parus major)*. Proceedings of the Royal Society B: Biological Sciences, 265(1408), 1867–1870. https://doi.org/10.1098/rspb.1998.0514

West, M. J., King, A. P., & White, D. J. (2003). The case for developmental ecology. Animal Behaviour, 66(4), 617–622. https://doi.org/10.1006/anbe.2003.2221

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2006). Density effects on life-history traits in a wild population of the great tit Parus major: Analyses of long-term data with GIS techniques. Journal of Animal Ecology, 75(2), 604–615. https://doi.org/10.1111/j.1365-2656.2006.01078.x

Wilkin, T. A., Perrins, C. M., & Sheldon, B. C. (2007). The use of GIS in estimating spatial variation in habitat quality: A case study of lay-date in the Great Tit *(Parus major)*. Ibis, 149(SUPPL. 2), 110–118. https://doi.org/10.1111/j.1474-919X.2007.00757.x

Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B., & Nussey, D. H. (2010). An ecologist's guide to the animal model. Journal of Animal Ecology, 79(1), 13–26. https://doi.org/10.1111/j.1365-2656.2009.01639.x

Wilson, D. S. (1998). Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society B: Biological Sciences, 353(1366), 199–205. https://doi.org/10.1098/rstb.1998.0202

Yasué, M., & Dearden, P. (2008). Replacement Nesting and Double-Brooding in Malaysian Plovers Charadrius peronii: Effects of Season and Food Availability. Ardea, 96(1), 59–72. https://doi.org/10.5253/078.096.0107

Yocum, G. D., Žďárek, J., Joplin, K. H., Lee, R. E., Smith, D. C., Manter, K. D., & Denlinger, D. L. (1994). Alteration of the eclosion rhythm and eclosion behavior in the flesh fly, Sarcophaga crassipalpis, by low and high temperature stress. Journal of Insect Physiology, 40(1), 13–21. https://doi.org/10.1016/0022-1910(94)90107-4

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Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits

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Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits

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Abstract

Intraspecific variation is necessary for evolutionary change and population resilience, but the extent to which it contributes to either depends on the causes of this variation. Understanding the causes of individual variation in traits involved with reproductive timing is important in the face of environmental change, especially in systems where reproduction must coincide with seasonal resource availability. However, separating the genetic and environmental causes of variation is not straightforward, and there has been limited consideration of how small-scale environmental effects might lead to similarity between individuals that occupy similar environments, potentially biasing estimates of genetic heritability. In ecological systems, environments are often complex in spatial structure, and it may therefore be important to account for similarities in the environments experienced by individuals within a population beyond considering spatial distances alone. Here, we construct multi-matrix quantitative genetic animal models using over 11,000 breeding records (spanning 35 generations) of individually-marked great tits (*Parus major*) and information about breeding proximity and habitat characteristics to quantify the drivers of variability in two key seasonal reproductive timing traits. We show that the environment experienced by related individuals explains around a fifth of the variation seen in reproductive timing, and accounting for this leads to decreased estimates of heritability. Our results thus demonstrate that environmental sharing between relatives can strongly affect estimates of heritability and therefore alter our expectations of the evolutionary response to selection.

Keywords: animal model, quantitative genetics, *Parus major*, phenology, environmental variation

Introduction

Changing environments, resulting from a combination of biotic and abiotic processes, but particularly accelerated by human influences (IPCC, 2022) pose a challenge for individuals and populations in today's world. Most of the traits that determine success in the face of such challenges are likely to be continuously distributed quantitative traits. To understand the evolutionary causes and consequences of intraspecific variation in quantitative traits, it is necessary to estimate additive genetic variance and heritability (Falconer & Mackay, 1996). Narrow-sense heritability quantifies the proportional contribution of additive genetic variance to the observed phenotypic variance; its mis-estimation can lead to erroneous conclusions about a population's evolutionary potential and resilience. Quantitative genetic methods, developed initially for animal and plant breeding, are now applied widely to wild populations, using the resemblance of phenotypes between relatives, along with the consideration of environment effects that contribute towards variation, to estimate the heritability of a trait (Bonnet et al., 2022; Falconer & Mackay, 1996; Kruuk, 2004; Lynch & Walsh, 1998; Postma & Charmantier, 2007; Wilson et al., 2010).

Understanding the causes of variation in traits that are associated with timing (i.e., "phenological traits") is particularly important as they are closely associated with the environment (Forrest & Miller-Rushing, 2010; Pau et al., 2011), and often show considerable variation across time and space, which is maintained despite close links with reproductive success (Reed et al., 2010). Phenology encompasses a wide range of seasonal timing traits, from breeding timing in birds to hibernation in mammals and flowering in plants; most phenological traits show continuous variation across individuals within the population (Cole & Sheldon, 2017; Germain et al., 2016; Matthysen et al., 2021). Understanding the causes of this individual variation and accurately estimating the heritability of phenological traits is increasingly important with accelerating global change (Forrest & Miller-Rushing, 2010). For organisms that breed seasonally, selection is often expected to favor timing events to coincide with temporally varying resources in other trophic levels (Kharouba & Wolkovich, 2020; Park & Post, 2022; Perrins, 1969; Renner & Zohner, 2018; Samplonius et al., 2021). As such, timing has likely consequences for breeding success and survival and is therefore an important life history trait to understand in the context of environmental change (Simmonds et al., 2020; Thomas et al., 2001).

Variation in phenological traits have been linked to various abiotic factors at a range of temporal and spatial scales, including altitudinal and latitudinal gradients, climatic

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conditions, habitat quality, and food availability (Lane et al., 2018; Réale et al., 2003; Rubolini et al., 2007; Wilkin et al., 2007a). In particular, increasing temperatures have been strongly linked to advancement in breeding time for a number of species (Both et al., 2004; Fitter et al., 1995; Moyes et al., 2011; Tryjanowski et al., 2003). Most frequently, these phenological shifts have been demonstrated at the population level by analyzing changes in mean phenotypes in relation to a mean measure of the environment. However, for many organisms, the assumption that all individuals within a population experience the same environment is an oversimplification and will likely lead to an inaccurate estimation of the relative importance of additive genetic and environmental effects for phenological variation. Therefore, quantifying individual level patterns in phenology is vital for understanding the population level patterns (Cole et al., 2021; Gervais et al., 2022), and the capacity for adaptation to climate change (Charmantier et al., 2014; Forrest & Miller-Rushing, 2010; Houle, 1992).

Related individuals within a population share genes, and when traits are heritable, we assume they will show more similar phenotypes due to shared genetic effects. When the relatedness between individuals is known, the genetic contribution to phenotypic variation can be estimated using quantitative genetic "animal" models (Wilson et al., 2010). However, focusing solely on shared genetic effects may result in overestimation of the genetic contribution to phenotypic similarity, particularly when shared environmental factors are also present (Kruuk & Hadfield, 2007). In natural populations, the environment may be highly heterogenous across many dimensions, so individuals within populations will experience different environmental conditions, contributing to the observed variation in phenotypes. Individuals that share an environment may therefore exhibit more similar phenotypes, known as "common environment" effects. Incorporating common environment effects into models allows the estimation of phenotypic variation attributed to shared environments (Regan et al., 2017; Rutschmann et al., 2020). Accounting for shared environments becomes especially important when individuals sharing these environments also share genetic effects. Related individuals often share environments due to factors such as limited dispersal, inheritance of breeding locations, habitat imprinting, maternal effects, and temporal overlap (Davis & Stamps, 2004; Van Der Jeugd & McCleery, 2002).

Animal model approaches have historically considered only a few key sources of common environment effects, most commonly maternal identity, birth year, breeding attempt identity or habitat type (e.g., Liedvogel et al., 2012; McCleery et al., 2004; Wilson et al., 2005). Not accounting for these shared environments among individuals risks assuming that observed phenotypic similarity is due to shared genes, and previous research has suggested this may lead to upward biased estimates of heritability (Gervais et al., 2022; Kruuk & Hadfield, 2007; Regan et al., 2017; Rutschmann et al., 2020; Stopher et al., 2012). Properly accounting for these shared environments can reduce the bias in attributing variation to genetic effects and allow a more comprehensive understanding of the contributions of genetic and environmental sharing to overall phenotypic variation.

Separating the influences on phenotypic variation of individuals that share environments, share genetics effects or share both requires a dataset which contains individuals with varying degrees of shared environments and genetics. Some studies have addressed nonindependence between shared genes and shared environments by incorporating spatial autocorrelation (Kruuk & Hadfield, 2007; Van Der Jeugd & McCleery, 2002). Whilst these approaches give an improved picture, they assume that spatial proximity is the key factor, or a reliable proxy for environmental similarity. Other studies have highlighted the limitations of this method and go further, considering home-range overlap and space sharing between individuals, which allows consideration of more than just distance between individuals (Germain et al., 2016; Regan et al., 2017; Rutschmann et al., 2020; Stopher et al., 2012).

However, this approach still overlooks the potential for individuals that share similar environments not being close to one another in space. Indeed, while in many ecological systems the expectation is that places closer together will be more similar, this assumption will not always be correct, particularly given that environments are often complex in their spatial structure over distances relevant to the scales that individual organisms operate over. Therefore, to accurately estimate the additive genetic contribution to phenotypic variation, there must be consideration of how phenotypes are influenced by similarities in the environment (both biotic and abiotic) experienced by individuals at an appropriate scale, regardless of their spatial proximity. For example, it is easy to conceive of arrangements of patchy environments such that individuals close together may experience very different environments, whilst those further apart may actually experience more similar environments. As such, little work has considered the contribution of environmental similarity between individuals not close in space or individuals that are close in space but subject to different environmental conditions.

A recent approach proposed by Thomson et al. (2018) and further applied by (Gervais et al., 2022) addresses this issue by using a multi-matrix animal model, including a matrix of environmental similarity alongside the matrix of genetic relatedness. Accounting for common environment effects will be important for understanding how and when heritability estimates may be biased (Gervais et al., 2022; Thomson et al., 2018), A popular model system for exploring genetic and environmental contributions to phenotypic variation has been breeding time in birds, normally studied as the date the first egg of the clutch is laid or the date that the first egg(s) in the clutch hatches. Estimates of heritability of breeding time in birds range from 0.001 to 0.45 (Teplitsky et al., 2010; van Noordwijk et al., 1981), although relatively few studies have explicitly explored the role of shared environments, other than by fitting grouping variables to control for these. Compared to other reproductive traits in birds, like clutch size, breeding timing shows lower heritability, but greater variation between and within years, suggesting there is a larger influence of environmental factors (Evans et al., 2020; Van Der Jeugd & McCleery, 2002). We expect breeding timing to be closely tied to the environment, as individuals are expected to use phenological cues to provide information on when there will be food available to feed their young and hence to choose a breeding time.

In this study, we assess the quantitative genetics of variation in breeding time in great tits studied at Wytham woods near Oxford over a 63 year period. Previous work has estimated heritability of timing in this population (Evans et al., 2020; Garant et al., 2008; Liedvogel et al., 2012; McCleery et al., 2004; Van Der Jeugd & McCleery, 2002), but has not addressed the spatial and environmental determinants of timing and the effect of their inclusion on heritability. Here we substantially extend this work by partitioning the variance in two traits associated with breeding timing (laying and hatching date) whilst accounting for different aspects of shared environments. Our aims were (a) to quantify how much between-individual variation is due to spatial autocorrelation and/or breeding environment factors, and (b) establish how including these factors in the models impacts heritability estimates.

Methods

Study system

This study used data from the long-term study of great tits (*Parus major)* in Wytham Woods, Oxfordshire over the years 1960 to 2022. Great tits rely on timing their breeding with the local temporally variable food supply, timing peak resource requirements of nestlings with a peak in their primary consumer prey, which in turn depends on the leaf development of deciduous trees (Hinks et al., 2015). Great tits are cavity nesters, and in this population, the majority of the breeding population nests in the 1,019 nest boxes placed throughout the woods (Harvey et al., 1979), which are monitored over the breeding season (from March—May) each year following a standardized protocol.

Birds are uniquely identified with metal British Trust for Ornithology (BTO) rings; since 2007 all birds have also been fitted with plastic rings, which contain a passive integrated transponder (PIT tag). Parent birds were identified at the nest when provisioning young. Radio Frequency Identification (RFID) antenna can read the PIT tags, so are placed around nest box entrance holes, allowing identification of individuals whilst feeding nestlings, without the need to catch them. Birds that cannot be identified using this method (likely unringed individuals) are trapped at the nest box when nestlings are at least 10 days old. They are then fitted with metal BTO leg rings and PIT tags. All individual identification was done by catching before the use of PIT tags. All nestlings are ringed and PIT tagged on day 15 before they leave the nest. For nests that fail or are abandoned before fledging, often only mother ID is recorded. Mist netting is carried out over the autumn and winter to catch and ring as many immigrant birds as possible.

Breeding data

Two traits were used to represent breeding timing: laying date, defined as the day the first egg of a clutch was laid, assuming that females lay one egg a day early in the morning, and hatching date, defined as the day the first egg was hatched. Nest boxes are visited at least once a week from late March until eggs are found; if there is more than one egg on first observation of eggs in the nest, the date of the first egg is inferred by counting back, assuming one egg is laid per day. Once eggs are observed to be warm, indicating incubation has begun, nests are not visited again until the expected hatch date (12 days after clutch completion). Onset of incubation and incubation duration can vary between individuals; if nestlings are not observed on the predicted hatch date, the nests are visited every other day until hatching or until the nest is declared abandoned. Newly hatched nestlings have a distinctive appearance, allowing fieldworkers to establish whether the largest young in a nest are more than a day old. If there is any ambiguity, 3 and 4 of the largest nestlings are weighed to determine age (Supplementary Table 3). This protocol ensures that all hatch dates should be accurate to ±1 day. Dates are expressed here in April Days (April 1st = 1).

Overall, there were 17,996 recorded breeding attempts over 63 years, from 1960 to 2022. From this sample only breeding attempts where the mother was identified and had a recorded laying date were kept (removing 5,848 attempts); further, any breeding attempts from known second broods were removed (260 and 19 attempts for mothers and known fathers respectively), as well as removing any laying dates that were 30 days after the first 5% of laying dates that year within subsets of the woods (the study site is split into 9 sections, based loosely on habitat types, for logistic purposes; 126 attempts), to account for unknown second broods (Van Der Jeugd & McCleery, 2002), and any broods that were experimentally manipulated or do not have complete habitat data (1,673 attempts); overall this left a sample of 11,658 breeding attempts for analysis. We kept breeding attempts where mothers were known, in preference to fathers, as here we opt to treat laying date as a maternal trait both given that the heritability of laying date in males is less than a fifth that of females (Evans et al., 2020) and because this makes the quantification of shared breeding environments tractable.

Pedigree construction

Identification of individuals at the nest box enabled the creation of a social pedigree across 63 years. The social pedigree assumes that the adult birds identified incubating or feeding nestlings at a nest are the biological parents. Other than clerical error, the maternal pedigree should be accurate, as there are no known cases of maternal identity mismatching social parent identity (Patrick et al., 2012). There are relatively low levels of extra-pair paternity recorded in this population (of the order of 12%: Patrick et al., 2012). Extra-pair paternity at this level (under 20%) is not thought to significantly influence quantitative genetic estimates, assuming it is not strongly biased with respect to traits of interest (Charmantier & Réale, 2005; Firth et al., 2015), and given our focus on timing as a maternal trait, we consider this a reasonable assumption. The pedigree analyzed here includes 14,506 individuals (including only individuals with recorded breeding attempts who contribute information to this analysis) and extends for up to 35 generations, with 7,431 maternities and 6,761 paternities, 4,260 full siblings, 3,033 maternal half siblings, and 2,114 paternal half siblings.

Analysis

We constructed animal models in ASReml-R (Butler et al., 2007) to partition the phenotypic variance in each of the traits into genetic and environmental variance components and re-assess the heritability (Kruuk, 2004; Wilson et al., 2010). The pedigree was used to create a matrix of expected relatedness between all individuals, allowing the consideration of many different relationships instead of just parents and offspring. Raw laying/hatching date data was used, given in April Days (April 1st = 1). The age of the female at breeding was included as a fixed effect as a 2-level factor, first-year breeders (1-year-old) or older adult (older than 1 year) (Evans et al., 2020).

In all models we included year of breeding as a random effect (V_{BY}) to partition the variance attributable to variation in the environment during the year of breeding; in this population previous studies have found marked phenotypic plasticity across years (Charmantier et al., 2008). We also included individual identity of the breeding female, linked to the pedigree, as a random effect (V_A) to estimate the additive genetic effect, which is the influence of the genes that belong to the individual in which the trait was measured. Individual identity of the breeding female was also included as a permanent environment effect (V_{PE}), to adjust for multiple records of individuals over years, accounting for nonheritable effects that will cause variation that is conserved across the repeated records of individuals (e.g., natal effects) (Kruuk & Hadfield, 2007; Lynch & Walsh, 1998).

Accounting for environmental similarity

First, a model was run with just the factors outlined above (the minimal model). We then ran additional models, extending the minimal model by adding: an individual nest box random effect (nestbox model), a matrix of spatial proximity (spatial proximity model), a matrix of environmental similarity (breeding environment model), and a model including all three simultaneously.

The minimal model simply decomposes the phenotypic variance (V_P) into breeding year effect (V_{BY}), female permanent environment effect (V_{PE}), genetic effects (additive genetic effect of female (V_A), and the residual variance (V_R) which accounts for variation arising from environmental effects that have not been explicitly included in the model.

$$V_P = V_{BY} + V_A + V_{PE} + V_R \quad (\textit{minimal model})$$

The nestbox model included "nest box" as a random effect (V_{NB}), which accounted for similarities in breeding timing of different females breeding in the same boxes over time that was due to similar breeding environments. Individual nest boxes were used between 1 and 35 times each in this data set (median = 11).

$$V_P = V_{BY} + V_A + V_{PE} + \mathbf{V_{NB}} + V_R \quad (\textit{nestbox model})$$

The spatial proximity model and breeding environment model included an "S-matrix" that describes the similarity of a non-genetic effect between individuals, and works in the same way the genetic relatedness matrix does, to estimate the contribution of variance associated with environmental effect; this approach was first applied by (Stopher et al., 2012).

The spatial proximity model contained a spatial proximity matrix. This was constructed by taking the breeding location of each individual bird and calculating the distance between all possible combinations of birds across all years. If an individual was recorded breeding more than once in different nest boxes (28% of individuals), the mean location point was taken. We expect this will not affect the results significantly as breeding dispersal in this population is limited to short distances: median of 60.75 m (Further details in Supplementary Figure 3).

The distance values were scaled from 0 to 1, with 1 along the diagonal such that individuals have a similarity of 1 with themselves, and 0 was the maximum distance between a pair of individuals (3,971.92 m). The matrix was linked to the animal model to estimate the proportion of variance explained by the distance between individuals ($V_{SPATIAL}$):

$$V_P = V_{BY} + V_A + V_{PE} + \mathbf{V_{SPATIAL}} + V_R \ (\textit{spatial proximity model})$$

The breeding environment model was constructed to account for effects of small-scale environmental variation, independently of the effect of distance. We aimed to create a measure that can act as a good proxy for the environment experienced by individual breeding birds in close proximity to their nest box. This was done by including a matrix of breeding environment similarity between individuals, including the following factors assigned to each individual nestbox: altitude, edge distance index, northness, oak-richness within 75 m, and population density (expressed as the square root of territory size). In this population of great tits, females lay earlier at lower altitudes, on north facing slopes, at more interior sites, when oak tree density within 75 m of the box is higher, and at lower population densities (when they have larger territories) (Wilkin et al., 2006; Wilkin et al., 2007a, 2007b). The correlation of these chosen factors with each other and each individual factor with the spatial proximity matrix and environmental similarity matrix are shown in Supplementary Table 4 and further information on the construction of the environmental similarity matrix is also given in the Supplementary.

The environmental factors were chosen as they are factors that vary over small spatial scales in Wytham, and have been previously shown to be related to variation in laying date, are likely to have remained the same over the years of the study (i.e., physical features of the environment and not climatic factors; boxes have a fixed location).

As with distance, for birds that were recorded breeding more than once, a mean for all environmental values over years was taken. This approach was taken because in this study population breeding dispersal (between years) is minimal; therefore, measures of breeding environment between boxes used for consecutive breeding attempts show considerable similarity compared to the possible range of differences in environment across the whole population (further information in Supplementary Figures 3 and 4). We then used methods suggested by (Thomson et al., 2018) to combine the environmental measures with values of breeding environment similarity between all individuals. Each variable was centered and scaled, and then combined using Euclidean distance measure in multivariate space between all individuals with every other individual to obtain the straight-line distance between 2 vectors of environmental measures in multivariate space. This creates a similarity matrix, which aims to capture a substantial amount of the similarity in the environment experienced by individuals as a single value. This similarity value was again scaled to give a value of 1 along the diagonal, with 0 as the distance between birds in the most dissimilar environments (histogram of the distribution of breeding environment similarity values in Supplementary Figure 5).

$$V_P = V_{BY} + V_A + V_{PE} + \mathbf{V_{BREED\ ENV.}} + V_R \ (\textit{breeding environment model})$$

Finally, we attempted to model both the spatial proximity and breeding environment similarity matrices together. However, we encountered convergence problems with the model, likely due to a lack of power in the data to decompose both environmental matrix effects simultaneously.

In order to understand the contribution of spatial proximity and environmental similarity to variation in breeding timing, we carried out two sets of comparisons. First, we visualized the relationship between the two matrices: spatial proximity and environmental similarity, to ensure there was representation of genetically related individuals experiencing more and less close/similar environments. Second, we also ran mantel correlation tests to broadly quantify the correlations between the different matrices (Mantel, 1967).

Assessing heritability

We used the within-year phenotypic variance, which is the sum of all variance components except breeding year, conditioned upon the fixed effect of female age at breeding, to estimate the heritability (Evans et al., 2020). This is for two reasons: firstly, when selection is estimated for these traits, it is typically done on a year-specific basis (Charmantier et al., 2008; Noordwijk et al., 1995). Secondly, there has been a long-term advancement in breeding timing in this population; as most individuals in the population only live to breed for 1 or 2 years, this will likely lead to overestimation of annual variance above what will be actually experienced by individuals.

Heritability is therefore given as the proportion of within-year phenotypic variation ($V_{P\,within\,year}$) assigned to additive genetic variance (V_A).

$$h^2 = \frac{V_A}{V_{P\,within\,year}}$$

Standard errors of proportional variance components and heritabilities are calculated using the *vpredict* function from the Asreml-R package, and uses the delta method (Butler et al., 2007). The proportion of variance explained by each of the variance components was calculated as the ratio of the relevant component to the within-year phenotypic variance $V_{P\,within\,year}$. To assess the significance of the variance components, we used likelihood ratio tests, assuming a χ^2 distribution with one degree of freedom (Wilson et al., 2010). We also plot some model diagnostic tests to assess model fit (further details in the Supplementary Materials).

Results

Initial findings

An influential previous analysis of these data used mother-daughter regression split by three dispersal classes to demonstrate environmental dependence of heritability (Van Der Jeugd & McCleery, 2002). For completeness, we show that the findings in (Van Der Jeugd & McCleery, 2002) are robust to repeated analysis using parent-offspring regressions with a substantially increased data set (see Supplementary information Section 1: Supplementary Figures 1 and 2 and Supplementary Tables 1 and 2). Since this approach does not make full use of the relatedness structure and doesn't allow modeling of continuous environmental distance, we focus from here onwards on results using multi-matrix animal models.

Visually comparing the spatial proximity and environmental similarity matrices suggests that they are correlated at short distances but that this correlation declines as distance increases (Supplementary Figure 6). In line with this, mantel tests showed a correlation of 0.192 between the spatial proximity and breeding environment similarity matrices (Supplementary Table 4).

Laying date

As expected, breeding year explained a considerable amount of variation in laying date in all models (ranging from 48.8% ± 8.8% to 60.2% ± 10.9%, see Table 1 and Figure 1A). The nest box model significantly improved the model fit compared to the minimal model without the nest box effect ($\chi^2_{(1)} = 237, p < 0.001$), with the nest box random effect explaining almost 3% of the variation. Within-year heritability was very similar between these two models; adding the nestbox random effect decreased the estimate by 0.7 percentage points, corresponding to a change of 3.5% (minimal model: 20.1% ± 5.8%, nestbox model: 19.4% ± 5.4%: Table 1 and Figure 1C). Fixed effects are reported in Supplementary Table 5. The fixed effect of mother's age at breeding did not change much across models.

Both the spatial proximity and breeding environment similarity terms significantly improved the model fit compared to the minimal model (minimal model vs spatial model: $\chi^2_{(1)} = 760$, $p < 0.001$; minimal model vs breeding environment model: $\chi^2_{(1)} = 496$, $p < 0.001$). Upon comparing model fit using the Akaike Information Criterion (AIC), we observe that the spatial model exhibits a slightly lower AIC compared to the breeding environment model (AIC: 50976 vs. 51240). Despite this difference, both models demonstrate satisfactory performance in diagnostic evaluations. Therefore, the comparison between these two models remains scientifically valuable, particularly as our aim is not to derive a perfect estimate of the heritability of laying date within this population, but instead to explore how different methods of accounting for environmental similarity within animal models of wild populations influences the conclusions we draw from them. Hence, we feel it is important to discuss the results from both models, as it contributes to a more comprehensive understanding of the underlying data structure and is useful for understanding how heritability estimates may be affected by accounting for shared environments in various ways.

The spatial proximity matrix and the breeding environment similarity matrix explained 21.7% ± 4.0% and 21.9% ± 3.7% of the variation in laying date, respectively. The incorporation of these S-matrices reduced the proportion of variation explained by breeding year by 19% and 16% compared to the nestbox model (from 60.2% in the nestbox model to 49.0% in the spatial model and 48.8% in the breeding environment model). Both models produced similar results for the proportion of variation explained by additive genetic effect (i.e., in relation to narrow-sense heritability (spatial 6.1% and breeding environment, 5.4%)). The individual permanent environment effect was also similar, breeding environment model compared to the spatial model (3.8% vs 4.6%). The amount of residual variation was reduced when including either matrix by around 16% (from 23.1% to 19.4% and 19.3%).

Including either S-matrix led to within-year heritability estimates of approximately two thirds the estimate from the nestbox model. The spatial model estimated a narrow-sense heritability of 11.9% ± 1.7% and the breeding environment model was slightly lower at 10.6% ± 1.6%, reducing the heritability estimate by over 40% (Table 1 and Figure 1C).

Hatching date

Laying date and hatching date are very closely correlated (Pearson's $r_{(10893)} = 0.952$, $r^2 = 0.905$, the interval between laying and hatching has a median of 21 days with a SD of 2.735), so we therefore expected very similar results. As for laying date, breeding year explained the greatest proportion of variation in hatching date in all four models (ranging from 52.0% ± 9.4% to 65.0% ± 11.7%: Table 1 and Figure 1B). Compared to each equivalent laying date model, breeding

Table 1. Variance components from animal models (models 1–4).

Trait	1—minimal model		2—incl. nest box		3—incl. spatial matrix		4—incl. breed env. Matrix	
	Est **(*SE*)**	***Rel to*** $\boldsymbol{V_P}$	***Est*** **(*SE*)**	***Rel to*** $\boldsymbol{V_P}$	***Est*** **(*SE*)**	***Rel to*** $\boldsymbol{V_P}$	***Est*** **(*SE*)**	***Rel to*** $\boldsymbol{V_P}$
LAYDATE								
V_{BY}	49.093 (8.857)	0.600 (0.108)	49.024 (8.843)	0.602 (0.109)	49.125 (8.860)	0.490 (0.088)	49.055 (0.850)	0.488 (0.088)
V_A	6.562 (0.848)	0.080 (0.010)	6.265 (0.794)	0.077 (0.010)	6.091 (0.753)	0.061 (0.008)	5.443 (0.758)	0.054 (0.008)
V_{PE}	6.588 (0.864)	0.081 (0.011)	4.896 (0.808)	0.060 (0.010)	3.822 (0.764)	0.038 (0.008)	4.642 (0.799)	0.046 (0.008)
V_{NB}	–	–	2.429 (0.233)	0.030 (0.003)	–	–	–	–
$V_{SPATIAL}$	–	–	–	–	21.732 (4.030)	0.217 (0.040)	–	–
$V_{BREED\ ENV.}$	–	–	–	–	–	–	22.013 (3.742)	0.219 (0.037)
V_R	19.522 (0.421)	0.239 (0.005)	18.778 (0.420)	0.231 (0.005)	19.462 (0.414)	0.194 (0.004)	19.441 (0.415)	0.193 (0.004)
V_P	81.766		81.391		100.231		100.594	
$V_{P-within\ year}$	32.696		32.391		51.065		51.514	
h^2 *within year*	**0.201 (0.025)**		**0.194 (0.024)**		**0.119 (0.017)**		**0.106 (0.016)**	
HATCHDATE								
V_{BY}	46.107 (8.316)	0.648 (0.117)	45.912 (8.279)	0.650 (0.117)	45.933 (8.283)	0.544 (0.098)	45.780 (8.256)	0.520 (0.094)
V_A	5.160 (0.674)	0.073 (0.009)	4.873 (0.621)	0.069 (0.009)	4.640 (0.580)	0.055 (0.007)	4.189 (0.585)	0.048 (0.007)
V_{PE}	4.840 (0.682)	0.068 (0.010)	3.190 (0.627)	0.045 (0.009)	2.418 (0.585)	0.029 (0.007)	2.900 (0.615)	0.033 (0.007)
V_{NB}	–	–	2.244 (0.202)	0.032 (0.003)	–	–	–	–
$V_{SPATIAL}$	–	–	–	–	16.483 (3.013)	0.195 (0.036)	–	–
$V_{BREED\ ENV.}$	–	–	–	–	–	–	20.19 (3.240)	0.230 (0.037)
V_R	15.018 (0.338)	0.211 (0.005)	14.434 (0.336)	0.204 (0.005)	15.011 (0.332)	0.178 (0.004)	14.982 (0.333)	0.170 (0.004)
V_P	71.126		70.654		84.485		88.071	
$V_{P-within\ year}$	25.018		24.179		38.547		42.299	
h^2 *within year*	**0.206 (0.026)**		**0.197 (0.024)**		**0.120 (0.017)**		**0.099 (0.016)**	

Note. Details of models found in methods. Est (SE) gives the raw estimate and standard error, Rel to V_P is the ratio of each variance component to V_P, V_{BY} = breeding year, V_{PE} = focal individual permanent environment effect, V_A = focal individual additive genetic effect, V_{NB} = nest box random effect, $V_{SPATIAL}$ = spatial proximity matrix, $V_{BREED\ ENV.}$ = breeding environment similarity matrix, V_R = residual variance, V_P = total phenotypic variance as sum of all variance component, $V_{P\text{-}within\ year}$ = total phenotypic variance as sum of all variance component excluding V_{BY}, h^2 *within year* = within year heritability as proportion of V_A to $V_{P\text{-}within\ year}$.

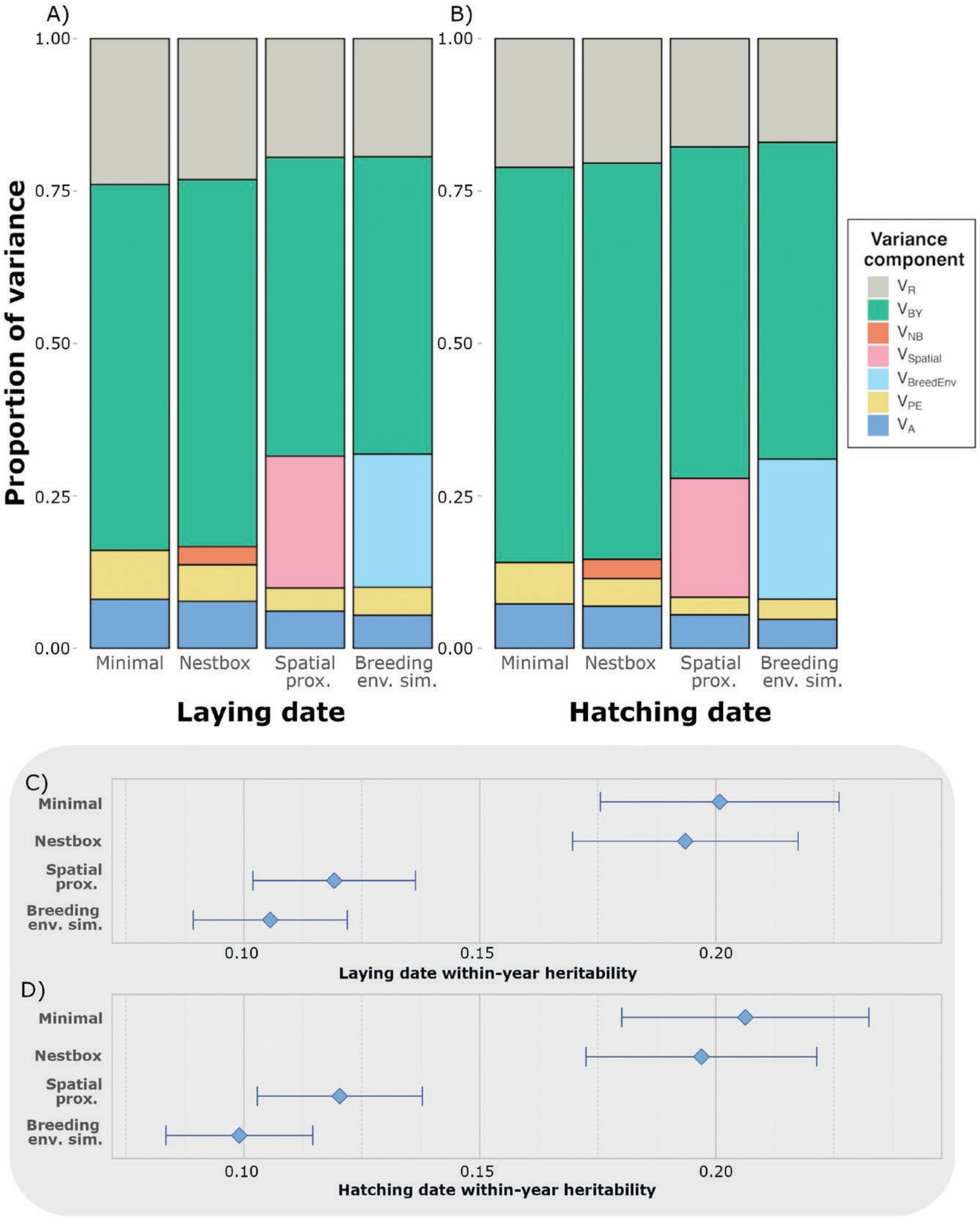

Figure 1. Proportion of variance assigned to each component for the 4 different models (specific information on all models in the methods), for (A) laying date and (B) hatching date. Colors correspond to each component. V_{BY} = breeding year, $V_{SPATIAL}$ = spatial proximity matrix, $V_{BREED\ ENV.}$ = breeding environment similarity matrix, V_{PE} = focal individual permanent environment effect, V_{NB} = nest box random effect, V_A = focal individual additive genetic effect, V_R = residual variance. In (C) and (D) within-year heritability estimates (estimated as the proportion of variance explained by V_A out of the within year $V_{P\text{-within year}}$) are shown for all 4 models for laying date and hatching date respectively. Error bars show standard error.

year contributed just under 5 percentage points more to variation in hatching date.

Including nest box as a random effect significantly improved the model fit compared to the minimal model ($\chi^2_{(1)} = 288$, $p < 0.001$), with the nest box random effect explaining 3.2% ± 0.3% of the variation. Within-year heritability only decreased slightly, from 20.6% ± 2.6% in the minimal model to 19.7% ± 2.4% in the nestbox model (Table 1 and Figure 1D). The fixed effect of mother's age at breeding does not change much across models, but is slightly lower for hatching date than for laying date (Supplementary Table 5).

Both S-matrices significantly improved the model fit compared to the minimal model (nestbox model vs spatial model: $\chi^2_{(1)} = 871$, $p < 0.001$, nestbox model vs breeding environment model: $\chi^2_{(1)} = 601$, $p < 0.001$). Upon comparing model fit using the Akaike Information Criterion (AIC), we observe that the spatial model exhibits a slightly lower AIC compared to the breeding environment model (AIC: 44613 vs. 44883). Despite this difference, both models demonstrate satisfactory performance in diagnostic evaluations, and as described in the results for laying date above we feel comparison between these two models remains scientifically valuable.

The spatial proximity matrix explained 19.5% ± 3.6% of variation seen in hatching date, and the breeding environment similarity matrix explained 23.0% ± 3.7%. Incorporation of either S-matrix reduced the proportion of variation explained by breeding year compared to the nestbox model—from 65.0% to 54.4% (spatial) and 52.0% (breeding environment).

There was little difference between the proportion of variance explained by additive genetic effects between the spatial and breeding environment model (spatial model, 5.5% and breeding model, 4.8%). The individual permanent environment effect explained was also very similar between the spatial model and the breeding environment model (2.9% vs 3.3% respectively).

The proportion of residual variance very similar same between models (17.8% ± 0.4% and 17.0% ± 0.4%). Including both matrices reduced the within-year heritability estimates by 39% and 50% compared to the nestbox model (19.7% to 12.0% and 9.9% (Table 1 and Figure 1D)).

Discussion

We demonstrate the importance of accounting for small-scale environmental variation when estimating heritability of a phenological trait in a wild population, showing that neglecting this variation leads to overestimation of heritability. The direct estimate of the heritability of breeding timing in this population of great tits was almost halved when the similarities in the breeding environments experienced by individuals were taken into consideration. Previous assessment of the effects of spatial and environmental similarity on phenological timing and heritability in this population have been limited: a single previous study used mother-daughter regressions across three distance classes of female natal dispersal and observed decreasing heritability of both laying and hatching date over greater dispersal distances (Van Der Jeugd & McCleery, 2002). We repeated these methods with updated data, and the results remain the same (Supplementary Section 1). These results support our main findings that failing to account for spatial and environment similarity between individuals will inflate heritability and clearly show the importance of accounting for shared environments between related individuals. Our study advances understanding in this area by using the full pedigree within multi-matrix animal models and accounting for smaller-scale environmental similarity in a more comprehensive way.

Similar results were found for both laying date and hatching date, which is expected as they are closely related. We found larger effects of year and slightly reduced additive genetic and permanent environment effects when considering hatching date compared to laying date. This may be due to the fact that individuals are able to adjust their hatching date after laying by controlling the number of eggs laid and the onset of incubation (Cresswell & McCleery, 2003; Simmonds et al., 2017). This could allow hatching to vary more between years in response to the environment; however, the difference is small and does not result in significant differences in heritability estimates between the two traits. We also found that the relative size of the permanent environment effect was reduced for these phenological traits when including either matrix compared to a random nestbox effect. The permanent environment effect captures unique individual environmental and genetic variation between individuals that is not otherwise accounted for in the model, for example by the additive genetic variance component. A decrease in the proportion of variance explained by the permanent environment effect suggests that some variation previously assigned to this unexplained between-individual variation was better explained specifically by the breeding environments those individuals experience across their lifetime. Hence, accounting for breeding location gives a better perspective on what is driving the permanent environment effects.

In the context of considering both spatial proximity and environmental similarity, we found that there was relatively little correlation between these two factors in our population (mantel correlation of 0.192). For a relatively small habitat patch such as this and with rather short distance dispersal, we might expect there to be a relatively strong relationship between spatial and environmental similarity. However, we might see low correlation in this case due to the structure of the habitat and the measures chosen to calculate the environmental similarity. This could mean that birds dispersing not too far may be experiencing a different environment to their mother, making the environmental similarity an important factor to consider on top of just distance in space. Further, both matrices separately accounted for approximately 20% of the variation observed in laying date and in hatching date, suggesting that they capture separate but similarly-sized effects. Further work involving direct comparison of both spatial and environmental similarity in this population and other populations, would be very valuable, but currently challenging given the methodological difficulties in estimating variance components simultaneously. However, simulation studies, where the precise environmental structure and data structure can be controlled, may be particularly fruitful in gaining further insights on where spatial or environmental sources of similarity will be especially important sources of individual phenotypic variation.

One of the reasons for the previous lack of consideration of environmental similarity in shaping heritability estimates may be the challenges associated with measuring this. Indeed, considering a measure of environmental similarity is limited by the choice of environmental factors used to create it. All such studies have to make assumptions about how to choose factors which may represent the relevant environment. In doing so, we may not capture the full importance of the environment, and methods which combine various factors of the environment (such as ours here) may underestimate their effect. Conversely, when relatives often share environments, leading to high covariance between genetic and environmental effects, assigning all of the covariance to the environment may lead to underestimation of heritability (Shaw & Shaw, 2014). While it is difficult to fully mitigate these issues (due to physical limitations on data collection, complexities with overloading models given how multi-dimensional the environment is, and difficulties picking apart tightly covarying genetic and environment effects without running experiments), long-term study systems with detailed information (such as ours) provide a first step to integrating this consideration properly when considering heritability in the wild.

The causes of any genotype-environment covariance are also important. If it results from a genetically mediated breeding environment choice then this could actually be considered part of the 'genetic' heritability of the trait (Munar-Delgado et al., 2023). Although consistent differences between wild individuals in their habitat choice are commonplace (Bell et al., 2009; Leclerc et al., 2016) few studies have been able to quantify the degree to which variation in habitat choice is driven by genetics (but see Gaither et al., 2018; Jaenike & Holt, 1991). In cases where breeding habitat choice is, at least partly, genetically determined, and thus breeding environments are, to some degree, heritable, the overall heritability or effective heritability, would be underestimated by assuming similarity in the environments used by individuals is driven purely by nongenetic processes (e.g., limited dispersal). For example, heritability of habitat selection has recently been found in a roe deer population, and therefore considering environmental effects within animal models may lead to incorrectly downward biasing heritability estimates of behavioral and morphological traits (Gervais et al., 2022). The decision about whether or not to consider nongenetically inherited environmental variance within estimates of heritability is complex and depends greatly on the biological context (Munar-Delgado et al., 2023). We do not claim that our estimates are the "true" heritability, but more aim to highlight the importance of thinking about the biological relevance of considering genetic and nongenetic inheritance of environments, and how these decisions can have a large impact on the estimates derived. It is currently unclear how heritable environmental choice is in birds, and whether it is a mechanism through which genetics influence lay date. Thus, our findings may represent only a part of the underlying mechanism.

Our primary results align well with current general investigation into this area, with other studies showing the importance of accounting for spatial variation when estimating heritability with quantitative genetic models (Regan et al., 2017; Rutschmann et al., 2020; Stopher et al., 2012; Thomson et al., 2018; Van Der Jeugd & McCleery, 2002). Birds that breed seasonally can be influenced by the environment at small local scales, and the timing of laying of great tits has been shown to vary with food availability and quality (Cole et al., 2021; Hinks et al., 2015), habitat composition (Matthysen et al., 2021) and territory size (Wilkin et al., 2006). Indeed, phenotypic plasticity is important for short term adjustments, and in the Wytham population individual plastic adjustments in timing of breeding have been key in tracking the rapidly changing environment (Charmantier et al., 2008). The impact of these small-scale environmental effects on estimates of the heritability of timing of breeding in wild bird populations has not previously been quantified. Furthermore, the reduction in permanent environment effects when considering environmental similarity that we report here has also been found in other systems, such as for behavioral traits in roe and red deer (Gervais et al., 2022; Stopher et al., 2012).

Our analyses clearly highlight the need for more careful consideration of breeding environment similarity across space, especially in wild populations where the environment can vary greatly. Specifically, as we found that breeding environment similarity between individuals explains similar amounts of variation as spatial proximity, it may be that in some cases it is perhaps desirable to use this measure of breeding environment similarity instead of spatial proximity to capture variation in phenotypes due to both space and environment. Yet, how the relative proportion of variation explained by spatial compared with breeding environment similarity matrices varies depending on context remains unknown, as well as how the life history of the species may shape this. For example, generation time and natal dispersal distance will impact how likely related individuals are to experience similar environments. In species with long and random dispersal distances, we may expect environmental similarity to play a more important role in contribution to variation in a trait; in contrast, for a species with limited dispersal or even inherited territories, it would be less important to consider this. As such, investigations around when it is most appropriate to consider environmental similarity over spatial similarity would now be useful. Such analyses would likely focus on considering factors such as the dispersal distances of a species and the grain of habitat variability experienced by the population. For example, in species with shorter dispersal distances and a larger grain of habitat variability (meaning environments close by are more similar), offspring are more likely to experience similar breeding environments to their parents. However, if the grain of habitat variability is very small (meaning nearby environments could be quite different), offspring that disperse short distances may end up actually experiencing different environments to their parents. In such cases, it becomes more important to consider not just spatial proximity but also breeding environment similarity. Furthermore, we have assumed a linear decrease in similarity across both spatial and environmental distance, as this aligns with previous work in Wytham (Hinks et al., 2015; Van Der Jeugd & McCleery, 2002; Wilkin et al., 2007b), but it may be important to consider how similarity may decrease with distance, both across space and environment, beyond a simple linear decrease. This could potentially be explored in future research to gain a better understanding of what measurements of common environment effects are most appropriate for a given population or species.

In a broader sense still, the possibility of inherited environments raises questions about how selection of environments could be transmitted from parents to offspring. It is important to consider the heritability of environment choice so that heritability estimates are not biased downwards by removing genetic variation that underpins similarity between parents and offspring. In this context, studies like ours could be used to investigate whether individuals actively choose to nest in environments more similar to where they were born, which could be contributing to the genetic heritability of the trait.

Summary

Understanding the additive genetic and environmental contributions to phenotypic variation in phenological traits is important for a range of questions about their evolution and for understanding their potential to respond to changing environments. It is clear that if common environment effects are not considered, estimates of heritability and trait evolvability will be biased. Our study shows that accounting for the shared environment is important for understanding the genetic basis of reproductive timing variation in wild individuals and is useful for enabling understanding of the causes and consequences of different components of phenotypic variation. As global change continues to impact phenology, it is crucial to continue to develop methods that account for small-scale environmental variation. Our approach, which includes a measure of breeding environment similarity, aims to capture both spatial autocorrelation and environmental similarity of individuals not necessarily close in space. Long-term study systems, which detail fine-scale individual level information across generations (such as ours), provide great opportunity for considering space and environment types and would therefore be useful in examining the effects of global change within a natural population in this context.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Code and data to reproduce all analyses is available at https://github.com/carysvjones/AnimalMod_Envir.git

Author contributions

All authors conceptualized the idea. All authors have participated in data collection. Carys V. Jones conducted data analysis with input from Charlotte E. Regan. Carys V. Jones produced first draft of the manuscript. Charlotte E. Regan, Ella F. Cole, Josh A. Firth, and Ben C. Sheldon provided detailed feedback on methodology, and contributed critically to drafts.

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References

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bonnet, T., Morrissey, M. B., de Villemereuil, P., Alberts, S. C., Arcese, P., Bailey, L. D., Boutin, S., Brekke, P., Brent, L. J. N., Camenisch, G., Charmantier, A., Clutton-Brock, T. H., Cockburn, A., Coltman, D. W., Courtiol, A., Davidian, E., Evans, S. R., Ewen, J. G., Festa-Bianchet, M., … Kruuk, L. E. B. (2022). Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science*, *376*(6596), 1012–1016. https://doi.org/10.1126/science.abk0853

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Jrvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P. -A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Trk, J., & Visser, M. E. (2004). Largescale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society B: Biological Sciences*, *271*(1549), 1657–1662. https://doi.org/10.1098/rspb.2004.2770

Butler, D. G., Cullis, B. R., Gilmour, A. R., & Gogel, B. J. (2007). Analysis of mixed models for S language environments ASReml-R. *Queensland Department of Primary Industries and Fisheries NSW Department of Primary Industries, QE02001*, *145*, 1.

Charmantier, A., Garant, D., & Kruuk, L. E. B. (2014). *Quantitative genetics in the wild*. Oxford University Press.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*(5877), 800–803. https://doi.org/10.1126/science.1157174

Charmantier, A., & Réale, D. (2005). How do misassigned paternities affect the estimation of heritability in the wild? *Molecular Ecology*, *14*(9), 2839–2850. https://doi.org/10.1111/j.1365-294X.2005.02619.x

Cole, E. F., Regan, C. E., & Sheldon, B. C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. *Nature Climate Change*, *11*(10), 872–878. https://doi.org/10.1038/s41558-021-01140-4

Cole, E. F., & Sheldon, B. C. (2017). The shifting phenological landscape: Within- and between-species variation in leaf emergence in a mixed-deciduous woodland. *Ecology and Evolution*, *7*(4), 1135–1147. https://doi.org/10.1002/ece3.2718

Cresswell, W., & McCleery, R. (2003). How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, *72*(2), 356–366. https://doi.org/10.1046/j.1365-2656.2003.00701.x

Davis, J. M., & Stamps, J. A. (2004). The effect of natal experience on habitat preferences. *Trends in Ecology and Evolution*, *19*(8), 411–416. https://doi.org/10.1016/j.tree.2004.04.006

Evans, S. R., Postma, E., & Sheldon, B. C. (2020). It takes two: Heritable male effects on reproductive timing but not clutch size in a wild bird population*. *Evolution*, *74*(10), 2320–2331. https://doi.org/10.1111/evo.13980

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics*. Longman Group Ltd.

Firth, J. A., Hadfield, J. D., Santure, A. W., Slate, J., & Sheldon, B. C. (2015). The influence of nonrandom extra-pair paternity on heritability estimates derived from wild pedigrees. *Evolution*, *69*(5), 1336–1344. https://doi.org/10.1111/evo.12649

Fitter, A. H., Fitter, R. S. R., Harris, I. T. B., & Williamson, M. H. (1995). Relationships between first flowering date and temperature in the flora of a locality in Central England. *Functional Ecology*, *9*(1), 55–60. https://doi.org/10.2307/2390090

Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *365*(1555), 3101–3112. https://doi.org/10.1098/rstb.2010.0145

Gaither, M. R., Gkafas, G. A., de Jong, M., Sarigol, F., Neat, F., Regnier, T., Moore, D., Gröcke, D. R., Hall, N., Liu, X., Kenny, J., Lucaci, A., Hughes, M., Haldenby, S., & Hoelzel, A. R. (2018). Genomics of habitat choice and adaptive evolution in a deep-sea fish. *Nature Ecology & Evolution*, *2*(4), 680–687. https://doi.org/10.1038/s41559-018-0482-x

Garant, D., Hadfield, J. D., Kruuk, L. E. B., & Sheldon, B. C. (2008). Stability of genetic variance and covariance for reproductive characters in the face of climate change in a wild bird population. *Molecular Ecology*, *17*(1), 179–188. https://doi.org/10.1111/j.1365-294x.2007.03436.x

Germain, R. R., Wolak, M. E., Arcese, P., Losdat, S., & Reid, J. M. (2016). Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows. *The Journal of Animal Ecology*, *85*(6), 1613–1624. https://doi.org/10.1111/1365-2656.12575

Gervais, L., Morellet, N., David, I., Hewison, A. J. M., Réale, D., Goulard, M., Chaval, Y., Lourtet, B., Cargnelutti, B., Merlet, J., Quéméré, E., & Pujol, B. (2022). Quantifying heritability and estimating evolutionary potential in the wild when individuals that share genes also share environments. *Journal of Animal Ecology*, *91*(6), 1239–1250. https://doi.org/10.1111/1365-2656.13677

Harvey, P. H., Greenwood, P. T., & Perrins, C. M. (1979). Breeding area fidelity of great tits (Parus major). *Journal of Animal Ecology*, *48*(1), 305–313.

Hinks, A. E., Cole, E. F., Daniels, K. J., Wilkin, T. A., Nakagawa, S., & Sheldon, B. C. (2015). Scale-dependent phenological synchrony between songbirds and their caterpillar food source. *The American Naturalist*, *186*(1), 84–97. https://doi.org/10.1086/681572

Houle, D. (1992). Comparing evolvability and variability. *Genetics*, *130*(1), 195–204. https://doi.org/10.1093/genetics/130.1.195

IPCC. (2022). Climate change 2022: impacts, adaptation, and vulnerability. In H. -O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3056). Cambridge University Press. Cambridge University Press, Cambridge, UK and New York, NY, USA. https://doi.org/10.1017/9781009325844

Jaenike, J., & Holt, R. D. (1991). Genetic variation for habitat preference: Evidence and explanations. *The American Naturalist*, *137*, S67–S90. https://doi.org/10.1086/285140

Kharouba, H. M., & Wolkovich, E. M. (2020). Disconnects between ecological theory and data in phenological mismatch research. *Nature Climate Change*, *10*(5), 406–415. https://doi.org/10.1038/s41558-020-0752-x

Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the "animal model.". *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*(1446), 873–890. https://doi.org/10.1098/rstb.2003.1437

Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology*, *20*(5), 1890–1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Lane, J. E., McAdam, A. G., McFarlane, S. E., Williams, C. T., Humphries, M. M., Coltman, D. W., Gorrell, J. C., & Boutin, S. (2018). Phenological shifts in North American red squirrels: Disentangling the roles of phenotypic plasticity and microevolution. *Journal of Evolutionary Biology*, *31*(6), 810–821. https://doi.org/10.1111/jeb.13263

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J. E., Kindberg, J., & Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. *Oecologia*, *180*(3), 697–705. https://doi.org/10.1007/s00442-015-3500-6

Liedvogel, M., Cornwallis, C. K., & Sheldon, B. C. (2012). Integrating candidate gene and quantitative genetic approaches to understand variation in timing of breeding in wild tit populations. *Journal of Evolutionary Biology*, *25*(5), 813–823. https://doi.org/10.1111/j.1420-9101.2012.02480.x

Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits*. Sinauer Associates, Inc.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*(2), 209–220.

Matthysen, E., Adriaensen, F., Van de Kerckhove, P., & Vandekerkhove, K. (2021). Great and blue tit laying dates vary with fine-scale variation in local tree composition but not tree budburst. *Journal of Ornithology*, *162*(3), 709–722. https://doi.org/10.1007/s10336-021-01872-2

McCleery, R. H., Pettifor, R. A., Armbruster, P., Meyer, K., Sheldon, B. C., & Perrins, C. M. (2004). Components of variance underlying fitness in a natural population of the great tit Parus major. *The American Naturalist*, *164*(3), E62–E72. https://doi.org/10.1086/422660

Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., Morris, S., Pemberton, J. M., Kruuk, L. E. B., & Clutton-Brock, T. H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology*, *17*(7), 2455–2469. https://doi.org/10.1111/j.1365-2486.2010.02382.x

Munar-Delgado, G., Araya-Ajoy, Y. G., & Edelaar, P. (2023). Estimation of additive genetic variance when there are gene–environment correlations: Pitfalls, solutions and unexplored questions. *Methods in Ecology and Evolution*, *14*(5), 1245–1258. https://doi.org/10.1111/2041-210X.14098

Noordwijk, A. J. V., McCleery, R. H., & Perrins, C. M. (1995). Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *The Journal of Animal Ecology*, *64*(4), 451. https://doi.org/10.2307/5648

Park, J. S., & Post, E. (2022). Seasonal timing on a cyclical Earth: Towards a theoretical framework for the evolution of phenology. *PLoS Biology*, *20*(12), e3001952. https://doi.org/10.1371/journal.pbio.3001952

Patrick, S. C., Chapman, J. R., Dugdale, H. L., Quinn, J. L., & Sheldon, B. C. (2012). Promiscuity, paternity and personality in the great tit. *Proceedings Biological Sciences*, *279*(1734), 1724–1730. https://doi.org/10.1098/rspb.2011.1820

Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., Betancourt, J. L., & Cleland, E. E. (2011). Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, *17*(12), 3633–3643. https://doi.org/10.1111/j.1365-2486.2011.02515.x

Perrins, C. M. (1969). The timing of birds' breeding seasons. *Ibis*, *112*, 242–255.

Postma, E., & Charmantier, A. (2007). What "animal models" can and cannot tell ornithologists about the genetics of wild populations. *Journal of Ornithology*, *148*(S2), 633–642. https://doi.org/10.1007/s10336-007-0191-8

Réale, D., McAdam, A. G., Boutin, S., & Berteaux, D. (2003). Genetic and plastic responses of a northern mammal to climate change. *Proceedings Biological Sciences*, *270*(1515), 591–596. https://doi.org/10.1098/rspb.2002.2224

Reed, T. E., Waples, R. S., Schindler, D. E., Hard, J. J., & Kinnison, M. T. (2010). Phenotypic plasticity and population viability: The importance of environmental predictability. *Proceedings Biological Sciences*, *277*(1699), 3391–3400. https://doi.org/10.1098/rspb.2010.0771

Regan, C. E., Pilkington, J. G., Bérénos, C., Pemberton, J. M., Smiseth, P. T., & Wilson, A. J. (2017). Accounting for female space sharing in St. Kilda Soay sheep (Ovis aries) results in little change in heritability estimates. *Journal of Evolutionary Biology*, *30*(1), 96–111. https://doi.org/10.1111/jeb.12990

Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Rubolini, D., Møller, A. P., Rainio, K., & Lehikoinen, E. (2007). Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among european bird species. *Climate Research*, *35*(1–2), 135–146. https://doi.org/10.3354/cr00720

Rutschmann, A., de Villemereuil, P., Brekke, P., Ewen, J. G., Anderson, N., & Santure, A. W. (2020). Consequences of space sharing on individual phenotypes in the New Zealand hihi. *Evolutionary Ecology*, *34*(5), 821–839. https://doi.org/10.1007/s10682-020-10063-z

Samplonius, J. M., Atkinson, A., Hassall, C., Keogan, K., Thackeray, S. J., Assmann, J. J., Burgess, M. D., Johansson, J., Macphie, K. H., Pearce-Higgins, J. W., Simmonds, E. G., Varpe, O., Weir, J. C., Childs, D. Z., Cole, E. F., Daunt, F., Hart, T., Lewis, O. T., Pettorelli, N., … Phillimore, A. B. (2021). Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. *Nature Ecology and Evolution*, *5*(2), 155–164. https://doi.org/10.1038/s41559-020-01357-0

Shaw, R. G., & Shaw, F. H. (2014). Quantitative genetic study of the adaptive process. *Heredity*, *112*(1), 13–20. https://doi.org/10.1038/hdy.2013.42

Simmonds, E. G., Cole, E. F., Sheldon, B. C., & Coulson, T. (2020). Testing the effect of quantitative genetic inheritance in structured models on projections of population dynamics. *Oikos*, *129*(4), 559–571. https://doi.org/10.1111/oik.06985

Simmonds, E. G., Sheldon, B. C., Coulson, T., & Cole, E. F. (2017). Incubation behavior adjustments, driven by ambient temperature variation, improve synchrony between hatch dates and caterpillar peak in a wild bird population. *Ecology and Evolution*, *7*(22), 9415–9425. https://doi.org/10.1002/ece3.3446

Stopher, K. V., Walling, C. A., Morris, A., Guinness, F. E., Clutton-Brock, T. H., Pemberton, J. M., & Nussey, D. H. (2012). Shared spatial effects on quantitative genetic parameters: Accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. *Evolution*, *66*(8), 2411–2426. https://doi.org/10.1111/j.1558-5646.2012.01620.x

Teplitsky, C., Mills, J. A., Yarrall, J. W., & Merilä, J. (2010). Indirect genetic effects in a sex-limited trait: The case of breeding time in red-billed gulls. *Journal of Evolutionary Biology*, *23*(5), 935–944. https://doi.org/10.1111/j.1420-9101.2010.01959.x

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M., & Speakman, J. R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, *291*(5513), 2598–2600. https://doi.org/10.1126/science.1057487

Thomson, C. E., Winney, I. S., Salles, O. C., & Pujol, B. (2018). A guide to using a multiple-matrix animal model to disentangle genetic and nongenetic causes of phenotypic variance. *PLOS ONE*, *13*(10), e0197720. https://doi.org/10.1371/journal.pone.0197720

Tryjanowski, P., Rybacki, M., & Sparks, T. (2003). Changes in the first spawning dates of common frogs and common toads in western Poland in 1978-2002. *Annales Zoologici Fennici*, *40*(5), 459–464.

Van Der Jeugd, H. P., & McCleery, R. (2002). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *Journal of Evolutionary Biology*, *15*(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

van Noordwijk, A. J., van Balen, J. H., & Scharloo, W. (1981). Genetic variation in the timing of reproduction in the great tit. *Oecologia*, *49*(2), 158–166. https://doi.org/10.1007/BF00349183

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2006). Density effects on life-history traits in a wild population of the great tit Parus major: Analyses of long-term data with GIS techniques. *The Journal of Animal Ecology*, *75*(2), 604–615. https://doi.org/10.1111/j.1365-2656.2006.01078.x

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2007a). Edge effects in the great tit: Analyses of long-term data with GIS techniques. *Conservation Biology: The Journal of the Society for Conservation Biology*, *21*(5), 1207–1217. https://doi.org/10.1111/j.1523-1739.2007.00767.x

Wilkin, T. A., Perrins, C. M., & Sheldon, B. C. (2007b). The use of GIS in estimating spatial variation in habitat quality: A case study of lay-date in the great tit parus major. *Ibis*, *149*(s2), 110–118. https://doi.org/10.1111/j.1474-919x.2007.00757.x

Wilson, A. J., Coltman, D. W., Pemberton, J. M., Overall, A. D. J., Byrne, K. A., & Kruuk, L. E. B. (2005). Maternal genetic effects set the potential for evolution in a free-living vertebrate population. *Journal of Evolutionary Biology*, *18*(2), 405–414. https://doi.org/10.1111/j.1420-9101.2004.00824.x

Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B., & Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, *79*(1), 13–26. https://doi.org/10.1111/j.1365-2656.2009.01639.x

3

The influence of age and social interactions on plasticity in breeding phenology in a wild bird population

The influence of age and social interactions on plasticity in breeding phenology in a wild bird population

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Abstract

In seasonally-breeding species, selection is expected to favour parents timing reproduction so that peak energetic demand of offspring aligns with resource distribution. Phenotypic plasticity allows individuals to fine-tune their reproductive timing, but many factors might influence plasticity in timing, and drive spatio-temporal variation across populations. Age is likely to affect plasticity in timing as greater experience can shape breeding performance, of which phenological timing is a component. However, there is limited understanding of how age relates to breeding timing given spatial variation in local phenology across habitats, and the role of age-related social mechanisms in mediating this, such as density effects and social learning. We use data from >10,000 great tit breeding events to examine age-specific breeding timing and the effects of local age structure. We find that adult individuals breed earlier than juveniles even when accounting for local phenological variation, providing evidence of advanced breeding with age. We find no evidence that local age structure affects juvenile timing, but that adults breed relatively later when their neighbours are also old. This indicates that juveniles do not use social cues from older more experienced birds to time breeding, potentially due to limited phenotypic plasticity. We suggest that later breeding among adults in adult-biased neighbourhoods could be underpinned by both adaptive and nonadaptive mechanisms. Given that climate change affects phenology across trophic levels, our findings of age-related breeding timing at the individual- and neighbourhood-level are relevant for understanding the drivers of phenotypic plasticity in wild populations in changing environments.

Introduction

In species with seasonal breeding, selection favours parents timing reproduction so that peak energetic demand of young matches with greatest resource availability (Kreitzman & Foster 2010; Schwartz 2003). As such, breeding phenology is under selection to coincide with time-varying resources, often from other trophic levels (Daan et al. 1989; Kharouba & Wolkovich 2020; Park & Post 2022). Phenotypic plasticity, where individuals with a given genotype express different phenotypes depending on environmental conditions (DeWitt & Scheiner 2004; Pigliucci 2001; Stager et al. 2024), allows individuals to fine-tune their reproductive timing such that it matches with temporal variation in resource availability (Charmantier et al. 2008; Nussey et al. 2007; Vedder et al. 2013). However, factors that might influence plasticity in reproductive timing within individuals, and mechanisms that generate spatio-temporal variation in breeding timing across populations, are often neglected when assessing the drivers of breeding phenology.

First (a), for phenotypic plasticity to improve the timing of breeding to better match to the local environment, individuals must be able to forecast the timing of environmental events (Lande 2009; Scheiner 1993). In seasonal environments, this is often achieved using indirect cues, such as temperature, photoperiod, phenological events that are indirectly related to resource availability, or the behaviour of conspecifics (Reed et al. 2010), meaning individuals that are better at recognising and responding to these cues will better time their breeding. Evidence across taxa suggests that breeding performance improves with age, leading to peak performance followed by a decrease in late-life through reproductive senescence (Charlesworth 1994; Clutton-Brock 1988, 1989; Heinze & Schrempf 2008; Nussey et al. 2013). The constraint hypothesis states that this is underpinned by increasing competence mediated by a longer period of learning through previous breeding (Curio 1983; Nol & Smith 1987; Pärt 2001). With regards to phenological timing, the constraint hypothesis might lead to better matching to a local optimum with age as older individuals use previous experience to more effectively track cues related to resource phenology and adjust their breeding timing in response (Fig. 1a). Indeed, there are often repeatable age-related differences in the timing of seasonal breeding, with a general trend of older individuals breeding earlier, particularly in birds (Forslund & Pärt 1995; Martin 1995; Mills & Shaw 1980;

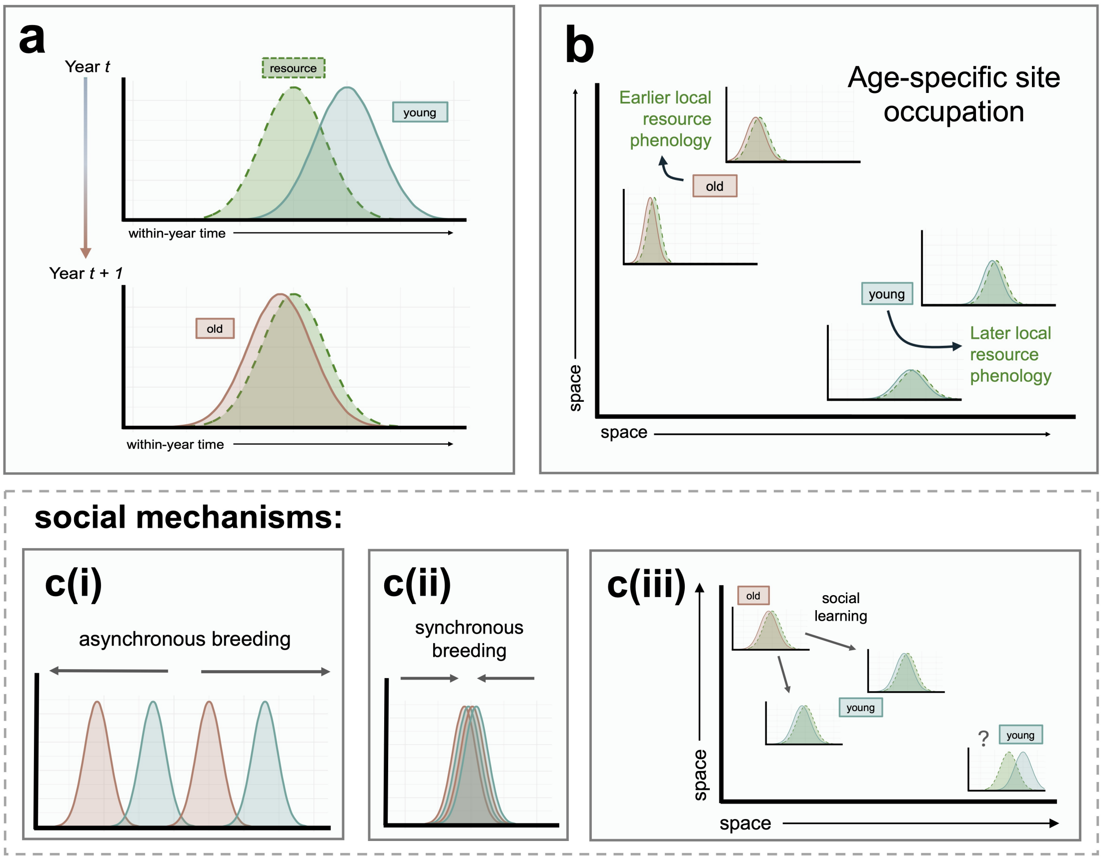

Figure 1: Overview of mechanisms that might shape phenological timing within and between individuals referred to in the introduction. In all plots, green dashed distributions illustrate phenological timing of a resource, blue distributions refer to phenological timing of young individuals, and red distributions refer to phenological timing of old individuals. In a) phenological timing advances as individuals better match a local resource peak with age. In b) there is spatial variation in local resource phenology, and age-specific occupation of sites, but individuals match to their local phenology equally independent of age. In c(i) local breeding phenology is asynchronous between individuals, in c(ii) it is synchronous, and in c(iii) young individuals copy the breeding phenology of older individuals when in close spatial proximity; for example younger individuals may advance their breeding timing to match their older and earlier breeding neighbours and therefore be better matched to the local resource peak, whilst young individuals without older neighbours nearby may breed later than their local resource peak.

Newton 1989; Nol & Smith 1987; Sæther 1990).

Second (b), other factors might influence phenological timing where earlier breeding with age might not be driven by increased phenotypic plasticity in relation to matching to the local environment. In fact, plasticity in behavioural traits is often higher in younger individuals (Araya-Ajoy & Dingemanse 2017; Atwell & Wagner 2014; Ericsson et al. 2016). An understudied mechanism which could lead to age-related differences in breeding timing is age-specificity in breeding habitat choice, across which there is variation in the timing of local resource phenology. If older individuals breed in higher quality sites (Brewer et al. 2009; Ferrer & Bisson 2003; Garneau et al. 2008; Stepanuk et al. 2021) which have earlier local phenology compared to the population mean, but all individuals equally match to local resource optima regardless of age, then older individuals will breed earlier on average (Fig. 1b). Therefore, rather than plastically changing breeding timing given previous experience, timing might largely be driven by spatial variation in phenology across the environment, across which there is age-specific occupation of sites. Indeed, recent work shows that accounting for environmental similarity across breeding sites decreases estimates of the heritability of reproductive timing (Jones et al. 2024), and in this way the same might be true not just for similarity in breeding timing between related individuals, but also for those of the same age.

Third (c), a neglected aspect that might influence breeding timing, and plasticity in this, is the operation of social mechanisms among individuals within the local breeding environment, and how these relate to age. We identify three potential social mechanisms here: (ci) effects due to density; (cii) effects due to selection favouring local synchrony within trophic levels; and (ciii) effects due to social learning of local optima.

(ci) At a proximate scale, breeding density of conspecifics in territorial species can negatively affect reproductive timing if there is higher competition, which may - for instance - hinder the rate at which critical resources are obtained, such as food or breeding sites (Wilkin et al. 2006). This might induce asynchronous breeding across neighbourhoods as some individuals' breeding attempts are delayed (Fig. 1ci). Further, the effects of density might be mediated by local age structure, because older individuals are generally of higher social dominance (Piper 1997; Poston 1997; Sol et al. 2000; Woodman et al. 2024b), thus enhancing the competitive landscape of local breeding environments.

(cii) On an ultimate scale, we might see selection for breeding asynchrony between conspecifics in local breeding environments, such that the negative effects of density-driven competition are avoided, including the need for territory defence, reduced foraging times or increased chance of mortality during aggressive interactions (Both & Visser 2000; Facka & Powell 2021; Goubault et al. 2005; Ward et al. 2006; Wilkin et al. 2006; Ydenberg & Krebs 1987). However, this might involve a trade-off between timing to best fit the social environment versus matching to a temporally-variable resource in the physical environment. Conversely, in some cases selection may favour breeding synchrony among territorial conspecifics if social familiarity is adaptive (Akçay et al. 2009; Frostman & Sherman 2004; Gokcekus et al. 2023; Grabowska-Zhang et al. 2012b; Siracusa et al. 2021; Temeles 1994). In such cases, social familiarity might promote mutual benefits during synchronised breeding such as relaxed competition allowing for coinciding optimal breeding timing to match the local environment, or increased cooperation such as joint predator defence between neighbours (Grabowska-Zhang et al. 2012a; Griffiths et al. 2003; Jungwirth et al. 2015; Rosell et al. 2008; Strodl & Schausberger 2012; Fig. 1cii).

(ciii) Finally, the adjustment of breeding timing may be mediated by social learning. Further, such social learning might be age-specific, as younger individuals may adjust their timing by copying older individuals who have greater familiarity of the local environment from previous breeding (Perrins & McCleery 1985; Piper 2011; Slagsvold & Wiebe 2018), and thus might better forecast the timing of phenological events (Fig. 1ciii). Social cues are important in other reproductive behaviours, such as mate choice (Dugatkin 1992; Gibson & Höglund 1992) and breeding habitat selection (Doligez et al. 2002; Pärt & Doligez 2003; Valone & Templeton 2002). These breeding behaviours often show age-specificity in the degree and direction of social copying, with a common pattern of young tending to learn from older individuals (Dugatkin & Godin 1993; Höglund et al. 1995; Valone 2007; Woodman et al. 2024b). Given that the constraint hypothesis predicts older individuals to better time their reproduction (mechanism 1), and there is high potential for adjusting breeding timing based on social cues, we might expect that individuals breeding for the first time copy and therefore have similarly-timed reproduction to older individuals when exposed to a greater number of experienced breeders in their social environment. However, the operation of these mechanisms that link age-based phenological timing to age-related social mechanisms are currently unknown due to the difficulty of assessing this in wild populations.

In this study, we use 46 years of data from a natural population of great tits *Parus major* detailing individual-level breeding behaviour of 6,850 individuals to assess age-related breeding phenology and understand how the social environment shapes this. First, we assess whether breeding is differentially timed in juvenile and adult individuals, and if age-specific differences in reproductive timing are maintained when accounting for fine-scale phenological differences in the environment. Second, we determine how variation in the age structure of breeding social environments affects reproductive timing in juvenile and adult individuals.

Methods

Study system and data collection

The great tit *Parus major* is a passerine bird found in woodlands across Europe, with breeding ages ranging 1–9, averaging 1.8 years (Perrins 1979; Woodman et al. 2022). Although there are some continuous changes with age (Bouwhuis et al. 2009), the main age effects on many individual-level traits linked to experience are captured by two age-classes: first-years (hereafter juveniles) and older (hereafter adults, Greenwood et al. 1979; Perrins 1979; Sandell and Smith 1991; Gosler 1993; Farine et al. 2015). The species is socially monogamous, with pairs defending territories during annual breeding seasons April–June (Hinde 1952). During breeding, great tits provision their young primarily with a local temporally-variable food supply of caterpillars (Gosler 1993). As such, peak energetic demand of young should be matched to the peak in caterpillar abundance, which itself depends on the leaf development of deciduous trees in the local environment (Hinks et al. 2015).

Data used here are from a long-term study in Wytham Woods, Oxford (51°46'N, 1°20'W), a 385ha mixed deciduous woodland (Savill et al. 2010). The great tit population has been monitored since 1947, where breeding adults and their chicks have been marked with unique British Trust for Ornithology (BTO) rings since the 1960s. Additionally, standard reproductive metrics are collected including clutch size, lay date (the day the first egg of a clutch is laid), hatch date, number of chicks, and number of fledglings (Perrins 1965). Individuals breed almost exclusively in the 1020 nest-boxes which are in fixed positions with known GPS coordinates (Krebs 1971; Wilkin et al. 2006). All chicks are ringed at 14 days of age, while adults are trapped at nest-boxes and identified by ring number, or marked with a new ring if they are immigrants. Age is based on year of hatching for local birds, or plumage characteristics for immigrants which can discern between juveniles and those older than this (Svensson 1992). Although immigration rates are high (46%), most are first caught as juveniles (78%) and can therefore be aged accurately.

Data selection

We used a dataset that assigned the year of hatching to all individuals since 1950, across which exact year of hatching was known for 88.8% of 46,062 identified breeding individuals (Woodman et al. 2022). In this study, we included birds in analyses that attempted to breed between 1978–2023, for which individual identity data were more complete compared to earlier dates (nest-box design was also changed in 1973 from wood boxes that backed directly onto tree trunks to woodcrete boxes suspended by a wire, which changed predation regime, Dunn 1977). Individuals that were first caught post-fledging are assumed to be immigrants, as locally-hatched tits are marked as nestlings in nest-boxes and the proportion of great tits hatched in natural cavities is very low (Kidd et al. 2015). Immigrants that entered the population with adult plumage were assigned a minimum age of 2, and subsequent age estimates were based on this (6.7% and 10.0% of breeding females and males; in these cases, individuals can still be categorised into 'juvenile' and 'adult' categories with certainty). Age was therefore assigned to 80.8% and 71.5% of breeding females and males respectively where at least one egg was laid (due to nests failing prior to adult capture, and unsuccessful trapping attempts, parental identity was unknown in some cases).

Local age-related breeding timing

In order to capture breeding timing both relative to other individuals in an annual breeding population, and also given fine-scale phenological differences in local resource distributions, we calculated two measures of reproductive timing. First, we took each year and centred the lay dates of all breeding attempts such that the mean lay date was 0 for every year. This provides an absolute measure of breeding timing relative to the entire population while removing between-year variability in population-level average breeding timing, which has advanced over time with climate change (Charmantier et al. 2008; Cole et al. 2021).

Second, we calculated a measure of breeding timing relative to fine-scale phenological differences across the study site (hereafter 'local breeding timing mismatch'). Great tit lay dates are linked to local tree phenology, particularly in terms of bud-burst dates of oaks *Quercus* spp. within their foraging range. Individual timing of oak bud-burst is highly repeatable between years relative to other oaks in the population, but varies across small spatial scales (Cole & Sheldon 2017; Hinks et al. 2015). Therefore, we took every breeding attempt within each year, and calculated the difference between a focal female's lay date and the lay date expected given the breeding locality, giving a measure of breeding timing relative to that of the average for a specific local environment. We calculated the average lay date for each locality by taking the median of all year-centred lay dates 1965–2023 associated with the focal nest-box in which the breeding attempt took place (additional years of data were used to calculate the long-term average because since 1978 data for individual identity is more complete, but before this date standardised and complete data collection of laying dates were still recorded). In the analysis we used a subset of boxes that had been occupied at least 10 times over the study period (leaving 80% of all boxes; Fig. S1) to ensure that the box-level median lay date was representative, as boxes with low occupancy over years are more likely to be skewed by individual breeding attempts. We also calculated average lay date for each locality at a coarser spatial scale (supporting information). The average lay date associated with a nest-box is not biased by age-specific occupation in the long-term, as this does not show temporal repeatability within this study system (Woodman et al. 2024a).

To assess the role of age-related social mechanisms on breeding timing, we considered how the age structure of breeding neighbourhoods interacts with lay date in terms of absolute breeding timing, and local breeding timing mismatch. Great tit lay dates are primarily considered a female

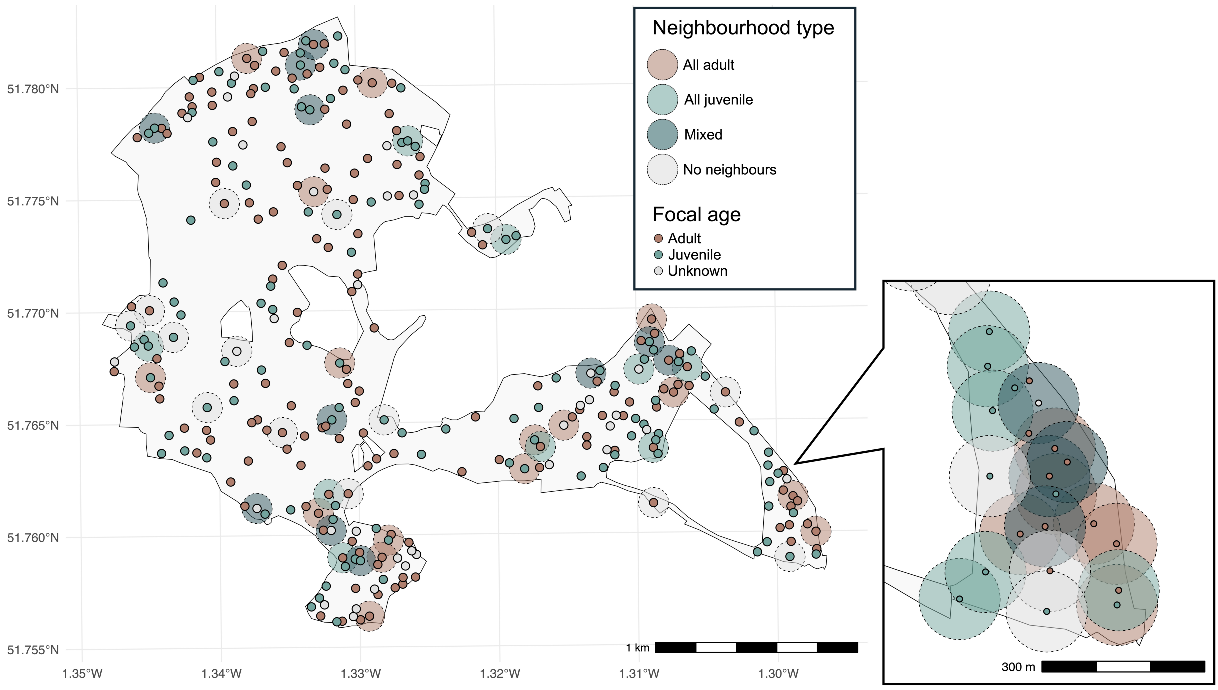

Figure 2: Illustration of variation in neighbourhood age structures across Wytham within a single year (2009). We demonstrate the variation in age structure neighbourhood types by randomly sampling 50 occupied boxes in the plot of the entire study system, and provide an enlarged section on the right of all neighbourhoods within a specific subset of Wytham. Each point is a nest-box, occupied by either an adult (red), juvenile (blue) or unknown (grey) female. Around each box a 75m radius buffer was placed to calculate whether a focal female has all adult (red), all juvenile (light blue), mixed aged (dark blue), or no neighbours (grey).

trait, as the timing is principally controlled by the female, and heritability of the trait is less than a fifth in males compared to females (Evans et al. 2020; Jones et al. 2024; Perrins & McCleery 1989). Therefore, we considered how a female's lay date varied depending on the age composition of its female neighbours. We defined neighbours as individuals that bred within 75m of each other. While there are alternative ways to determine neighbourhoods in territorial species (e.g. Thiessen polygons, Gokcekus et al. 2023; Schlicht et al. 2014; Wilkin et al. 2006; Woodman et al. 2024a), these are more appropriate when considering neighbours during concurrent chick-rearing behaviour. Here, we are concerned with behaviour prior to egg-laying, which is the period during which social mechanisms might affect breeding timing between neighbours.

Although the precise spatial scale at which individuals interact during this period is not known, we chose 75m as an appropriate scale based on previous studies that assess space-use during pre-breeding behaviour in great tits (Both & Visser 2000; Firth et al. 2018; Krebs 1971). For every breeding female, we calculated the number of their female neighbours that were adults. We removed cases where a nest-box was used for a second time (0.30%) and females' second broods (0.75%) within years, as these occur much later (Perrins 1965, 1979) and it can be assumed that the timing of these attempts are not underpinned by the same mechanisms as first breeding events.

Statistical analyses

We used Bayesian regression models to assess the effect of neighbourhood age structure on lay date as (1) absolute breeding timing and (2) local breeding timing mismatch. Bayesian regression models were chosen due to their flexibility in handling complex hierarchical structures and the ability to incorporate prior information, which is particularly useful in ecological studies such as this where data can be noisy. The models also provide full posterior distributions of the estimated parameters, allowing for nuanced interpretation of the results.

We constructed separate Gaussian models to estimate the marginal effects of local age structure on breeding timing defined by a categorised measure of neighbourhood type (either 'all juvenile', 'all adult', 'mixed', where both age classes exist within the neighbourhood, or 'no neighbours', where no birds bred within 75m of the focal female; Fig. 2). We chose a categorical instead of continuous measure to allow for a more biologically-meaningful interpretation of interactions between different age structures and breeding timing. Additionally, using a continuous measure would not allow for clear differentiation of the 'no neighbours' category, as 0% adult neighbours could either mean no neighbours at all or only juvenile neighbours (see also supporting information).

To account for between-year differences in breeding timing variance, and repeated measures of the same nest-box or female across years, we included year, nest-box and female ID as random effects. In all models, we included the age of the focal female as an interaction term to test for differences in the effect of neighbourhood age structure on breeding timing depending on the focal female's age (Table S1).

These models were run using *brms* version 2.21.0 (Bürkner 2017), an interface to the Hamilton Monte Carlo engine Stan (Stan Development Team 2024). Models were run using uninformative flat priors and the *marginaleffects* package was used to process posterior distributions (Arel-Bundock et al. 2024). Model convergence was checked using the effective number of samples and inspection of chain trace plots. We report posterior median estimates and their 95% credible intervals.

Results

In total, we recorded 10,931 breeding attempts by 6,850 female great tits across 46 years. There was profound spatial variation in the average phenology of breeding sites, with the average year-centred lay date of nest-boxes ranging from -8.4 to 10.3 (i.e. approximately 19 days difference in the average lay date at nest-boxes accounting for between-year differences in breeding populations' overall timing). The number of neighbours found breeding within 75m of a focal female ranged from 0–9. Both annual population size and age structure showed marked temporal variation (proportion of juvenile females ranged from 29.7–67.8%; female population size ranged from 145–470), which together led to great spatio-temporal variation in the range of neighbourhood age structure types across the study system (Fig. S2).

Our results support previous studies showing average absolute breeding timing (laying date accounting for annual differences) of juvenile birds is a little more than 2 days later than adult birds (lay date difference in days posterior median [95% credible intervals]: 2.22 [1.73, 2.70]). Further, we find that when calculating local breeding timing mismatch, therefore accounting for spatial variation in local phenology, the average difference between adults and juveniles is also close to 2 days (2.09 [1.61, 2.57]).

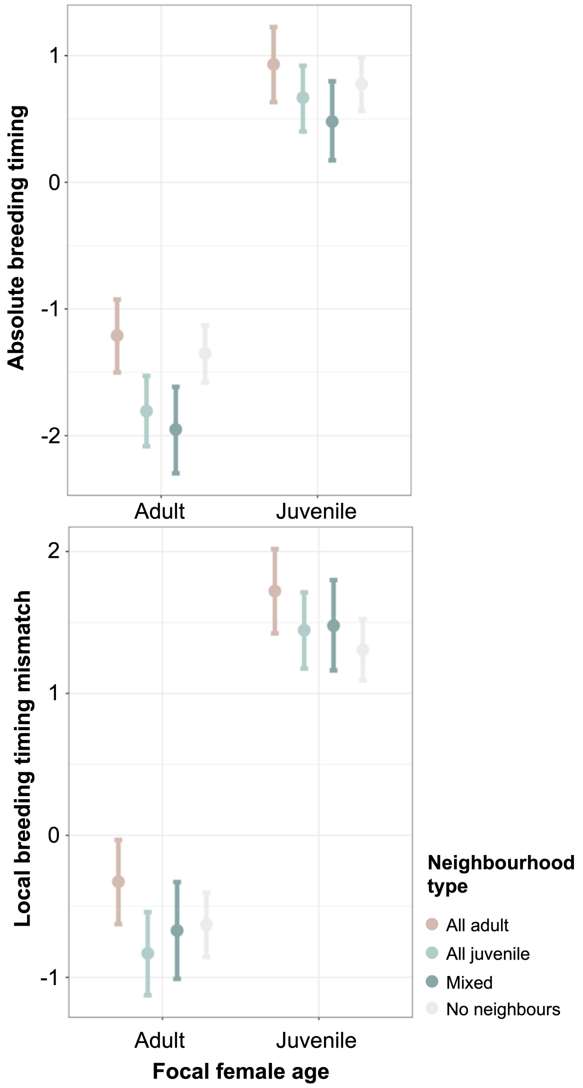

Figure 3: Marginal predictions of breeding timing in adult and juvenile great tits depending on their neighbourhood age structure as defined by: a) absolute breeding timing; or b) local breeding timing mismatch.

Neighbourhood age structure had a stronger influence on adult birds' absolute laying date and local breeding timing mismatch compared to juveniles (Fig. 3). There was not a significant difference between the absolute laying date of juvenile birds depending on whether they are surrounded by all adult or all juvenile neighbours (all adult neighbours: 0.93 [0.63, 1.23], all juvenile neighbours: 0.67 [0.40, 0.92]). Adult birds with all adult neighbours had later absolute laying dates compared to those with all juvenile neighbours, but they still laid earlier than the mean within years (all adult neighbours: -1.21 [-1.50, -0.93], all juvenile neighbours: -1.81 [-2.08, -1.53]). Similar patterns were found assessing local breeding timing mismatch, in that adults showed slightly later average breeding when surrounded by all adult neighbours compared to all juvenile neighbours (all adult neighbours: -0.33 [-0.63, -0.03], all juvenile neighbours: -0.83 [-1.13, -0.54]), whereas the same pattern was not seen as strongly in juvenile birds (all adult neighbours: 1.72 [1.42, 2.02], all juvenile neighbours: 1.45 [1.18, 1.71]).

Birds within mixed age-cohort neighbourhoods had very similar laying dates to birds with all juvenile neighbours regardless of the focal female's age, though there are minor differences depending on whether laying date is measured as absolute or local breeding timing mismatch (Fig. 3). Both absolute lay date and local breeding timing mismatch for individuals that have no neighbours varies across models (Table S2 for all results).

Discussion

Using 10,931 records of breeding female great tits across 46 years, we quantified whether age-specific earlier breeding in adult great tits is maintained considering fine-scale variation in local phenology, and whether such timing is affected by the age structure of the social breeding environment. We find that adult females breed earlier than juveniles not only compared to the population-average, but also given local phenological variability, providing evidence of significant age-related differences in breeding behaviour, which is potentially consistent with the constraint hypothesis. Given persistent differences in breeding timing relative to local environmental variation between juvenile and older individuals, we find no evidence that the age structure of breeding neighbourhoods has an effect on the timing of juveniles' reproductive attempts, but that adults breed relatively later when their neighbours are also adults compared to when they have all juvenile neighbours.

Adult females had earlier lay dates not only relative to the breeding population within any year, but also considering local environmental differences in phenology. While it is well-established that there are often repeatable age-related differences in breeding timing across taxa (Forslund & Pärt 1995; Morgan et al. 2013; Newton 1989; Nussey et al. 2006; Sæther 1990), the role of age-specific habitat-use in phenologically-variable environments in driving this pattern is often overlooked. Our findings suggest that there is not co-variation between age and average local resource phenology in breeding sites. If there was age-specific site occupation where adults breed in habitats with earlier local resource phenology, then given our findings that adults breed earlier than juveniles regardless of local phenology, we would expect an even greater difference between the absolute breeding timing of juveniles and adults at the population-level. Instead, the difference in average breeding timing between juveniles and adults is similar whether assessing local breeding timing mismatch or absolute breeding timing, suggesting earlier breeding in adults is driven by advancement relative to their local average phenology across which there is not age-specific occupation.

Given theories of increasing reproductive performance with age under the constraint hypothesis, this might suggest that adults with greater experience advance their lay dates to enhance breeding performance (Harvey et al. 1979b; Perrins & McCleery 1985, 1989), such as through better matching breeding with temporally-variable resource distributions, even when there is fine-scale phenological variation (Cole et al. 2021; Hinks et al. 2015). This is consistent with findings in other age-related reproductive behaviours in closely-related blue tits *Cyanistes caeruleus*, where adults use knowledge from previous breeding of average patch reproductive success to make decisions regarding settlement, whereas juveniles are unable to do so as they lack breeding experience (Parejo et al. 2007). However, implicit in this suggestion would be that advancement of breeding timing leads to better precision of matching chick rearing behaviour with local resource phenology, whereas in fact advancement could represent cases where breeding occurs so early that there is a mismatch between peak energetic demand of offspring and resource availability. Future work could decouple age-related advancement of breeding timing with increasing precision to local resource phenology through more detailed data collection of phenological timing across multiple trophic levels at local scales across phenologically-variable environments.

Irrespective of their neighbourhood age structure, we find that juvenile great tits lay later relative to both the population average, and the average of its local environment. This suggests that birds undertaking their first reproductive attempts do not use social cues to adjust breeding timing. Adult great tits breed earlier on average (Harvey et al. 1979b; Perrins 1965; Sæther 1990), and as shown in the present study, earlier breeding exhibited by adults occurs even when accounting for fine-scale phenological variation across territories. Therefore, if juveniles were to use social cues from neighbours to adjust their own timing, we would expect differences among their lay dates depending on whether they are mainly exposed to adult or juvenile neighbours, or if they exist in areas of low density and thus have little social opportunity. However, despite the extent of the data used here, we find no evidence of social cues affecting breeding timing in juveniles.

The fact that there is no evidence of juveniles copying the breeding timing of conspecifics is interesting given the wider socio-ecology of great tits and other short-lived territorial species. This is because tit *Paridae* species often show age-specific trends where younger individuals rely more on copying conspecifics in behaviours associated with foraging (Aplin et al. 2017), and are more plastic in changing such behaviours in response to social cues (Aplin et al. 2012, 2013). However, we find no evidence that juveniles copy phenological timing behaviour in the same way. This suggests that juveniles instead predominantly use cues within their physical environment to time breeding, such as budburst in local tree species or increasing temperatures (Reed et al. 2010).

While it is expected that younger individuals have less experience-based information of when to time breeding attempts, this does not explain why they show limited ability to use social cues from those in their breeding environment. This may be driven by lower phenotypic plasticity in juveniles. For example, recent work shows that juvenile blue tits show minimal phenotypic plasticity with regards to adjusting lay date to temperature (Bonamour et al. 2020). It is suggested that younger individuals may have not accumulated enough resources to adequately modulate laying date in response to temperature, which for example might require an earlier onset of egg production (Nilsson & Råberg 2001; Perrins 1996; Visser & Lessells 2001). Therefore, the same might be the case here, where juveniles are unable to adjust their laying date in response to the timing of more experienced neighbours due to the associated energetic cost.

We find a greater difference in breeding timing among adults depending on the age structure of their neighbourhoods compared to juveniles. Specifically, we find that breeding timing relative to the entire population is later in adults with either no or only adult neighbours. When breeding timing is calculated accounting for local phenological variability, adults with juvenile, mixed-age cohort or no neighbours breed earlier (and with a greater mismatch to the box-level average) compared to those with only adult neighbours (Fig. 3). The difference in breeding timing in adults with no neighbours depending on whether this is calculated accounting for local phenological variation or not highlights the potential for estimates of age-related breeding timing to be biased based on fine-scale phenological variability. Specifically, when comparing against a within-year population average, adults with no neighbours breed later than those in juvenile or mixed age-cohort neighbourhoods. However, accounting for average phenological variation across territories, adults with no neighbours are more similar in their relative breeding timing to those with juvenile neighbours. When assessing the relationship between the number of neighbours and the average phenological timing of nest-boxes in the long-term, we find that there is a relationship where boxes with fewer neighbours are timed slightly later on average (Fig. S3). This is likely driven by habitat heterogeneity within the study site, where areas of high nest-box density tend to be in regions with habitat features associated with earlier phenology (i.e. lower altitude and nearer the woodland edge, Fig. S4; Wilkin et al. 2007a, 2007b). It is unlikely that this relationship is confounded with age-biased use of territories over time, as there is no temporal repeatability in age-specific occupation of nest-boxes in this study system (Woodman et al. 2024a).

Previous research has suggested that in seasonally-breeding species, selection might act to promote early breeding to increase reproductive success (Arnold et al. 2004; Perrins 1970; Verhulst & Tinbergen 1991). However, breeding later than this optimum is frequently observed, suggesting that there are either physiological constraints that prevent individuals breeding when reproductive output is maximised, or breeding time is the outcome of an optimisation process where there are sometimes fitness costs associated with early breeding (Arcese & Smith 1988; Brown & Brown 2000; Davies & Lundberg 1985; Nager & van Noordwijk 1992; Nilsson 1994; Perrins 1996). However, the proximate mechanisms that might induce trade-offs in breeding timing are still not well understood.

Our finding of differences in average breeding timing among adults depending on their neighbourhood age structure might provide initial evidence that social mechanisms are involved in the trade-off associated with breeding timing. One such social mechanism might be related to how familiarity among territorial neighbours can increase reproductive success during synchronised breeding events (Akçay et al. 2009; Frostman & Sherman 2004; Grabowska-Zhang et al. 2012b; Siracusa et al. 2021). Given that adults are more likely to be familiar with each other from previous breeding and winter flocking behaviour compared to juveniles or mixed age-cohorts (Gokcekus et al. 2023), we might expect their neighbourhoods to synchronise breeding to obtain mutual benefits, such as cooperative nest defence (Grabowska-Zhang et al. 2012a). Synchronised breeding among individuals might induce on average later breeding than the local optimum, where individuals which could breed earlier delay egg laying to match with their neighbours. Indeed, research using captive starlings *Sturnus vulgaris* found that adults housed next to experimentally-induced late breeders (through food rationing) delay their own laying to synchronise with the experimental birds, whereas a control group that was isolated from the rationed birds bred earlier (Meijer & Langer 1995). This finding, in combination with the suggestions made here, point to a potential socially adaptive mechanism that promotes on average later breeding to increase reproductive synchronisation among adults.

Alternatively, delayed breeding among adults with adult-biased breeding neighbourhoods might be driven by non-adaptive mechanisms. In this case, instead of later laying being a result of a trade-off between early and later breeding to maximise reproductive success, non-adaptive delayed breeding might occur due to age-specific social mechanisms. For example, in many taxa, older individuals are dominant in competitive interactions, allowing them to monopolise resources (Piper 1997; Poston 1997; Sol et al. 2000; Woodman et al. 2024b), including in great tits (Krebs 1971, 1982; Sandell & Smith 1991). Therefore, adult great tits that either have no neighbours in areas of low density, or acquire territories near subdominant juvenile neighbours, might be able to breed earlier due to their social dominance or lack of competition. This might allow dominant adults to monopolise local food resources thus reaching the necessary energetic demands for egg laying at earlier dates (Nager & van Noordwijk 1992; Perrins 1996; Visser & Lessells 2001).

Alternatively, socially dominant adults might acquire breeding territories at earlier dates, particularly if this territory was occupied in previous years (Greenwood et al. 1979; Harvey et al. 1979a), allowing for earlier egg-laying compared to subdominant neighbouring individuals that take longer to acquire territories. In these cases, adults breeding in adult-biased breeding environments might experience greater competition, delaying the rate at which they can obtain critical breeding resources and leading to later average lay dates. This is consistent with findings that suggest higher breeding densities lead to greater competition, thus delaying lay dates in territorial species (Wilkin et al. 2006). Future research would ideally use experimental manipulations to disentangle the relative role of adaptive versus nonadaptive mechanisms in mediating breeding timing in territorial species depending on local age structure and familiarity among older individuals. Further, experiments could be used to separate out the roles of age *per se* versus familiarity (i.e. either social familiarity from previous association with neighbours, or environmental familiarity with the breeding location from prior reproduction) in driving differences in breeding timing among adults. However, these sorts of experiments are complex and may not be possible to carry out in wild systems such as the one used in this study.

The findings presented here may be relevant in the context of the effects of climate change on breeding phenology. Over recent decades, climate change has advanced the timing of phenological events due to earlier and warmer temperatures (Davis et al. 2005; Visser & Both 2005; Zettlemoyer & DeMarche 2022). In some cases, this has advanced interacting species' phenological events to different extents, leading to phenological asynchrony where seasonal breeding in one species occurs later than peak abundance of resources from another (Radchuk et al. 2019; Renner & Zohner 2018; Visser & Gienapp 2019). This poses a considerable potential concern for birds in a deciduous tree–caterpillar–passerine-bird food chain, such as great tits, where there is evidence for an evolved response to climate-induced changes in phenology (Both et al. 2004, 2009; Burgess et al. 2018; Dunn et al. 2010; Marrot et al. 2018; Simmonds et al. 2020; Visser et al. 1998, 2004, 2006). Given large-scale climatic changes to phenology, it is important to understand potential drivers of plasticity in populations due to processes operating at various levels, such as the suggestions made here of persistent age-specific differences in the timing of breeding, reduced plasticity in juveniles manifested as an inability to copy experienced adults in their social environment, and differences among adult lay dates associated with local age structure.

Further, age effects on phenology at the individual- and neighbourhood-level might be relevant given our current understanding of the effects of climate on population demography. Short-lived seasonally-breeding species show profound fluctuations in population age structure (Gamelon et al. 2016; Woodman et al. 2022). For example, the age structure of breeding great tit populations in a given year can range from being almost entirely composed of adults to being almost 90% juvenile individuals, which appears to be linked to climatic variation affecting age-specific survival and recruitment (Woodman et al. 2024c). As such, climate change induced changes to population age structure might be synergistic in their effects on population reproductive output. This is because fluctuations in age structure affect output due to age-specific reproduction and density dependent dynamics (Bouwhuis et al. 2009, 2010; Gamelon et al. 2016; Perrins & McCleery 1985), but also because population-level matching to changes in phenology may be affected by the overall distribution of age and how age is spatially-structured within a population, given our findings presented here. Future work should further our understanding on how climatic induced changes to age structure in wild populations affects population-level reproductive output mediated by phenological synchrony, how this is influenced by within-population structuring of age, and whether the sensitivity of breeding timing given local age structure is affected by spatio-temporal environmental variability.

Conclusions

Using long-term data from a wild territorial bird species in which reproductive success is mediated by phenological timing, we show that adult individuals breed earlier than juveniles even when accounting for fine-scale local phenological variability, thus providing evidence of increased phenotypic plasticity in adults consistent with the constraint hypothesis. We find no evidence that the age structure of breeding neighbourhoods affects the timing of reproduction in younger individuals breeding for the first-time in their life-history, suggesting that such individuals do not use social cues when timing breeding, possibly due to reduced phenotypic plasticity. In contrast, we find that local age structure relates to reproductive timing in adults, where relatively later breeding is observed when their neighbours consist of other older individuals. This could be underpinned either by adaptive mechanisms, where increased familiarity leads to synchronised later breeding to obtain joint benefits, or nonadaptive mechanisms, where greater competition delays breeding. Our study provides a framework to study how social mechanisms influence reproductive timing in territorial breeding populations, not just with regard to age, but other individual-level traits and site-level attributes. Finally, we highlight the potential for climate change to have complex synergistic effects on wild population dynamics, not just by altering average phenological timing across a population, but also because changes to overall population age structure induced by environmental change will influence within-population structuring of age and population-level phenological synchrony.

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References

Akçay, Ç., Wood, W.E., Searcy, W.A., Templeton, C.N., Campbell, S.E. & Beecher, M.D. (2009). Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. Anim Behav, 78, 97–102.

Aplin, L.M., Farine, D.R., Morand-Ferron, J. & Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society B: Biological Sciences, 279, 4199–4205.

Aplin, L.M., Sheldon, B.C. & McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. Proc Natl Acad Sci U S A, 114, 7830–7837.

Aplin, L.M., Sheldon, B.C. & Morand-Ferron, J. (2013). Milk bottles revisited: Social learning and individual variation in the blue tit, Cyanistes caeruleus. Anim Behav, 85, 1225–1232.

Araya-Ajoy, Y.G. & Dingemanse, N.J. (2017). Repeatability, heritability, and age-dependence of seasonal plasticity in aggressiveness in a wild passerine bird. Journal of Animal Ecology, 86, 227–238.

Arcese, P. & Smith, J.N.M. (1988). Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology, 57, 119–136.

Arel-Bundock, V., Greifer, N. & Heiss, A. (2024). How to interpret statistical models using marginaleffects in R and Python. Journal of Statistical Software, 111(9), 1–32. https://doi.org/10.18637/

Arnold, J.M., Hatch, J.J. & Nisbet, I.C.T. (2004). Seasonal declines in reproductive success of the common tern Sterna hirundo: Timing or parental quality? J Avian Biol, 35, 33–45.

Atwell, A. & Wagner, W.E. (2014). Female mate choice plasticity is affected by the interaction between male density and female age in a field cricket. Anim Behav, 98, 177–183.

Bonamour, S., Chevin, L.M., Réale, D., Teplitsky, C. & Charmantier, A. (2020). Age-dependent phenological plasticity in a wild bird. Journal of Animal Ecology, 89, 2733–2741.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., et al. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society B: Biological Sciences, 271, 1657–1662.

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. & Visser, M.E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? Journal of Animal Ecology, 78, 73–83.

Both, C. & Visser, M.E. (2000). Breeding territory size affects fitness: An experimental study on competition at the individual level. Journal of Animal Ecology, 69, 1021–1030.

Bouwhuis, S., Van Noordwijk, A.J., Sheldon, B.C., Verhulst, S. & Visser, M.E. (2010). Similar patterns of age-specific reproduction in an island and mainland population of great tits Parus major. J Avian Biol, 41, 615–620.

Bouwhuis, S., Sheldon, B.C., Verhulst, S. & Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B: Biological Sciences, 276, 2769–2777.

Brewer, S.K., DiStefano, R.J. & Rabeni, C.F. (2009). The influence of age-specific habitat selection by a stream crayfish community (Orconectes spp.) on secondary production. Hydrobiologia, 619, 1–10.

Brown, C.R. & Brown, M.B. (2000). Weather-mediated natural selection on arrival time in cliff swallows (Petrochelidon pyrrhonota). Behav Ecol Sociobiol, 47, 339–345.

Burgess, M.D., Smith, K.W., Evans, K.L., Leech, D., Pearce-Higgins, J.W., Branston, C.J., et al. (2018). Tritrophic phenological match-mismatch in space and time. Nat Ecol Evol, 2, 970–975.

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. J Stat Softw, 80, 1–28.

Charlesworth, B. (1994). Evolution in age-structured populations. Cambridge University Press Cambridge.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science (1979), 320, 800–803.

Clutton-Brock, T.H. (1988). Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago.

———. (1989). Mammalian Mating Systems. Proceedings of the Royal Society B: Biological Sciences, 236, 339–372.

Cole, E.F., Regan, C.E. & Sheldon, B.C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. Nat Clim Chang, 11, 872–878.

Cole, E.F. & Sheldon, B.C. (2017). The shifting phenological landscape: Within- and between-species variation in leaf emergence in a mixed-deciduous woodland. Ecol Evol, 7, 1135–1147.

Curio, E. (1983). Why do young birds reproduce less well? Ibis, 125, 400–404.

Daan, S., Dijkstra, C., Drent, R. & Meijer, T. (1989). Food supply and the annual timing of avian reproduction. Acta XIX Congressus Internationalis Ornithologici, Volume I. 19th International Ornithological Congress, I, 392–407.

Davies, N.B. & Lundberg, A. (1985). The influence of food on time budgets and timing of breeding of the Dunnock Prunella modularis. Ibis, 127, 100–110.

Davis, M.B., Shaw, R.G. & Etterson, J.R. (2005). Evolutionary responses to changing climate. Ecology, 86, 1704–1714.

DeWitt, T.J. & Scheiner, S.M. (2004). Phenotypic plasticity: functional and conceptual approaches. Oxford University Press.

Doligez, B., Danchin, E. & Clobert, J. (2002). Public information and breeding habitat selection in a wild bird population. Science (1979), 297, 1168–1170.

Dugatkin, L.A. (1992). Sexual Selection and Imitation: Females Copy the Mate Choice of Others. Am Nat, 139, 1384–1389.

Dugatkin, L.A. & Godin, J.G.J. (1993). Female mate copying in the guppy (poecilia reticulata): Age-dependent effects. Behavioral Ecology, 4, 289–292.

Dunn, E. (1977). Predation by Weasels (Mustela nivalis) on Breeding Tits (Parus Spp.) in Relation to the Density of Tits. Journal of Animal Ecology, 46, 633–652.

Dunn, P.O., Winkler, D.W., Møller, A.P., Fiedler, W. & Berthold, P. (2010). Effects of climate change on timing of breeding and reproductive success in birds. Effects of climate change on birds, 11, 17.

Ericsson, M., Henriksen, R., Bélteky, J., Sundman, A.S., Shionoya, K. & Jensen, P. (2016). Long-term and transgenerational effects of stress experienced during different life phases in chickens (Gallus gallus). PLoS One, 11.

Evans, S.R., Postma, E. & Sheldon, B.C. (2020). It takes two: Heritable male effects on reproductive timing but not clutch size in a wild bird population. Evolution (N Y), 74, 2320–2331.

Facka, A.N. & Powell, R.A. (2021). Intraspecific competition, habitat quality, niche partitioning, and causes of intrasexual territoriality for a reintroduced carnivoran. Front Ecol Evol, 9.

Farine, D.R., Firth, J.A., Aplin, L.M., Crates, R.A., Culina, A., Garroway, C.J., et al. (2015). The role of social and ecological processes in structuring animal populations: A case study from automated tracking of wild birds. R Soc Open Sci, 2.

Ferrer, M. & Bisson, I. (2003). Age and territory-quality effects on fecundity in the Spanish Imperial Eagle (Aquila adalberti). Auk, 120, 180–186.

Firth, J.A., Verhelst, B.L., Crates, R.A., Garroway, C.J. & Sheldon, B.C. (2018). Spatial, temporal and individual-based differences in nest-site visits and subsequent reproductive success in wild great tits. J Avian Biol, 49, 1–11.

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. Trends Ecol Evol, 10, 374–378.

Frostman, P. & Sherman, P.T. (2004). Behavioral response to familiar and unfamiliar neighbors in a territorial cichlid, Neolamprologus pulcher. Ichthyol Res, 51, 283–285.

Gamelon, M., Grøtan, V., Engen, S., Bjørkvoll, E., Visser, M.E. & Sæther, B.E. (2016). Density dependence in an age-structured population of great tits: Identifying the critical age classes. Ecology, 97, 2479–2490.

Garneau, D.E., Boudreau, T., Keech, M. & Post, E. (2008). Habitat use by black bears in relation to conspecifics and competitors. Mammalian Biology, 73, 48–57.

Gibson, R.M. & Höglund, J. (1992). Copying and sexual selection. Trends Ecol Evol, 7, 229–232.

Gokcekus, S., Firth, J.A., Regan, C., Cole, E.F., Sheldon, B.C. & Albery, G.F. (2023). Social Familiarity and Spatially Variable Environments Independently Determine Reproductive Fitness in a Wild Bird. American Naturalist, 201, 813–824.

Gosler, Andrew. (1993). The great tit . Hamlyn species guides. Hamlyn, London.

Goubault, M., Outreman, Y., Poinsot, D. & Cortesero, A.M. (2005). Patch exploitation strategies of parasitic wasps under intraspecific competition. Behavioral Ecology, 16, 693–701.

Grabowska-Zhang, A.M., Sheldon, B.C. & Hinde, C.A. (2012a). Long-term familiarity promotes joining in neighbour nest defence. Biol Lett, 8, 544–546.

Grabowska-Zhang, A.M., Wilkin, T.A. & Sheldon, B.C. (2012b). Effects of neighbor familiarity on reproductive success in the great tit (Parus major). Behavioral Ecology, 23, 322–333.

Greenwood, P.J., Harvey, P.H. & Perrins, C.M. (1979). The role of dispersal in the great tit (Parus major): The causes, consequences and heritability of natal dispersal. Journal of Animal Ecology, 48, 123–142.

Griffiths, S., Höjesjö, J. & Johnsson, J. (2003). Familiarity confers anti-predator and foraging advantages on juvenile brown trout. J Fish Biol, 63, 226.

Harvey, P.H., Greenwood, P.J. & Perrins, C.M. (1979a). Breeding area fidelity of great tits (Parus major). Journal of Animal Ecology, 48, 305–313.

Harvey, P.H., Greenwood, P.J., Perrins, C.M. & Martin, A.R. (1979b). Breeding success of great tits Parus major in relation to age of male and female parent. Ibis, 121, 216–219.

Heinze, J. & Schrempf, A. (2008). Aging and reproduction in social insects - A mini-review. Gerontology.

Hinde, R.A. (1952). The Behaviour of the Great Tit (Parus major) and Some Other Related Species. Behaviour, 2, 1–201.

Hinks, A.E., Cole, E.F., Daniels, K.J., Wilkin, T.A., Nakagawa, S. & Sheldon, B.C. (2015). Scale-dependent phenological synchrony between songbirds and their caterpillar food source. American Naturalist, 186, 84–97.

Höglund, J., Alatalo, R. V., Gibson, R.M. & Lundberg, A. (1995). Mate-choice copying in black grouse. Anim Behav, 49, 1627–1633.

Jones, C. V., Regan, C.E., Firth, J.A., Cole, E.F. & Sheldon, B.C. (2024). Environmental similarity between relatives reduces heritability of reproductive timing in wild great tits. bioRxiv.

Jungwirth, A., Josi, D., Walker, J. & Taborsky, M. (2015). Benefits of coloniality: Communal defence saves anti-predator effort in cooperative breeders. Funct Ecol, 29, 1218–1224.

Kharouba, H.M. & Wolkovich, E.M. (2020). Disconnects between ecological theory and data in phenological mismatch research. Nat Clim Chang.

Kidd, L.R., Sheldon, B.C., Simmonds, E.G. & Cole, E.F. (2015). Who escapes detection? Quantifying the causes and consequences of sampling biases in a long-term field study. Journal of Animal Ecology, 84, 1520–1529.

Krebs, J.R. (1971). Territory and Breeding Density in the Great Tit, Parus Major L. Ecology, 52, 2–22.

———. (1982). Territorial Defence in the Great Tit (Parus major): Do Residents Always Win? Behavioral Ecology and Sociobiology , 11, 185–194.

Kreitzman, L. & Foster, R. (2010). Seasons of life: the biological rhythms that enable living things to thrive and survive. Profile Books.

Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. J Evol Biol, 22, 1435–1446.

Marrot, P., Charmantier, A., Blondel, J. & Garant, D. (2018). Current spring warming as a driver of selection on reproductive timing in a wild passerine. Journal of Animal Ecology, 87, 754–764.

Martin, K. (1995). Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoology, 35, 340–348.

Meijer, T. & Langer, U. (1995). Food availability and egg-laying of captive European starlings. Condor, 97, 718–728.

Mills, J.A. & Shaw, P.W. (1980). The influence of age on laying date, clutch size, and egg size of the white-fronted tern, sterna striata. N Z J Zool, 7, 147–153.

Morgan, M.J., Wright, P.J. & Rideout, R.M. (2013). Effect of age and temperature on spawning time in two gadoid species. Fish Res, 138, 42–51.

Nager, R.G. & van Noordwijk, A.J. (1992). Energetic limitation in the egg-laying period of great tits. Proceedings of the Royal Society B: Biological Sciences, 249, 259–263.

Newton, I. (1989). Lifetime reproduction in birds.

Nilsson, J.-Å. (1994). Energetic bottle-necks during breeding and the reproductive cost of being too early. Journal of Animal Ecology, 63, 200–208.

Nilsson, J.-Å. & Råberg, L. (2001). The resting metabolic cost of egg laying and nestling feeding in great tits. Oecologia, 128, 187–192.

Nol, E. & Smith, J.N.M. (1987). Effects of age and breeding experience on seasonal reproductive success in the song sparrow. J Anim Ecol, 301–313.

Nussey, D.H., Froy, H., Lemaitre, J.F., Gaillard, J.M. & Austad, S.N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. Ageing Res Rev, 12, 214–225.

Nussey, D.H., Kruuk, L.E.B., Donald, A., Fowlie, M. & Clutton-Brock, T.H. (2006). The rate of senescence in maternal performance increases with early-life fecundity in red deer. Ecol Lett, 9, 1342–1350.

Nussey, D.H., Wilson, A.J. & Brommer, J.E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol, 20, 831–844.

Parejo, D., White, J. & Danchin, E. (2007). Settlement decisions in blue tits: Difference in the use of social information according to age and individual success. Naturwissenschaften, 94, 749–757.

Park, J.S. & Post, E. (2022). Seasonal timing on a cyclical Earth: Towards a theoretical framework for the evolution of phenology. PLoS Biol, 20.

Pärt, T. (2001). Experimental evidence of environmental effects on age–specific reproductive success: the importance of resource quality. Proc R Soc Lond B Biol Sci, 268, 2267–2271.

Pärt, T. & Doligez, B. (2003). Gathering public information for habitat selection: Prospecting birds cue on parental activity. Proceedings of the Royal Society B: Biological Sciences, 270, 1809–1813.

Perrins, C.M. (1965). Population fluctuations and clutch-size in the great tit, Parus major L. Journal of Animal Ecology, 34, 601–647.

———. (1970). The timing of birds' breeding seasons. Ibis, 112, 242–255.

———. (1979). British tits. 1st edn. Collins, London.

———. (1996). Eggs, egg formation and the timing of breeding. Ibis, 138, 2–15.

Perrins, C.M. & McCleery, R.H. (1985). The effect of age and pair bond on the breeding success of Great Tits Parus major. Ibis, 127, 306–315.

———. (1989). Laying dates and clutch size in the great tit. Wilson Bull, 101, 236–253.

Pigliucci, M. (2001). Phenotypic plasticity: beyond nature and nurture. JHU Press.

Piper, W.H. (1997). Social Dominance in Birds. In: Current Ornithology (eds. Nolan, V., Ketterson, E.D. & Thompson, C.F.). Springer US, Boston, MA, pp. 125–187.

———. (2011). Making habitat selection more "familiar": A review. Behav Ecol Sociobiol, 65, 1329–1351.

Poston, J.P. (1997). Dominance, access to colonies, and queues for mating opportunities by male boat-tailed grackles. Behav Ecol Sociobiol, 41, 89–98.

Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C., et al. (2019). Adaptive responses of animals to climate change are most likely insufficient. Nat Commun, 10.

Reed, T.E., Robin, S.W., Schindler, D.E., Hard, J.J. & Kinnison, M.T. (2010). Phenotypic plasticity and population viability: The importance of environmental predictability. Proceedings of the Royal Society B: Biological Sciences, 277, 3391–3400.

Renner, S.S. & Zohner, C.M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu Rev Ecol Evol Syst, 49, 165–182.

Rosell, F., Gundersen, G. & Le Galliard, J.F. (2008). Territory ownership and familiarity status affect how much male root voles (Microtus oeconomus) invest in territory defence. Behav Ecol Sociobiol, 62, 1559–1568.

Sæther, B. (1990). Age-specific variation in reproductive performance of birds. Current Ornithology, 7, 251–283.

Sandell, M. & Smith, H.G. (1991). Dominance, prior occupancy, and winter residency in the great tit (Parus major). Behav Ecol Sociobiol, 29, 147–152.

Savill, P., Perrins, C., Kirby, K. & Fisher, N. (2010). Wytham Woods: Oxford's ecological laboratory. OUP Oxford.

Scheiner, S.M. (1993). Genetics and evolution of phenotypic plasticity. Annu Rev Ecol Syst, 24, 35–68.

Schlicht, L., Valcu, M. & Kempenaers, B. (2014). Thiessen polygons as a model for animal territory estimation. Ibis, 156, 215–219.

Schwartz, M.D. (2003). Phenology: an integrative environmental science. Springer.

Simmonds, E.G., Cole, E.F., Sheldon, B.C. & Coulson, T. (2020). Phenological asynchrony: a ticking time-bomb for seemingly stable populations? Ecol Lett.

Siracusa, E.R., Boutin, S., Dantzer, B., Lane, J.E., Coltman, D.W. & McAdam, A.G. (2021). Familiar Neighbors, but Not

Relatives, Enhance Fitness in a Territorial Mammal. Current Biology, 31, 438-445.e3.

Slagsvold, T. & Wiebe, K.L. (2018). Immigrants and locally recruited birds differ in prey delivered to their offspring in blue tits and great tits. Anim Behav, 139, 127–135.

Sol, D., Santos, D.M. & Cuadrado, M. (2000). Age-related feeding site selection in urban pigeons (Columba livia): Experimental evidence of the competition hypothesis. Can J Zool, 78, 144–149.

Stager, M., Velotta, J.P., Cheviron, Z.A. & Senner, N.R. (2024). Assessing the evidence for treating developmental plasticity and phenotypic flexibility as different phenomena. Funct Ecol.

Stan Development Team. (2024). Stan Modeling Language Users Guide and Reference Manual, Version 2.34.

Stepanuk, J., Heywood, E., Lopez, J., DiGiovanni Jr, R. & Thorne, L. (2021). Age-specific behavior and habitat use in humpback whales: implications for vessel strike. Mar Ecol Prog Ser, 663, 209–222.

Strodl, M.A. & Schausberger, P. (2012). Social familiarity reduces reaction times and enhances survival of group-living predatory mites under the risk of predation. PLoS One, 7.

Svensson, L. (1992). Identification guide to European passerines. 4th, revd. edn. Lars Svensson; British Trust for Ornithology, Stockholm: Thetford.

Temeles, E.J. (1994). The role of neighbours in territorial systems: when are they “dear enemies”? Anim Behav, 47, 339–350.

Valone, T.J. (2007). From eavesdropping on performance to copying the behavior of others: A review of public information use. Behav Ecol Sociobiol.

Valone, T.J. & Templeton, J.J. (2002). Public information for the assessment of quality: A widespread social phenomenon. Philosophical Transactions of the Royal Society B: Biological Sciences.

Vedder, O., Bouwhuis, S. & Sheldon, B.C. (2013). Quantitative Assessment of the Importance of Phenotypic Plasticity in Adaptation to Climate Change in Wild Bird Populations. PLoS Biol, 11.

Verhulst, S. & Tinbergen, J.M. (1991). Experimental evidence for a causal relationship between timing and success of reproduction in the great tit Parus m. major. Journal of Animal Ecology, 60, 269–282.

Visser, M.E. & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. Proceedings of the Royal Society B: Biological Sciences.

Visser, M.E., Both, C. & Lambrechts, M.M. (2004). Global climate change leads to mistimed avian reproduction. Adv Ecol Res, 35, 89–110.

Visser, M.E. & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. Nat Ecol Evol.

Visser, M.E., Holleman, L.J.M. & Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia, 147, 164–172.

Visser, M.E. & Lessells, C.M. (2001). The costs of egg production and incubation in great tits (Parus major). Proceedings of the Royal Society B: Biological Sciences, 268, 1271–1277.

Visser, M.E., Van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. (1998). Warmer springs lead to mistimed reproduction in great tits (Parus major). Proceedings of the Royal Society B: Biological Sciences, 265, 1867–1870.

Ward, A.J.W., Webster, M.M. & Hart, P.J.B. (2006). Intraspecific food competition in fishes. Fish and Fisheries.

Wilkin, T.A., Garant, D., Gosler, A.G. & Sheldon, B.C. (2006). Density effects on life-history traits in a wild population of the great tit Parus major: Analyses of long-term data with GIS techniques. Journal of Animal Ecology, 75, 604–615.

Wilkin, T.A., Garant, D., Gosler, A.G. & Sheldon, B.C. (2007a). Edge effects in the great tit: Analyses of long-term data with GIS techniques. Conservation Biology, 21, 1207–1217.

Wilkin, T.A., Perrins, C.M. & Sheldon, B.C. (2007b). The use of GIS in estimating spatial variation in habitat quality: A case study of lay-date in the Great Tit Parus major. Ibis, 149, 110–118.

Woodman, J.P., Cole, E.F., Firth, J.A., Perrins, C.M. & Sheldon, B.C. (2022). Disentangling the causes of age-assortative mating in bird populations with contrasting life-history strategies. Journal of Animal Ecology.

Woodman, J.P., Cole, E.F., Firth, J.A. & Sheldon, B.C. (2024a). Age-specificity in territory quality and spatial structure in a wild bird population. bioRxiv.

Woodman, J.P., Gokcekus, S., Beck, K.B., Green, J.P., Nussey, D.H. & Firth, J.A. (2024b). The ecology of ageing in wild societies: linking age structure and social behaviour. EcoEvoRxiv.

Woodman, J.P., Vriend, S.J.G., Adriaensen, F., Alvarez, E., Artemyev, A., Barba, E., et al. (2024c). Continent-wide drivers of spatial synchrony in age structure across wild great tit populations. bioRxiv.

Ydenberg, R.C. & Krebs, J.R. (1987). The tradeoff between territorial defense and foraging in the great tit (Parus major). Am Zool, 27, 337–346.

Zettlemoyer, M.A. & DeMarche, M.L. (2022). Dissecting impacts of phenological shifts for performance across biological scales. Trends Ecol Evol.

4

Pair fidelity and site familiarity effects on the timing of breeding in wild great tits

Pair fidelity and site familiarity effects on the timing of breeding in wild great tits

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Abstract

In seasonal environments, the timing of reproduction is critical for offspring survival, as synchronising breeding with peak resource availability maximises reproductive success. However, disentangling the factors that influence breeding timing is complex, particularly in wild populations where individual experience in various contexts may play a diverse role. Specifically, as individuals age, their increased experience could enhance their ability to time breeding effectively, potentially through pair fidelity (social familiarity with their breeding partner) or site fidelity (habitat familiarity with their local environment). Nevertheless, disentangling these aspects of experience and their potential influence on phenology has remained challenging due to requiring integrated analyses of long-term datasets detailing many individuals' reproduction events across many years and over various local environments (i.e. across the population). This study explores the contributions of pair and site fidelity to breeding timing in a population of wild great tits *(Parus major)* using 63 years of individual-level data from the Wytham Woods population across over 2,000 breeding attempts. While familiarity with a partner in this population (including those that meet earlier over winter and those that breed with the same partner across years) has been associated with earlier breeding and higher reproductive success, the role of site fidelity, where individuals return to familiar breeding locations, remains less understood. We find that birds with either familiar partners or nesting in a familiar nest box lay earlier relative to a population level measure of laying date and a more local scale measure. There is no clear additive effect of having both a familiar partner and nest box, but instead it appears that familiarity with either advances laying similarly. Our findings aim to clarify the role of partner and site fidelity in shaping reproductive strategies, particularly in environments where breeding timing is critical for survival and fitness. By distinguishing between these two sources of familiarity, we provide insight into how an individual bird's social relationships and local physical environment can shape their breeding timing. We discuss the importance of these findings for understanding how different types of individual level experience might shape phenology across various systems.

Introduction

In seasonal environments, the timing of reproduction is important, as offspring survival will be maximised when individuals can synchronise their breeding attempts with peaks in resource availability (Foster & Kreitzman, 2009; Schwartz, 2003). The determinants of breeding timing, and constraints upon it, are diverse and can be difficult to disentangle in wild populations. One factor that can contribute to the variation in reproductive success we see within populations in breeding timing is individual experience. As individuals age, and gain experience, we might expect them to improve their ability to better time their breeding (Curio, 1983; Nol & Smith, 1987). But, often the benefits of experience could arise either from consistently breeding with the same partner (pair fidelity) or from continued residence in the same breeding site or territory (site fidelity). We see pair and site fidelity widespread across species (Ens et al., 1996; Harvey et al., 1979; Leach et al., 2020; Pyle et al., 2001; Saino et al., 2002). The ability to breed earlier may result from both direct or indirect advantages of familiarity, potentially including but not limited to improved coordination between familiar partners, reduced conflict, better resource provisioning or better judgement of environmental cues (Black & Hulme, 1996; Culina et al., 2015; Gokcekus et al., 2023; Martin & Shepherdson, 2012).

Familiarity with a partner or environment, and their influences on breeding timing, may play a particularly important role in seasonal environments where the timing of reproduction is crucial. Breeding too early often can risk resource scarcity for nestlings, while breeding too late can result in a mismatch between peak resource demand and availability, or more difficult conditions for fledglings (Foster & Kreitzman, 2009; Schwartz, 2003). Many birds maximise their reproductive success by synchronising their peak resource requirements for chicks with the peak resource availability, achieved by adjusting their laying dates (Simmonds et al., 2020; Visser et al., 2021). This synchronisation is particularly challenging in ephemeral environments where resource availability can vary both spatially and temporally, often at fine scales (Gosler, 1993; Hinks et al., 2015). Whilst breeding timing is often assessed relative to the entire population, in environments with variation across small scales, it may also be valuable to consider localised measures of breeding timing relative to fine-scale phenological differences across the study site (hereafter 'local breeding timing mismatch').

In species where parental care requires coordination between mates, the increased coordination that might develop over repeated breeding attempts might lead to it being beneficial for individuals to re-mate with the same partners (Ens et al., 1996). As around 90% of bird species are socially monogamous, pair fidelity in birds is well studied and often associated with earlier laying, producing more fledglings, and achieving higher overall breeding success compared to those forming new pair bonds (Culina et al., 2020; Gokcekus et al., 2023, 2024; Perrins & McCleery, 1985). Furthermore, individuals that have spent more time together prior to breeding, are also shown to have earlier laying and increased reproductive success (Culina et al., 2020; Martin & Shepherdson, 2012). However, in some wild bird populations it appears that whilst pair fidelity is associated with earlier laying, this does not necessarily improve breeding success (Pampus et al., 2005). In some cases, separating and forming new pair bonds (referred to as divorce) may even be an adaptive strategy to increase reproductive success, particularly after experiencing a failed reproductive attempt (Culina et al., 2015).

Familiarity is not restricted to partner dynamics and social bonds, but can extend to familiarity with the local environment through breeding site fidelity. Often birds will return to the same or nearby sites to breed in consecutive years (Harvey et al., 1979; Pyle et al., 2001). This behaviour may arise because familiarity with the local environment enables individuals to better assess optimal breeding times (Perrins & McCleery, 1985). Alternatively, returning to a known site may reduce the time and effort that is required to locate and establish a new territory, allowing birds to initiate breeding earlier (Pärt, 1995). Site fidelity is often linked with partner dynamics; birds are more likely to change breeding locations between years following a failed reproductive attempt, the loss of a partner or divorce, and they are more likely to return to the same breeding site in consecutive years when they remain paired with a familiar partner (Harvey et al., 1979; Schieck & Hannon, 1989). This interplay means that current understanding surrounding whether any benefits of site fidelity on breeding timing are direct (e.g., familiarity with resources) or indirect (e.g., driven by partner fidelity) is relatively limited.

Due to pair and site familiarity being potentially confounding factors in understanding the drivers of breeding timing, addressing these challenges requires long-term and spatially detailed datasets. The Wytham great tit *(Parus major)* population provides such an opportunity, with decades of data on individual breeding locations, pair identities and breeding timing. Although pair familiarity and its effects on breeding timing have been explored, there's limited understanding of how this interacts with individuals' familiarity with their environment. In this study, we aim to disentangle the contributions of partner and site familiarity to breeding timing using 63 years of individual-level breeding data from wild great tits.

Methods

Study system and breeding data

This study used data from the long-term monitoring of great tits *(Parus major)* in Wytham Woods, Oxfordshire, spanning the years 1960 to 2022. Great tits are a common passerine bird found across much of Europe, with breeding ages ranging from 1 to 9 years and an average of 1.8 years (Perrins, 1969; Woodman et al., 2023).The species is strictly socially monogamous, with pairs defending territories during the breeding season, which occurs annually from April to June (Hinde, 1952). Great tits typically breed once per year (Chapter 5), aiming to align the peak energetic demands of their nestlings with the abundance of caterpillars, their primary prey during this period. The availability of caterpillars is tightly linked to the phenology of deciduous trees, specifically the timing of leaf development in the local environment (Gosler, 1993; Hinks et al., 2015).

Most of the breeding population of great tits in Wytham Woods nests in one of the 1,019 nest boxes distributed throughout the woodland, which are monitored annually during the breeding season from March to June following standardised protocols (Perrins, 1965). Individual birds are uniquely identified with metal British Trust for Ornithology (BTO) rings. Since 2007, plastic rings containing passive integrated transponder (PIT) tags have also been used. Parent birds are identified at the nest while provisioning their young, using Radio Frequency Identification (RFID) antennae positioned around nest box entrances, which detect PIT tags and allow for identification without trapping. Unringed birds are trapped at the nest box when their nestlings are at least 10 days old and are fitted with a metal BTO ring and a PIT tag. Prior to the introduction of PIT tags, all identification was conducted through trapping. Nestlings are ringed and PIT tagged on day 15, before fledging. Mist netting is conducted during autumn and winter to capture and ring immigrant birds.

The usual measure of breeding timing in this population is an absolute measure of laying date relative to the whole population in each given year. This is calculated by taking standardised laying dates of all breeding attempts within a year and centring them around the annual mean laying date (hereafter 'year-centred laying date'). This provides an absolute measure of breeding timing relative to the entire population while controlling for interannual variation in average breeding timing, which has shifted earlier over time in response to climate change (Charmantier et al., 2008; Cole et al., 2021).

Mismatch measure

To then get a measure of local breeding timing mismatch for individual breeding attempts relative to their local environment, we first calculate an average lay date for each breeding location (nest box) throughout the woods, by taking the median year-centred lay date of each nest box across the study period 1963-2022. We then calculate the difference between an individual female's year-centred lay date and the median lay date for her specific nest box. Great tit laying dates are closely linked to local tree phenology, particularly the timing of oak (Quercus spp.) bud-burst within their foraging range. Oak bud-burst timing is highly repeatable within trees between years, but exhibits spatial variation across small scales (Cole & Sheldon, 2017; Hinks et al., 2015). As part of this measure we included only nest boxes occupied at least 10 times over the study period (approximately 67% of all boxes: see Supplementary Figure 1) to ensure the median lay date was representative, and avoid bias introduced by nest boxes which have only a handful of breeding attempts across all years of the study. The long-term median lay date associated with a nest box was not influenced by age-related biases in occupation, as these show no temporal repeatability in this study system (Chapter 3).

Familiarity measures

To categorise the familiarity between breeding pairs we used a binary measure, indicating whether a pair had bred together at least once previously (yes or no). Similarly, to categorise familiarity with a breeding site we used a binary measure of whether a female has nested in the same nest box previously or not. To consider the impact of longer term familiarity with a partner we then ran the same models again but using a count measure, which quantified the total number of times a pair had bred together over the years. This measure allowed for the identification and consideration of females that bred with the same male more than twice. Although such instances represent a small sample size, they may help us understand whether any benefits of breeding with the same partner increase as the number of times they breed together or not (additional details provided in Supplementary Figure 2A). For familiarity with a breeding site we also look at a count measure quantifying the number of times the female has nested in that particular box over her lifetime (Supplementary Figure 2B).

Analysis

We used Bayesian regression models to explore the effects of familiarity with breeding partners and breeding locations on breeding timing and success. Our analysis focused on three main questions:

1. How does pair familiarity affect year-centred laying date and local breeding timing mismatch to local average?
2. How does nest box familiarity affect year-centred laying date and local breeding timing mismatch to local average?
3. How do nest box familiarity and pair familiarity interact and affect year-centred laying date and local breeding timing mismatch to local average?

To address the first and second question we used Gaussian regression models to estimate the effect of pair and nest box familiarity on a) local breeding mismatch and b) year-centred laying date. For both familiarity measures we ran a model using the i) binary familiarity measure and another using the ii) count measure (as described above). For the nest box familiarity model we first model only nest box familiarity, and then we run another model with binary nest box familiarity and an interaction term with binary pair familiarity, to see how these effects interact. To account for temporal variation and repeated measurements at both the individual and breeding location levels, we incorporated random effects for year (to account for variation between years) and mother identity (to account for individual variation) and nest box identity (to account for environmental or site-specific factors).

For all models, except those using pair familiarity as a count measure, we excluded all first breeding attempts of females, focusing solely on second or subsequent breeding attempts. This allowed us to compare whether timing varies based on familiarity with a partner or nest box separate from an individual female's personal experience.

We included the age of the breeding female as a fixed effect, to account for changes in laying date as birds age. We know the main effects of age on timing in this population are captured by grouping juveniles and adults (Farine et al., 2015; Gosler, 1993), however here we exclude juveniles from the analysis, and want to ensure we capture any continuous changes with age (Bouwhuis et al., 2009). A summary of model structure for all above models can be found in Supplementary Table 1.

We used a Bayesian framework to fit the models, incorporating prior information and estimating posterior distributions for all parameters. We set weak regularising priors for all predictors with a normal distribution centred on 0 with a standard deviation of 2, and exponential priors around 1 for the standard deviations of the random intercepts for nest box, mother, and year, as well as on the residual error term. Convergence and model fit was assessed using posterior predictive checks. Models were run using the 'brms' package (Bürkner, 2017) using 'CmdStanR' interface (Gabry et al., 2024), and the outputs were analysed using the 'marginaleffects' package (Vincent Arel-Bundock et al., 2024).

Results

Data subset

There are 9093 breeding attempts between 1960-2022 for which we know the identity of both parents. 4763 of these breeding attempts (53%) include a female that is recorded in more than one year breeding, comprising 1957 unique females. Of those, 799 (41%) individual females were recorded with the same male for two or more attempts, and 631 (32%) individual females nested in the same box for multiple attempts across years.

The subset used in most models takes only females' second breeding attempts (in different years) and beyond: this leaves 2806 breeding attempts;. 909 of these are with a partner that female has previously bred with, and 733 of those attempts are in a nest box previously used. Of those 360 had a familiar partner and a familiar nest box, 373 had a familiar nest box but a new partner, 549 had a familiar partner but a new box and 1524 had a new partner and a new nest box. Local breeding timing mismatch of this subset ranges from -18.27 days to 35.87 days, with a median of -0.88 days (distribution shown in Supplementary Figure 3).

1) Partner Familiarity

All marginal effects and predictions are reported as medians with 95% confidence intervals. Partner familiarity was assessed as both a binary measure and a count of prior breeding events with the same partner. When familiarity was treated as a binary variable, females breeding with familiar partners bred earlier relative to the local average laying date by 0.94 days [0.53, 1.35] compared to those with unfamiliar partners (Figure 1A and Supplementary Table 2). A similar difference was seen in year-centred laying date, with females with familiar partners breeding 1.14 days [0.74, 1.55] earlier compared to those with unfamiliar partners (Supplementary Figure 4A and Supplementary Table 2).

When familiarity was quantified as the number of previous breeding events with the same partner, the primary difference occurred between the first and second breeding attempts. Specifically, local breeding timing mismatch was 0.73 days [0.39, 1.07] more negative for birds breeding with the same male for a second time compared to a first time (Figure 1B and Supplementary Table 2). Beyond the second time breeding together, further pairings showed no significant changes in mismatch. This same pattern was seen when using the year-centred laying date measure, with females breeding with males for a second time 0.94 days [0.60, 1.27] earlier than first time pairs, and further pairings showing no significant changes in laying date (Supplementary Figure 4B and Supplementary Table 2).

2) Nest box familiarity

Nest box familiarity also influenced laying dates. For models including just the nest box familiarity measure, females breeding in a familiar nest box laid eggs earlier relative to local average breeding date by 0.67 days [0.26, 1.09](Figure 1C and Supplementary Table 2) compared to those breeding in an unfamiliar nest box, and also had an earlier year-centred laying date by 0.96 days [0.56, 1.38](Supplementary Figure 4C and Supplementary Table 2). When using the count measure of nest box familiarity we see a significant difference in both local breeding timing mismatch and year-centred laying date between females nesting in a box for a first and second time (local breeding timing mismatch: 0.49 days [0.15, 0.81]; Figure 1D and and Supplementary Table 2, and year-centred laying date: 0.68 days [0.37, 0.99]; Supplementary Figure 4D and Supplementary Table 2). Both measures of laying date also get slightly earlier for females nesting for a third time in a nest box compared to a second time, this is significant for year-centred laying date but not for local breeding timing mismatch (year-centred laying

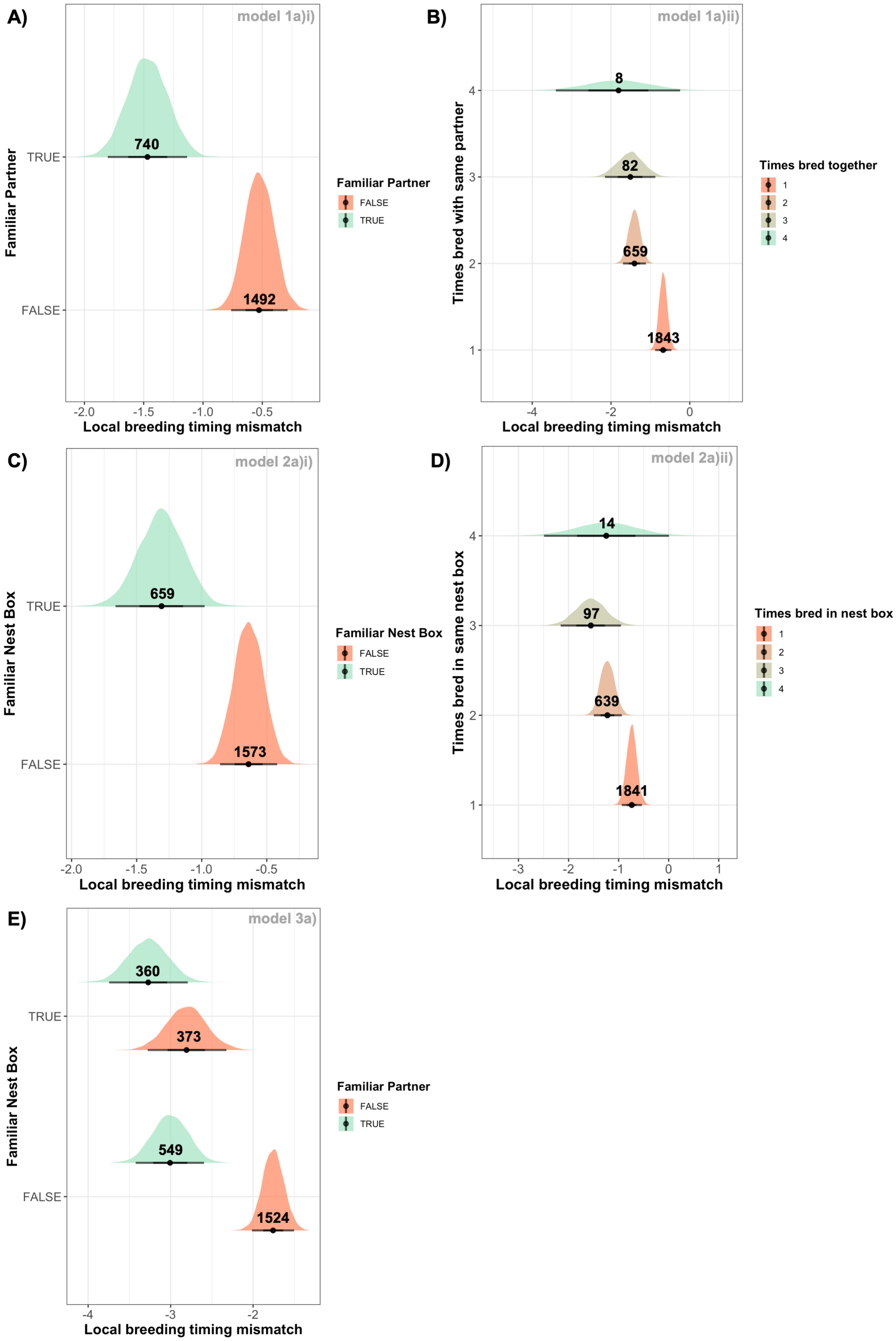

Figure 1: Marginal posterior predictions of local breeding timing mismatch for each of the models run (models labelled in top right corner of each plot correspond to model structures in Supplementary Table 1.) Response variables for each model: **A)** binary partner familiarity **B)** partner familiarity count (with 5 times removed, as there is only 1 instance) **C)** binary nest box familiarity **D)** nest box familiarity count (with 5 times removed as there is only 2 instances) **E)** binary partner familiarity and interaction with nest box familiarity.

date: 0.71 days [0.22, 1.20]; Supplementary Figure 4D and Supplementary Table 2, and local breeding timing mismatch: 0.33 days [-0.14, 0.82]; Figure 1D and Supplementary Table 2)

3) Joint models

In unfamiliar nest boxes, females paired with familiar partners bred earlier (local breeding timing mismatch: by 1.11 days [0.61, 1.65]; Figure 1E and Supplementary Table 2, and year-centred laying date: by 1.25 days [0.77, 1.74]; Supplementary Figure 4E and Supplementary Table 2) than those with unfamiliar partners. Similarly, in familiar nest boxes, females with familiar partners had a more negative local breeding timing mismatch and an earlier year-centred laying date (local breeding timing mismatch : by 0.33 days [-0.36, 1.03]; Figure 1E and Supplementary Table 2, year-centred laying date: by 0.46 days [-0.21, 1.14]; Supplementary Figure 4E and Supplementary Table 2) than those with unfamiliar partners, however these were not significantly different.

This translates to birds with a familiar partner and nest box laying earliest, significantly earlier, both relative to local breeding timing mismatch and year-centred laying date, than those with neither a familiar partner or box, but not significantly earlier than those with only a familiar partner or only a familiar nest box (Figure 1E and Supplementary Figure 4E). Hence, we see no evidence that these two types of familiarity act additively: while the effect of a familiar partner is slightly larger than that of a familiar nest box, there is no additional effect of combining these two types of familiarity.

Age at breeding, fitted as a fixed effect in all models, shows a small positive effect over time as age increases beyond 2 years, local breeding mismatch becomes less negative and year-centred laying date gets later (further detail in Supplementary Table 3).

Discussion

Our findings demonstrate that partner and nest box familiarity did not increase matching breeding timing to a local phenological average but instead consistently advanced laying dates overall and relative to the local average. We do not directly measure the fitness implications of familiarity with a partner or with a nest box, however, as earlier breeding on average leads to higher breeding success in this population with a decline in success across the season (Perrins & McCleery, 1989), we feel it is safe to assume that earlier breeding is advantageous to individuals. Our findings support previous research in this population demonstrating that maintaining a consistent breeding partner can facilitate earlier breeding (Culina et al., 2020; Gokcekus et al., 2023). As the number of times a female bred with the same partner or in the same box increased, after controlling for age, laying date advanced significantly from the first to second instance, but then plateaued in subsequent breeding attempts. This suggests that the primary effect of social familiarity on early laying is realised by simply having the same partner from the previous year (rather than even more increased familiarity as the years progress). A slight further advancement was seen from the second to third year breeding in the same nest box, although this effect was small. Even though the breeding advancements of repeated breeding with the same partner or in the same box do not continue to increase with repeated breeding beyond the initial improvement, the persistence of this effect across multiple breeding attempts highlights the advantages of familiarity in this system.

The relationship between nest box familiarity and earlier laying suggests that familiarity with the local environment, such as knowledge of resources and reduced competition for nest sites, can contribute to earlier breeding (Black & Hulme, 1996; Gokcekus et al., 2023; Harvey et al., 1979; Martin & Shepherdson, 2012). This could be considered direct benefits of familiarity with a territory, enabling earlier and potentially more optimal reproductive timing. Indirect effects may also contribute to these patterns; familiarity with a site could facilitate pair retention, reducing the time and energy needed to secure a new partner and territory, thus advancing breeding. Further, the opposite could also be true in that pair familiarity may allow site fidelity, with pairs that stay together being more able to quickly occupy and defend their nesting site from a previous year. Whilst some effects of site familiarity may be partially mediated by partner familiarity, we do see some evidence of the independent role of site familiarity in this system. Notably, when females bred with unfamiliar males, the effect of nest box familiarity on laying date was more pronounced. Furthermore, when females bred in familiar nest boxes with unfamiliar partners, laying dates were advanced compared to breeding with unfamiliar partners in unfamiliar boxes.

Overall, it appears pair fidelity may therefore be the main driver of earlier breeding, but with the absence of familiarity with a partner site fidelity allows individuals to breed earlier. It is notable that there is no additive effect of partner and site familiarity; females with familiar partners lay earlier regardless of familiarity with their nest box, and females with unfamiliar partners but a familiar nest box breed similarly early, and we see no significant extra advancement for those with both a familiar partner and nest box. One possible explanation for this could be that there is only so early it is possible for birds to lay because of other environmental or individual constraints, and so having a familiar partner allows individuals to reach that limit, but if you don't have a familiar partner then having a familiar nest box allows you to advance laying instead. This interplay between partner and site fidelity, where partner fidelity appears to be the main driver is also found in other systems, for instance in willow ptarmigans high site fidelity is maintained because of the benefits of breeding with a familiar partner (Schieck & Hannon, 1989), and in Cassin's auklet, they suggest fitness is more optimised by mate selection than site fidelity (Pyle et al., 2001).

Age is widely linked to improved reproductive competence (Curio, 1983; Nol & Smith, 1987; Perrins & McCleery, 1985)). In this population, juvenile females will breed on average later than adults, thought to be at least partly explained by the need for them to establish a new pair bond and a territory (Chapter 3; Perrins & McCleery, 1985). We then see a decline in reproductive performance of mothers three years and older (Bouwhuis et al., 2009). As this investigation was based on familiarity effects from the previous year, we exclude juveniles from our analysis, so our results are not driven by this pattern of later laying in the first year, we see that with increasing age (beyond 2 years old) females' laying date becomes later. However, the effects of familiarity appear to act independently of age, providing females with an advantage that offsets, at least partially, age-related delays in laying dates.

This effect of partner and site familiarity on breeding timing could reflect the individual birds' quality, where high-quality birds are better equipped to retain both partners and territories, allowing them to breed earlier, while lower-quality individuals may be more prone to partner loss or territory displacement with the knock on effect of later breeding. This raises the possibility that the observed effects of familiarity on breeding timing and success may partially reflect underlying differences in individual quality rather than familiarity per se (Culina et al., 2020). Future experimental work will be necessary to disentangle the effects of familiarity from intrinsic individual quality.

Familiarity-driven advances in breeding timing have important implications for how birds adjust their reproduction to changing environmental conditions. In the context of climate change, where resource phenology is shifting unpredictably, the ability to adapt breeding timing becomes increasingly vital (Perrins, 1969; Verhulst et al., 1995; Verhulst & Tinbergen, 1991). Familiarity with breeding sites may allow individuals to adjust more efficiently to local environmental variability, reducing the mismatch between laying dates and resource availability, maximising resources during chick-rearing. At the same time, our results raise questions about whether the benefits of earlier laying are primarily due to absolute timing (breeding earlier than others in the population) or synchrony with local resource peaks. These results don't point towards evidence for birds using environmental cues to align more precisely with the optimal timing for resource availability. However, in other work in this system (Chapter 3) we find that adult females surrounded by other adults tend to breed closer to their local average, suggesting that social information could potentially aid in fine-tuning reproductive timing. The interactions between partner and site fidelity suggest that both forms of familiarity may play complementary roles in enabling birds to optimise their reproductive timing.

One thing to consider is the way we estimate the "local average" laying date. By averaging laying dates within nest boxes over years, we aim to approximate local resource conditions, but this may not fully capture fine-scale environmental variation, such as caterpillar abundance or tree phenology. While such data are challenging to collect at a large spatial scale, future studies could improve these measures by directly assessing resource peaks relative to laying dates. Another avenue for future research is to explore the consequences of these familiarity metrics on breeding output and reproductive success. Does increased experience breeding with the same partner or in the same nest box confer greater fitness benefits for individuals? Furthermore, experiments designed to isolate the effects of social familiarity (partner retention) from environmental familiarity (site fidelity) would help clarify the mechanisms underlying these patterns.

Summary

Our findings highlight the potential role of familiarity in contributing to females' ability to breed earlier relative to both population-wide and local averages. This suggests that familiarity may play an important role in helping birds to adapt their breeding timing to changing environments. In the face of climate change, the flexibility conferred by familiarity, both social and environmental, may play a key role in maintaining synchrony with shifting phenology of resources, and ultimately influence reproductive success and population dynamics.

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References

Black, J. M., & Hulme, M. (1996). Partnerships in Birds: The Study of Monogamy: The Study of Monogamy. Oxford University Press, UK.

Bouwhuis, S., Sheldon, B. C., Verhulst, S., & Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B: Biological Sciences, 276(1668), 2769–2777. https://doi.org/10.1098/rspb.2009.0457

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science, 320(5877), 800–803. https://doi.org/10.1126/science.1157174

Cole, E. F., Regan, C. E., & Sheldon, B. C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. Nature Climate Change, 11(10), 872–878. https://doi.org/10.1038/s41558-021-01140-4

Cole, E. F., & Sheldon, B. C. (2017). The shifting phenological landscape: Within- and between-species variation in leaf emergence in a mixed-deciduous woodland. Ecology and Evolution, 7(4), 1135–1147. https://doi.org/10.1002/ece3.2718

Culina, A., Firth, J. A., & Hinde, C. A. (2020). Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population: Pairs that meet earlier do better. Proceedings of the Royal Society B: Biological Sciences, 287(1941). https://doi.org/10.1098/rspb.2020.1554rspb20201554

Culina, A., Radersma, R., & Sheldon, B. C. (2015). Trading up: The fitness consequences of divorce in monogamous birds. Biological Reviews, 90(4), 1015–1034. https://doi.org/10.1111/brv.12143

Curio, E. (1983). Why do young birds reproduce less well? Ibis, 125(3), 400–404. https://doi.org/10.1111/j.1474-919X.1983.tb03130.x

Ens, B., Choudhury, S., & Black, J. (1996). Mate fidelity and divorce in monogamous birds. Oxford University Press.

Farine, D. R., Firth, J. A., Aplin, L. M., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Milligan, N. D., Psorakis, I., Radersma, R., Verhelst, B., Voelkl, B., & Sheldon, B. C. (2015). The role of social and ecological processes in structuring animal populations: A case study from automated tracking of wild birds. Royal Society Open Science, 2(4). https://doi.org/10.1098/rsos.150057

Foster, R., & Kreitzman, L. (2009). Seasons of life: The biological rhythms that enable living things to thrive and survive. Yale University Press. https://ora.ox.ac.uk/objects/uuid:7fe87578-1b69-4b99-99ac-362ad7302175

Gabry, J., Češnovar, R., Johnson, A., & Bronder, S. (2024). R Interface to CmdStan. https://mc-stan.org/cmdstanr/

Gokcekus, S., Firth, J. A., Cole, E. F., Sheldon, B. C., & Albery, G. F. (2024). Different types of social links contrastingly shape reproductive wellbeing in a multi-level society of wild songbirds (p. 2024.02.02.578606). bioRxiv. https://doi.org/10.1101/2024.02.02.578606

Gokcekus, S., Firth, J. A., Regan, C., Cole, E. F., Sheldon, B. C., & Albery, G. F. (2023). Social Familiarity and Spatially Variable Environments Independently Determine Reproductive Fitness in a Wild Bird. The American Naturalist, 201(6), 813–824. https://doi.org/10.1086/724382

Gosler, A. (1993). The Great Tit. Hamlyn.

Harvey, P. H., Greenwood, P. T., & Perrins, C. M. (1979). Breeding Area Fidelity of Great Tits *(Parus major)*. Journal of Animal Ecology, 48(1), 305–313.

Hinde, R. A. (1952). The Behaviour of the Great Tit *(Parus Major)* and Some Other Related Species. Behaviour. Supplement, 2, III–201.

Hinks, A. E., Cole, E. F., Daniels, K. J., Wilkin, T. A., Nakagawa, S., & Sheldon, B. C. (2015). Scale-dependent phenological synchrony between songbirds and their caterpillar food source. American Naturalist, 186(1), 84–97. https://doi.org/10.1086/681572

Leach, A. G., Riecke, T. V., Sedinger, J. S., Ward, D. H., & Boyd, S. (2020). Mate fidelity improves survival and breeding propensity of a long-lived bird. Journal of Animal Ecology, 89(10), 2290–2299. https://doi.org/10.1111/1365-2656.13286

Martin, M. S., & Shepherdson, D. J. (2012). Role of Familiarity and Preference in Reproductive Success in Ex Situ Breeding Programs. Conservation Biology, 26(4), 649–656. https://doi.org/10.1111/j.1523-1739.2012.01880.x

Nol, E., & Smith, J. N. M. (1987). Effects of Age and Breeding Experience on Seasonal Reproductive Success in the Song Sparrow. Journal of Animal Ecology, 56(1), 301–313. https://doi.org/10.2307/4816

Pampus, M., Schmidt, K.-H., & Wiltschko, W. (2005). Pair bond and breeding success in Blue Tits *(Parus caeruleus)* and Great Tits *(Parus major)*. Ibis, 147(1), 92–108. https://doi.org/10.1111/j.1474-919x.2004.00376.x

Pärt, T. (1995). The importance of local familiarity and search costs for age- and sex-biased philopatry in the collared flycatcher. Animal Behaviour, 49(4), 1029–1038. https://doi.org/10.1006/anbe.1995.0132

Perrins, C. M. (1965). Population Fluctuations and Clutch-Size in the Great Tit. Journal of Animal Ecology, 34(3), 601–647.

Perrins, C. M. (1969). The timing of birds' breeding seasons. Ibis, 112, 242–255.

Perrins, C. M., & McCleery, R. H. (1985). The effect of age and pair bond on the breeding success of Great Tits *(Parus major)*. Ibis, 127(3), 306–315. https://doi.org/10.1111/j.1474-919X.1985.tb05072.x

Perrins, C. M., McCleery, R. H. (1989). Laying Dates and Clutch Size in the Great Tit. The Wilson Bulletin, 101(2), 236–253.

Pyle, P., Sydeman, W. J., & Hester, M. (2001). Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. Journal of Animal Ecology, 70(6), 1088–1097. https://doi.org/10.1046/j.0021-8790.2001.00567.x

Saino, N., Ambrosini, R., Martinelli, R., & Møller, A. P. (2002). Mate fidelity, senescence in breeding performance and reproductive trade-offs in the barn swallow. Journal of Animal Ecology, 71(2), 309–319. https://doi.org/10.1046/j.1365-2656.2002.00600.x

Schieck, J. O., & Hannon, S. J. (1989). Breeding site fidelity in willow ptarmigan: The influence of previous reproductive success and familiarity with partner and territory. Oecologia, 81(4), 465–472. https://doi.org/10.1007/BF00378953

Schwartz, M. (2003). Phenology: An Integrative Environmental Science. Springer Science & Business Media.

Simmonds, E. G., Cole, E. F., Sheldon, B. C., & Coulson, T. (2020). Phenological asynchrony: A ticking time-bomb for seemingly stable populations? Ecology Letters, 23(12) 1766–1775. https://doi.org/10.1111/ele.13603

Verhulst, S., & Tinbergen, J. M. (1991). Experimental Evidence for a Causal Relationship between Timing and Success of Reproduction in the Great Tit *(Parus m. Major)*. Journal of Animal Ecology, 60(1), 269–282. https://doi.org/10.2307/5459

Verhulst, S., van Balen, J. H., & Tinbergen, J. M. (1995). Seasonal Decline in Reproductive Success of the Great Tit: Variation in Time or Quality? Ecology, 76(8), 2392–2403. https://doi.org/10.2307/2265815

Visser, M. E., Lindner, M., Gienapp, P., Long, M. C., & Jenouvrier, S. (2021). Recent natural variability in global warming weakened phenological mismatch and selection on seasonal timing in great tits *(Parus major)*.

Woodman, J. P., Cole, E. F., Firth, J. A., Perrins, C. M., & Sheldon, B. C. (2023). Disentangling the causes of age-assortative mating in bird populations with contrasting life-history strategies. Journal of Animal Ecology, 92(5), 979–990. https://doi.org/10.1111/1365-2656.13851

5

Predictors of second breeding attempts in a predominantly single brooded bird population

Predictors of second breeding attempts in a predominantly single brooded bird population

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Abstract

In many bird species, reproduction is typically confined to a single breeding season within each year, often characterised by a single reproductive attempt. In seasonal environments, synchronising these reproduction attempts with a resource peak is often critical for maximising offspring survival. As such, much research on bird populations which typically have a single brood per season has focused on individuals' primary attempt each year, and excluded any second attempts (due to their infrequent nature) and thus overlooked the occurrence of multiple breeding attempts within the same season. However, even within populations which largely breed only once per season, sometimes a subset of individuals will engage in a second breeding attempt. Often a second breeding attempt is triggered by the failure of the initial attempt, but may also reflect genuine multi-brooding. Indeed, the occurrence of second breeding attempts in seasonal breeders is observed in various taxa, including birds and mammals. The prevalence of these multi breeding attempts, along with the ecological and individual factors that predict their occurrence, remains poorly understood, due to the difficulty of investigating these infrequent occurrences. Using 63 years of long-term data from a UK population of great tits *(Parus major)* comprising 250 second breeding attempts, we examined the determinants of multiple breeding attempts in a predominantly single-brooded system. We found that the occurrence of second breeding attempts in this population is non-random, and is shaped by individual factors, including age and timing of first-brood failure. Large-scale environmental factors, such as annual population size or breeding season length, have limited influence on the frequency of second breeding attempts, but that adults and earlier breeders are more likely to have second breeding attempts due to reattempting reproduction after an earlier failure. These findings provide new knowledge of the factors shaping second breeding attempts in wild populations, and add to our understanding of the drivers of second breeding attempts which offers valuable insight into reproductive strategies in seasonal environments.

Introduction

Reproductive strategies among species exhibit considerable diversity, from the number of offspring produced at one time, to the frequency of breeding attempts across both annual cycles and lifetimes (Stearns, 1976). In seasonal environments, the timing of reproduction is crucial, as offspring survival will be maximised when individuals can synchronise their breeding attempts with peaks in resource availability (Foster & Kreitzman, 2009; Schwartz, 2003). Some species and individuals engage in multiple breeding attempts per season, whilst others may only reproduce once. This variation, which can be observed both between and within species, populations and individuals, is often thought to be a life history strategy aimed at maximising an individual's reproductive success (Stearns, 1992). The decision of whether to produce multiple broods within a single season is likely to be influenced by conditions of both the environment and the breeding individual.

Second breeding attempts within a season can occur in two forms: either as a "true" second attempt following a successful first attempt, where offspring were raised to no longer require parental care (from here on we refer to these as "successive breeding attempts"), or as a "replacement" attempt following the failure of an initial attempt (from here on referred to as "replacement breeding attempts"). Both strategies are widespread across various taxa including birds and mammals (Enemar, 2009; Geupel & DeSante, 1990; Hayssen, 2008; Hoffmann et al., 2015; Rowley et al., 1991; Senécal et al., 2021; Tablado et al., 2009; Yasué & Dearden, 2008). Successive second breeding attempts are expected to occur more frequently in populations where environmental conditions, such as long breeding seasons and abundant resources, enable multiple successful attempts (Rowley et al., 1991; Yasué & Dearden, 2008). For short lived species, that may only have the opportunity to breed once or twice in their lifetimes, maximising annual reproductive output is essential for an individual's reproductive success (Sæther & Bakke, 2000). This could involve multiple successful breeding attempts within a season or the ability to replace a failed attempt when the conditions permit this. However, this is often not possible and within species, some populations may show this strategy whilst others will not, likely due to variation in environmental factors between geographic locations (Husby et al., 2009).

For species that synchronise their breeding with a seasonal resource peak, there are often limited opportunities for multiple successive breeding attempts. In these populations, replacement breeding attempts may play a crucial role in maximising reproductive success, offering an alternative strategy for individuals to compensate when an initial breeding attempt fails. For example, if a first attempt is mistimed and fails, a replacement attempt allows the pair to try again without missing the seasonal window entirely. This strategy could be especially valuable for species that face fluctuating environmental conditions (Yasué & Dearden, 2008). This would be particularly true for shorter lived species with limited breeding opportunities, where replacement attempts could provide an opportunity to increase fitness when successive second attempts are rare or unfeasible. Understanding the factors that facilitate replacement attempts is therefore useful for understanding how species may optimise breeding strategies under varying environmental pressures.

Birds, particularly small passerine species, offer a useful opportunity to study the occurrence of multiple breeding attempts within seasons (multibrooding), due to the availability of extensive long-term monitoring data of their breeding behaviour. Another advantage is the ability to observe the failure of breeding attempts early on, compared to (e.g.) wild mammals where it is often not possible to be certain a female is pregnant before live offspring is observed, so any losses that occur before birth will not be recorded (Brambell, 1948). Despite this potential, second breeding attempts are often understudied, and our knowledge of the predictors of multiple breeding attempts within well-studied species usually considered to be single-seasonal breeders remains limited. A variety of studies have used experimental manipulations to assess determinants of second brooding in wild populations and the trade offs between first and second broods within years (Lindén, 1988; Verhulst, 1998; Verhulst et al., 1997). But, few have explored these patterns in non-experimental situations in wild populations and even less so in populations that are predominantly single brooded and do not commonly have successive second attempts (Bukor et al., 2021; Husby et al., 2009; Senécal et al., 2021; Verboven et al., 2001; Verboven & Verhulst, 1996).

Great tits *(Parus major)* are facultative multibrooded passerines, and are known to have multiple broods frequently within a season in populations in mainland Europe, but less so in the UK (Bukor et al., 2021; Husby et al., 2009; Senécal et al., 2021). In great tits, the timing of breeding with the resource peak is key, and production of successive second broods in some populations has been linked with experimental work to the 'date hypothesis', which predicts that having a second clutch is driven by seasonal variation and opportunities to breed (Verboven & Verhulst, 1996). In support of this we see effects on multibrooding trends with climate change. In the Netherlands, the frequency of multibrooding in great tits has decreased due to shifts in the timing of resources, primarily driven by climate change (Husby et al., 2009; Visser et al., 2003). These patterns highlight the plasticity in reproductive strategies and underscore the need for understanding the environmental and individual factors driving these decisions.

In this study, we use 63 years of long-term data from a population of great tits that predominantly breeds once per season, with rare occurrences of successive multibrooding, but more frequent replacement broods, to explore the determinants of multiple breeding. Using this model system, we examine the prevalence of successive and replacement multiple breeding attempts and investigate the ecological and individual-level factors that might predict their occurrence in this population. We then discuss how understanding the drivers behind these reproductive strategies can provide insight into how individuals and populations may respond to changing environments, particularly with regard to adjusting the frequency of second breeding attempts, and how this may provide valuable insights into the evolution of reproductive strategies in wild populations.

Methods

Study system

We use data from the long-term monitoring of great tits *(Parus major)* in Wytham Woods, Oxfordshire spanning the years 1960 to 2022. Great tits are cavity nesters and most of the breeding population uses the 1,019 nest boxes that are distributed throughout the woods (Harvey et al., 1979) and monitored annually from March to June during the breeding season following a standardised protocol. Two types of identification are used to mark individual birds. Each caught bird has a unique metal British Trust for Ornithology (BTO) ring, and a plastic ring which contains a passive integrated transponder (PIT) tag (these have been used since 2007). Radio Frequency Identification (RFID) antennae, placed around nest box entrance holes, read the PIT tags, allowing for the identification of individuals whilst feeding nestlings without the need to catch them. Female birds may also be identified whilst incubating eggs using handheld RFID readers. Unringed birds, that cannot be identified using this method, are trapped at the nest box when nestlings are at least 10 days old. They are then fitted with metal BTO leg rings and PIT tags. Before the use of PIT tags, all individual identification was conducted by trapping birds. All nestlings are ringed and PIT tagged on day 15, before fledging. Additionally mist netting is conducted throughout the autumn and winter to capture and ring immigrant birds.

Birds in this population typically breed once per year, and aim to synchronise the peak resource demand of their nestlings with the peak in primary consumer prey, which in turn is closely linked to the leaf green up of deciduous trees (Hinks et al., 2015).

Nest failures are recorded during regular nest box visits, with the timing of failure identified as occurring either pre-hatching or in between hatching and fledging. In cases of nest failure before fledging, often only the mother's identification is recorded.

Breeding data

In order to look at the frequency of multibrooding in Wytham, we classify two categories: "successive" second breeding attempts and "replacement" second breeding attempts. A successive second attempt is a breeding attempt that occurs after a first breeding attempt by the same female within the same season successfully produces fledglings. A replacement attempt is defined as occurring when a first breeding attempt fails at some point before fledging occurs, and the same female goes on to attempt to breed again within the same season.

We used a subset of the data including just those breeding attempts where we know the identity of at least the breeding female; this allows us to identify multibrooding attempts with high confidence, but may mean that we miss others where the females were unidentified. Failure to identify parents could be due to a few reasons. A female can be identified earliest when she is incubating, however most females and males are likely to be identified when the chicks are around 5-14 days old. Every year a proportion of adults are never identified (18.8% (2901 out of 15440 total recorded breeding attempts) of nesting attempts over all years have neither parent identified, 21.3% (3289) have no mother identified and 37.5% (5791) no father). Breeding attempts that fail earlier on are less likely to have parents identified (individuals failing before hatching are 23.9 [21.6, 26.4] percentage points less likely to be identified than those failing between hatching and fledging: Supplementary Figure 1), and so it is possible we may be missing some multibrooding attempts.

Analysis

We used Bayesian regression models to explore patterns in second breeding attempts in the population. Our analysis focused on four main questions:

1. **Population level patterns of laying date advancement:** How have first egg dates advanced over time, and how does this vary between first and second breeding attempts?
2. **Timing of first breeding attempt:** If a female's first breeding attempt failed, is the timing of her first breeding attempt related to whether she will produce a replacement breeding attempt?
3. **Individual characteristics:** How does the age of individual birds and the timing of failure of their first breeding attempt influence their likelihood of producing a replacement breeding attempt?
4. **Demographic and phenological influences:** How do demographic and phenological characteristics of a year influence the proportion of replacement breeding attempts recorded?

To address the first and second questions we used Gaussian regression models to estimate 1) the marginal effects of breeding attempt type (first or second) on the advancement of laying dates over time and 2) the marginal effect of whether a female had a second attempt or not (0 = no, 1 = yes) on the timing of her first laying date. For questions three and four we used Bernoulli models, where the binary response variable was whether an individual female had a second breeding attempt or not following the failure of her first attempt (0 = no, 1 = yes).

For question 3 we consider how the age of individual birds influences their probability of producing a replacement breeding attempt, whilst controlling for the timing of their first breeding attempt (scaled within years), and the timing of failure of their first breeding attempt (categorised as before hatching or between hatching and fledging). We used two different categorisations of age: exact age (in years), and a binary grouping (juveniles: 1 year old, adults: $\geq$2 years old), based on previous findings that, although there are some continuous changes with age (Bouwhuis et al., 2009), the main effects of age on many individual-level traits are captured by these two age classes (Farine et al., 2015; Gosler, 1993; Perrins & McCleery, 1985).

For question 4 we tested how a number of different demographic and phenological characteristics influenced the likelihood of a second breeding attempt. The predictors included:

- **Earliness of a year**, measured as the median scaled laying date for each year
- **Variance of a year**, calculated as the difference between the earliest and latest of 1st egg dates within a year. To capture the length of the breeding season.
- **Population size**, measured as the number of first breeding attempts recorded within each year
- **Age structure of neighbourhoods**, as in Chapter 3, we calculated this for each bird's first breeding attempt within each year, where neighbours are defined as individuals that breed within 75 metres of each other, and split into 4 categories: 'adult' (all neighbours are ≥2 years old), 'juvenile' (all neighbours are 1 year old), 'both' (mix of adult and juvenile neighbours), and 'no neighbours' (no birds bred within 75 m of the focal female). The precise spatial scale at which individual birds interact throughout the breeding period is not known; we chose 75m as an appropriate scale based on previous studies that assess space-use in great tits (Firth et al., 2018; Krebs, 1971). We opted to use a categorical instead of continuous measure to allow for a more biologically meaningful interpretation of interactions between different age structures and breeding timing.

In all models, to account for temporal variation and repeated measurements at both the individual and breeding location levels, we incorporated random effects for year (to account for variation between years: in all models except model 1) and mother identity (to account for individual variation) and nest box identity (to account for environmental or site-specific factors). A summary of model structure for all above models can be found in Supplementary Table 1.

We used a Bayesian framework to fit the models, incorporating prior information and estimating posterior distributions for all parameters. We set weak regularising priors for all parameters using a normal distribution, for most parameters this is centred on 0 with a standard deviation of 2, apart from the prior for the intercept in the model for question 1 which is normal centred around 40 with standard deviation of 10. We used exponential priors around 1 on the standard deviations of the random intercepts for nest box, mother, and year, as well as on the residual error term. Convergence and model fit was assessed using posterior predictive checks. Models were run using the *'brms'* package (Bürkner, 2017) using *'CmdStanR'* interface (Gabry et al., 2024), and the outputs were analysed using the *'marginaleffects'* package (Vincent Arel-Bundock et al., 2024).

Results

Prevalence

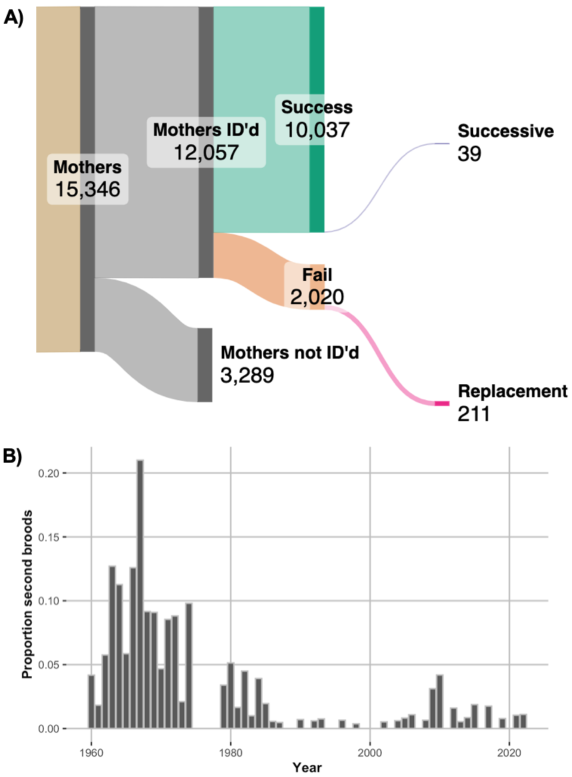


Figure 1: A) Sankey diagram showing how the data is subsetted as we remove those without females identified, and then split into those first breeding attempts that succeed and fail and how many of those females go on to have a second breeding attempt within the same year. B) Proportion of second breeding attempts across years of the study.

Occurrence of second breeding attempts

Across all study years in this predominantly single-brooded population, a total of 11,658 breeding attempts were recorded where the identity of the mother was known. Of these, 2.1% (250 attempts) were identified as second breeding attempts, where the same female is recorded producing two clutches within the same year (three third attempts and one fourth attempt were removed). Among these second attempts, 16% (39) were classified as successive second breeding attempts, where the first breeding attempt successfully fledged before a second was initiated. Of these, fledglings from 20 broods went on to recruit into the population, as they were recorded breeding in subsequent years (26 females and 15 males): therefore the possibility of brood failure soon after fledging can be excluded for the majority of these cases. The remaining 211 second attempts (84.4%) were replacement breeding attempts, where the first attempt failed at some point prior to fledging, and the female went on to re-attempt breeding Figure 1A summarises these data.

The number of second breeding attempts varies between years (ranging from 1 to 25 recorded attempts). Over time the proportion of replacement breeding attempts has decreased (the probability of having a second attempt decreases by 0.12 percentage points per year [0.10, 0.14]: Figure 1B). The identification rate of females has remained stable over time, with no significant trend detected (simple linear Bayesian model, birds not identified year, -0.0011 [-0.0025, 0.0003]: Supplementary Figure 3). So this decrease in prevalence of second breeding attempts is not due to changes in detection rates. As the number of successive second breeding attempts is small we focus further analysis on replacement breeding attempts.

Predictors

All marginal effects and predictions and reported as medians with 95% confidence intervals.

1) Population level patterns of laying date advancement

The advancement in first breeding attempts matches the advancement of laying date reported in previous studies, with an advancement of approximately 0.268 days per year [-0.277, -0.259] (Figure 2A and B), which equals to an advancement of around 17 days over the 63 year study period. However, there is no evidence of a corresponding advancement in the timing of second breeding attempts since 1960 (0.026 days per year [-0.030, 0.082]). This lack of advancement in second attempts is likely driven by a simultaneous change in the timing that first breeding attempts are failing. This can be seen in records of failures and in an increase in interval time between first and second breeding attempts. In earlier years of the study more first breeding attempts appear to fail before hatching (-1.22 [-1.41, -1.01] percentage point decrease in probability per year of failure before hatching), compared to in more recent years where failures are more likely to occur after hatching but before fledging (0.79 [0.61, 0.94] percentage point increase in probability per year of failure occurring between hatching and fledging), which by definition delays the onset of a second breeding attempt (Supplementary Figure 2).

Ecological drivers

2) Timing of first breeding attempt

Birds that failed in their first breeding attempt and subsequently laid a replacement clutch initiated their first attempt, on average, 5.37 days [4.40, 6.33] earlier than those that did not lay a replacement (Figure 2C). Additionally, juveniles laid their first clutch 2.43 days [1.74, 3.12] later than adults, consistent with previous findings (Chapter 3).

When comparing adults and juveniles based on whether they produced a second attempt, the age-related difference in timing was slightly larger for birds that did not reattempt (no second attempt: juveniles 2.66 days [-3.30, -2.01] later than adults) compared to those that did (juveniles 1.74 days [-3.56, 0.07] later than adults: Figure 2C).

Furthermore, both adults and juveniles that reattempted breeding laid their first clutch earlier than those that did not (adults: 4.53 days [3.22, 5.81] earlier, juveniles: 5.45 days [3.98, 6.87] earlier). Interestingly, juveniles that laid a replacement clutch did so 2.79 days [1.29, 4.24] earlier than adults that did not reattempt (Figure 2C).

3) Individual characteristics

Age and time of failure

Taking a subset of all failed first breeding attempts, and accounting for the laying date of individuals', adult birds were nearly twice as likely to initiate a second attempt compared to juveniles (adults 14.9% [13.0, 16.9], and juveniles 8.2% [6.9, 9.6], with a difference of 6.7% [4.4, 9.1]: Figure 3A)

Controlling for the timing of the first breeding attempt failure, birds that failed before hatching had a higher probability of making a second attempt in both age groups. Juveniles that fail before hatching have a higher probability of re-attempting breeding by 17.6 [14.4, 21.1] percentage points, whilst adults show a 27.6 [23.2, 32.0] percentage point increase. Even when grouped by failure timing, adults remain more likely than juveniles to make a second attempt (before hatching: by 13.4 [8.4, 18.5] percentage points, and between hatching and fledging: by 3.4 [2.0, 5.1] percentage points: Figure 3A).

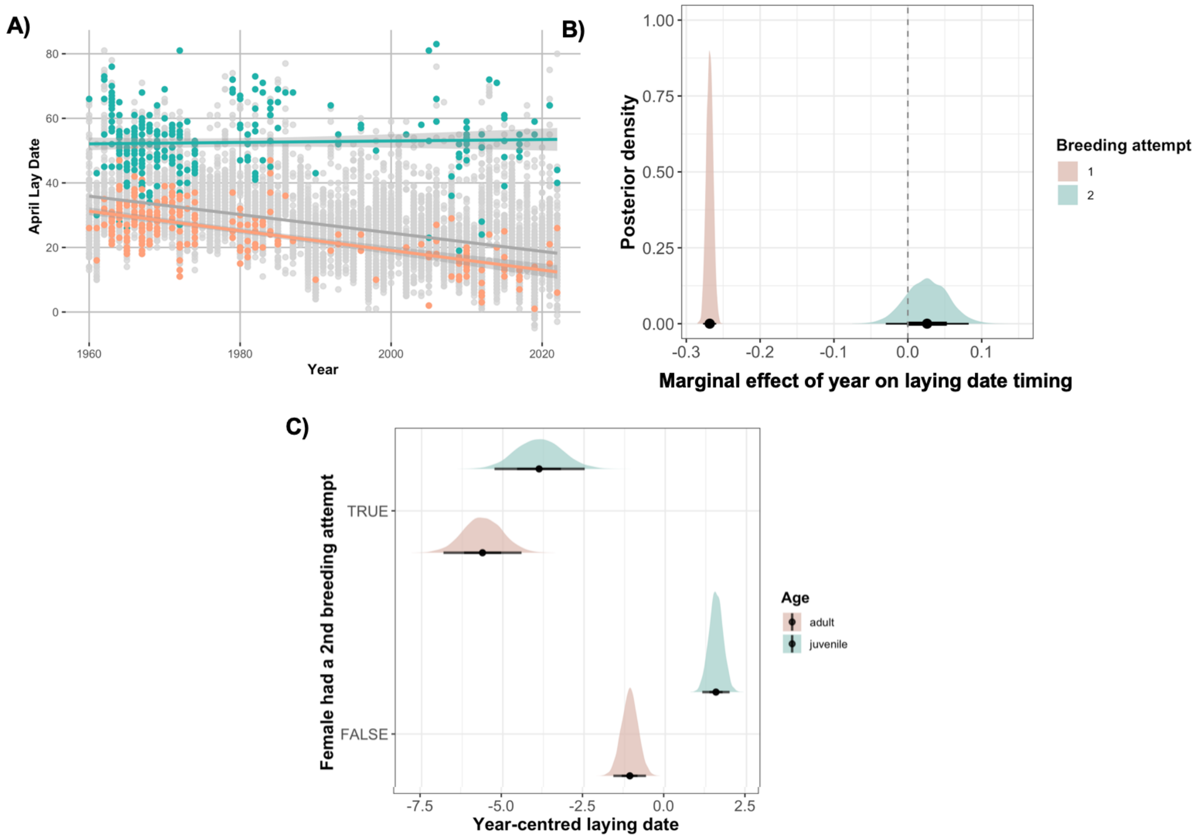


Figure 2: A) Trend over time of laying dates. The blue shows second breeding attempts, pink shows the timing of first breeding attempts of those that went on to have a second, and grey is all breeding attempts. B) Posterior distribution of marginal effects at the mean of laying date change over years for first and second breeding attempts (model 1). C) Posterior predicted means for year-centred laying date of first breeding attempts split by whether that female went on to have a second attempt or not and whether she was an adult or juvenile at time of breeding (model 2).

When the age of the breeding female is classified as years instead of the binary age groupings, we see the same pattern that females failing before hatching are overall more likely to produce second breeding attempts than those failing between hatching and fledging (Figure 3B). The biggest change in probability of second attempts is between one year and two year old birds, for both birds failing before hatching and between hatching and fledging (difference of -7.24 [-10.70, -4.34] percentage points for failures before hatching and -1.67 [-2.77, -0.86] percentage points for failures between hatching and fledging).

For females failing before hatching the probability of a second attempt increases slightly for three year old birds compared to two year olds (by 6.4 [1.74, 11.0]) percentage points, and then remains fairly steady, although the sample size for older birds is a lot smaller and so the confidence intervals grow considerably. For females failing between hatching and fledging, as age increases to three and four years old the probability of a second breeding attempt increases marginally, with a peak at four years, although not significantly different from three years old (2 vs 3 years old: 0.65 [-0.54, 2.25] percentage points difference, 3 vs 4 years old: 1.64 [-0.39, 4.02] percentage points difference), and then after this age it appears to decrease, although the sample size gets smaller and confidence intervals increase.

4) Demographic and phenological influences

Population size over years has no effect on the probability of second breeding attempts for both adults and juveniles (the increase in probability of a second breeding attempt as a function of population size: 0.007 [-0.04, 0.06] percentage points and 0.003 [-0.02, 0.03] percentage points for adults and juveniles respectively; Supplementary Figure 4). The within year variance of laying date also shows no effect on the probability of a female having a second breeding attempt, either for adults or for juveniles (-0.1 [-0.5, 0.3] percentage point difference, and -0.05 [-0.3, 0.1] percentage point difference for adults and juveniles respectively; Supplementary

Figure 4).

The model comparing neighbourhood age shows only a few notable differences in proportion of replacement breeding attempts related to neighbourhood age (Figure 4A). We find again that adults have a higher probability of having a second attempt after a failed first attempt. Between juveniles, those with juvenile neighbours have slightly higher probability of having a second breeding attempt than those with all adult neighbours, but not significantly different (4.71% [3.0, 6.1] and 2.92% [1.73, 4.70]). For adults, those with adult neighbours have a slightly higher probability of having a second attempt versus those with all juvenile neighbours, but not significantly different (8.75% [6.04, 11.26] and 5.86% [4.20, 8.51] respectively). For adults, those with no neighbours appear to have slightly higher probability of second breeding attempts than those with mixed or juvenile neighbours, but not significantly different from those with all adult neighbours. For both adults and juveniles with mixed neighbourhoods they have marginally lower probability of a second breeding attempt compared to those with no neighbours, however neither of these are significantly different from those that have all adult or all juvenile neighbours. Adults with mixed age neighbours have a slightly lower probability of having a second breeding attempt compared to adults with no neighbours and adults with all adult neighbours (5.33% [3.34, 7.20]) compared to 9.95% [8.00, 11.89]) and 8.81% [6.20, 11.31]) respectively). And juveniles with mixed neighbours also have a slightly lower probability of having a second breeding attempt compared to juveniles with no neighbours and juveniles with all juvenile neighbours (1.48% [0.66, 2.83] compared to 4.27% [3.07, 5.85]) and 4.79% [3.06, 6.03]) respectively).

In terms of annual differences, we found that for every day later the yearly median laying date is the probability of second breeding attempts for females who have a failure of their first brood decreases by 5.1 [1.9, 9.3] percentage points for adults and 2.6 [0.9, 5.1] percentage points for juveniles (Figure 4B); hence there is a suggestion that adults are more responsive to annual differences in phenology than juveniles, though the posterior probability distributions overlap substantially.

Discussion

Using 63 years of data from a wild, predominantly single-brooded, great tit population we identify the predictors of rare occurrences of second brooding and show that they do not occur at random. Instead, the likelihood of individuals having second breeding attempts is linked to an individual's age, the timing of their first laying date and the timing of failure of their first attempt, but less clearly linked to broader environmental factors.

Our study demonstrates that second breeding attempts, while present, are relatively uncommon in this population of great tits. Specifically, successive second breeding attempts, where a second attempt follows a successful first attempt, are rare, comprising only 39 of attempts. Although some females of successful attempts are unidentified, suggesting that this frequency could be a little higher, the percentage of successful unidentified females is low (3.8%), hence these types of second attempt cannot be very frequent. In contrast, replacement attempts, occurring after the failure of a first breeding attempt, are more frequent, particularly among adult birds whose first attempts fail before hatching. We observed variation in the frequency of second breeding attempts across the study years, with a possible link to changes in predation pressure. Our analysis indicates that the timing of first-breeding attempt failure has shifted over time, with early failures before hatching becoming less frequent and more failures occurring between hatching and fledging. One potential hypothesis is that the introduction of more predator-resistant woodcrete nest boxes in the 1980s helped to reduce predation of eggs by weasels (Mustela nivalis) (McCleery et al., 1996; Wilkin et al., 2007). This is reflected in the data as fewer replacement breeding attempts, not because necessarily there were fewer failures overall, but because failures later on in the reproductive process are less likely to produce a replacement breeding attempt, in part potentially just due to seasonal timing constraints. The rate of identifying individual birds has remained fairly consistent over time, which suggests that these observed differences in frequencies of known second breeding attempts are unlikely to be due to changes in detection efforts.

Ecological drivers of second breeding attempts

Our findings indicate that birds that make a second breeding attempt tend to have initiated their first breeding attempt earlier in the season, which is in line with what has been reported in other populations of great tits (Senécal et al., 2021; Verboven et al., 2001; Verboven & Verhulst, 1996). We also find that this pattern holds for both adult and juvenile birds. Interestingly, while juveniles generally breed later than adults, those that have a replacement attempt have -on average- an earlier first lay date than adults that fail but do not rebreed. We have previously found that on juvenile birds breed later than adults in general (Chapter 3),

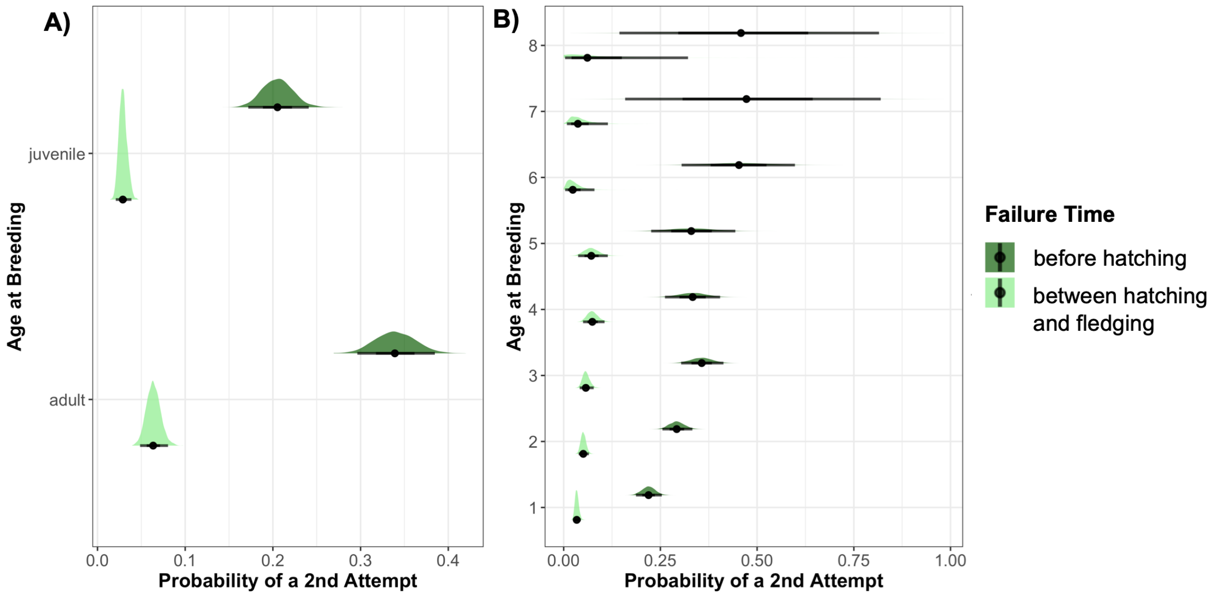
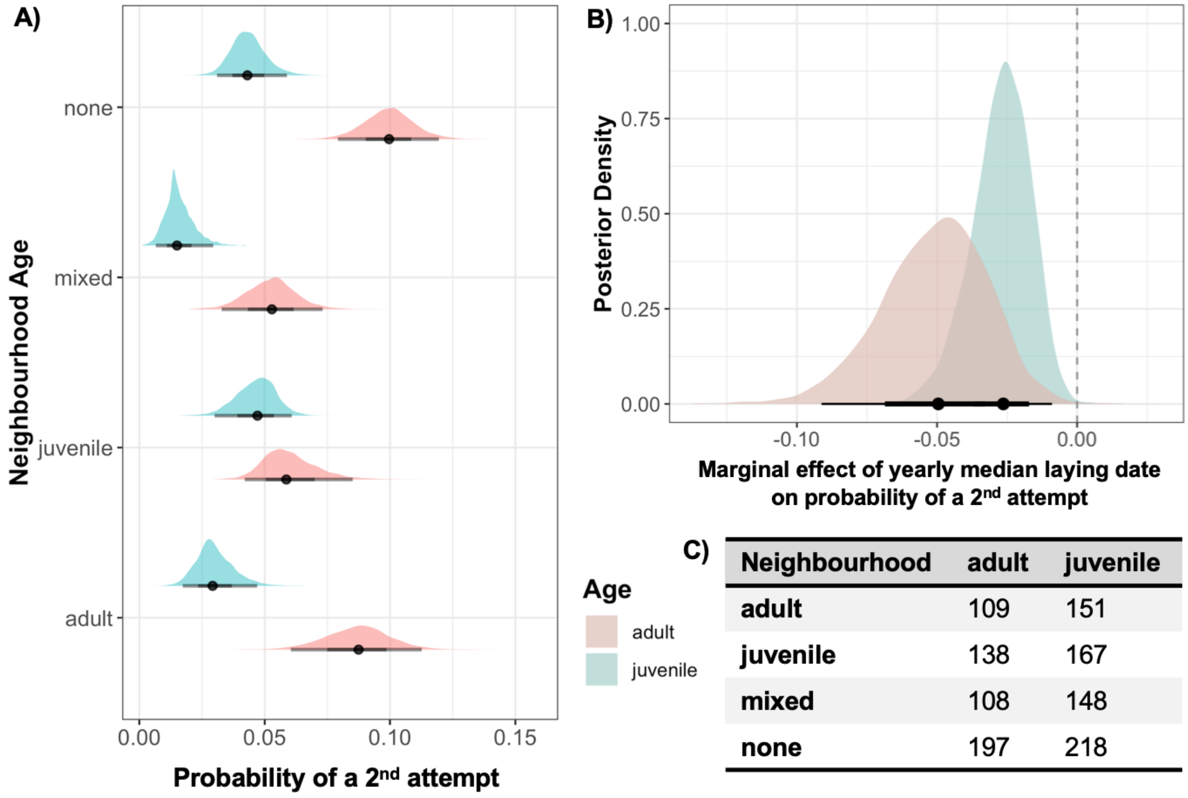


Figure 3: A) posterior predicted means for the probability of a female having a second attempt after the failure of her first attempt depending on the time at which her first brood failed and her age at breeding categorised by juvenile (1 year old) or adult (2+ years old) (model 3a). B) posterior predicted means for the probability of a female having a second attempt after the failure of her first attempt depending on the time which her first brood failed and her exact age at breeding. n = 1914, with 581 breeding attempts that fail before hatching, and 1333 that fail between hatching and fledging (model 3b).



Neighbourhood	adult	juvenile
adult	109	151
juvenile	138	167
mixed	108	148
none	197	218

Figure 4: A) posterior marginal predictions of the probability of having a second attempt after a failure, split by neighbourhood age group and age of breeding female (model 4). B) marginal effect of the yearly median laying date on the probability of females having a second breeding attempt (model 4). C) Sample size split between groupings, i.e. there are 109 adult females that have all adult neighbours, and 151 juvenile females who have all adult neighbours, and so on.

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and this aligns with our finding here that producing a second breeding attempt following a failed first breeding attempt is linked to the age of the bird and the timing of failure of their first attempt. Birds that experience early nest failures (before hatching), were considerably more likely to attempt a second breeding attempt than those failing after hatching but before fledging. This is potentially due to both the availability of time to renest as well as the reduced resource expenditure associated with early failures. Notably adults are more likely than juveniles to produce a second attempt in both failure timing groups, even when controlling for the timing of laying. Specifically, adults who fail before hatching are more likely to have a second attempt than juveniles who fail before hatching, and the same relationship is seen between adults and juveniles who fail between hatching and fledging. These age-related trends may reflect the advantages of breeding experience, which could enable adults to breed earlier and therefore have an increased chance of renesting after a failed attempt (Pyle et al., 2001).

Another interesting result is that juveniles who went on to have a second breeding attempt laid their first brood earlier, on average, than other adult birds that did not attempt a second brood. As noted previously, juveniles typically lay around two days later than adults (Chapter 3). This result suggests that only juveniles laying earlier are capable of initiating a second breeding attempt after a failed first attempt. Such opportunities may be more limited for juveniles than adults, as it is often believed that their timing is constrained by the additional time required to establish pair bonds and secure a territory (Culina et al., 2020).

We did not find any strong evidence that yearly population size or length of the breeding season each year significantly influenced the likelihood of replacement breeding attempts across years. However, years with an earlier median lay date showed a slight increase in second breeding attempts. This suggests year-to-year variation in seasonal timing may play a role in determining the frequency of second breeding attempts.

Analysis of neighbourhood age effects on the probability of second breeding attempts show that adults with all adult neighbours and juveniles with all juvenile neighbours show higher probability of second attempts than those with neighbours all of a different age, even though this is not always a statistically significant difference. One explanation for this general pattern could be that being surrounded by individuals of the same age reduces competition or enhances familiarity, potentially creating a more favourable social environment (Chapter 3). Familiarity among territorial neighbours has been shown to enhance reproductive success during synchronised breeding events in other populations (Grabowska-Zhang et al., 2012; Siracusa et al., 2021). Adult neighbours are more likely to be familiar with one another from prior breeding seasons or winter flocking behaviour (Culina et al., 2020; Gokcekus et al., 2023). In contrast, juveniles in all-juvenile neighbourhoods, compared to all-adult neighbourhoods, may not experience the disadvantages of competing against more experienced adults. Further research is needed to fully understand the role of neighbourhood composition in shaping second breeding attempts. Overall, the effects in relation to mixed age neighbourhoods are slightly more challenging to interpret, as these mixed age neighbours encompass some variation, it could be interesting to explore this further by looking at the proportions of juvenile and adult neighbours.

Importance of replacement breeding attempts for individual fitness

Replacement breeding attempts may offer potential benefits by allowing earlier breeders a second opportunity for reproductive success following an initial failure. For this population of great tits, where most individuals will only breed once or twice in their lifetimes (with an average breeding age of 1.8 years)(Woodman et al., 2023), replacement breeding attempts could play an important role in maximising reproductive output. Previous studies have demonstrated that birds laying earlier in the season tend to have higher reproductive success, with a decline across the season (Perrins & McCleery, 1989; Verhulst & Nilsson, 2008; Verhulst & Tinbergen, 1991). An early initial laying date may confer both direct and indirect reproductive advantages. Birds that breed earlier are more likely to have higher success rates for their first attempt, whilst also maintaining the possibility for having a second attempt if the first fails. Thus, early breeding not only aligns with the seasonal peak in reproductive success but also provides an additional opportunity to mitigate fitness loss following failure. This highlights the role of timing as a key factor in reproductive strategy. Furthermore, to fully understand the implications of replacement breeding attempts, further investigation is needed to evaluate how these secondary attempts influence individual fitness. This would provide valuable insights into the role of timing and adaptive flexibility in reproductive strategies.

In fluctuating environmental conditions, particularly as a result of climate change, the ability to produce a replacement breeding attempt may become increasingly important. Climate-induced changes in food availability, breeding conditions, and environmental stability may make the ability to have a second breeding attempt after a first failed attempt increasingly important for maintaining fitness and population stability. Patterns in occurrence of replacement breeding attempts in response to these changes could provide insights into how species might adapt their reproductive strategies in a warming climate. For instance, some species are already reducing the frequency of second breeding attempts (Husby et al., 2009; Visser et al., 2003), and others that typically produced a single brood per season, such as wrentits (Chamaea fasciata), have begun to exhibit multi-brooding behaviors under favorable conditions (Geupel & DeSante, 1990). Comparative studies across populations could help clarify whether such shifts are emerging in response to climate variability, and whether replacement and successive second breeding attempts are becoming more common under certain environmental scenarios. Understanding these dynamics is essential for predicting how reproductive strategies might evolve in response to ongoing climate changes.

It is also important to understand the drivers of second breeding attempts and their consequences on breeding success for knowing how these attempts may influence other analysis when these breeding attempts are included or excluded from datasets. Previous studies using these data often focus on initial breeding attempts, removing second attempts from analyses (Gokcekus et al., 2023; Jones et al., 2024; Van Der Jeugd & McCleery, 2002) However, it is important to consider second breeding attempts as a significant component of reproductive strategies, especially in populations where they do not occur randomly but are driven by individual-level factors like age and timing of failure. Further work directly examining how the inclusion or exclusion of second breeding attempts affects our estimates of ecological parameters are now warranted.

Summary

Distinguishing the roles of individual choice or ability versus external constraints in determining the frequency of second breeding attempts is challenging. Our results suggest second attempts are primarily driven by individual characteristics, such as age, timing of the first breeding attempt, and the timing of its failure, rather than by broader seasonal and environmental factors such as population size or timing and length of breeding season. Second breeding attempts in this population are not random, making it crucial to understand when they occur and their role in shaping breeding timing at the population level. As climate change shifts breeding patterns for many species, these attempts could represent a key component of reproductive strategy. This underscores the importance of incorporating second attempts into broader frameworks of reproductive timing and encourages further investigation across other systems. Further work could now focus on determining the causal effects of second breeding attempts for fitness. Using comparative studies across multiple species or experimental manipulations that induce second breeding attempts could provide valuable insights into their adaptive significance. By investigating the balance between individual choice and external constraints, we can gain new insights into strategies birds use to adjust timing traits and maximise reproductive success across different systems.

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References

Bouwhuis, S., Sheldon, B. C., Verhulst, S., & Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B: Biological Sciences, 276(1668), 2769–2777. https://doi.org/10.1098/rspb.2009.0457

Brambell, F. W. R. (1948). Prenatal Mortality in Mammals. Biological Reviews, 23(4), 370–407. https://doi.org/10.1111/j.1469-185X.1948.tb00565.x

Bukor, B., Seress, G., Pipoly, I., Sándor, K., Sinkovics, C., Vincze, E., & Liker, A. (2021). Double-brooding and annual breeding success of great tits in urban and forest habitats. Current Zoology, 68(5), 517–525. https://doi.org/10.1093/cz/zoab096

Culina, A., Firth, J. A., & Hinde, C. A. (2020). Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population: Pairs that meet earlier do better. Proceedings of the Royal Society B: Biological Sciences, 287(1941). https://doi.org/10.1098/rspb.2020.1554rspb20201554

Enemar, A. (2009). First, second and replacement broods in the breeding biology of a Treecreeper Certhia familiaris population. Ornis Svecica, 19(2), Article 2. https://doi.org/10.34080/os.v19.22654

Farine, D. R., Firth, J. A., Aplin, L. M., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Milligan, N. D., Psorakis, I., Radersma, R., Verhelst, B., Voelkl, B., & Sheldon, B. C. (2015). The role of social and ecological processes in structuring animal populations: A case study from automated tracking of wild birds. Royal Society Open Science, 2(4). https://doi.org/10.1098/rsos.150057

Firth, J. A., Cole, E. F., Ioannou, C. C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K., & Sheldon, B. C. (2018). Personality shapes pair bonding in a wild bird social system. Nature Ecology and Evolution, 2(11), 1696–1699. https://doi.org/10.1038/s41559-018-0670-8

Foster, R., & Kreitzman, L. (2009). Seasons of life: The biological rhythms that enable living things to thrive and survive. Yale University Press. https://ora.ox.ac.uk/objects/uuid:7fe87578-1b69-4b99-99ac-362ad7302175

Gabry, J., Češnovar, R., Johnson, A., & Bronder, S. (2024). R Interface to CmdStan. https://mc-stan.org/cmdstanr/

Geupel, G. R., & DeSante, D. F. (1990). Incidence and Determinants of Double Brooding in Wrentits. The Condor, 92(1), 67–75. https://doi.org/10.2307/1368384

Gokcekus, S., Firth, J. A., Regan, C., Cole, E. F., Sheldon, B. C., & Albery, G. F. (2023). Social Familiarity and Spatially Variable Environments Independently Determine Reproductive Fitness in a Wild Bird. The American Naturalist, 201(6), 813–824. https://doi.org/10.1086/724382

Gosler, A. (1993). The Great Tit. Hamlyn.

Grabowska-Zhang, A. M., Wilkin, T. A., & Sheldon, B. C. (2012). Effects of neighbor familiarity on reproductive success in the great tit *(Parus major)*. Behavioral Ecology, 23(2), 322–333. https://doi.org/10.1093/beheco/arr189

Harvey, P. H., Greenwood, P. T., & Perrins, C. M. (1979). Breeding Area Fidelity of Great Tits *(Parus major)*. Journal of Animal Ecology, 48(1), 305–313.

Hayssen, V. (2008). Reproductive Effort in Squirrels: Ecological, Phylogenetic, Allometric, and Latitudinal Patterns. Journal of Mammalogy, 89(3), 582–606. https://doi.org/10.1644/07-MAMM-A-064R2.1

Hinks, A. E., Cole, E. F., Daniels, K. J., Wilkin, T. A., Nakagawa, S., & Sheldon, B. C. (2015). Scale-dependent phenological synchrony between songbirds and their caterpillar food source. American Naturalist, 186(1), 84–97. https://doi.org/10.1086/681572

Hoffmann, J., Postma, E., & Schaub, M. (2015). Factors influencing double brooding in Eurasian Hoopoes Upupa epops. Ibis, 157(1), 17–30. https://doi.org/10.1111/ibi.12188

Husby, A., Kruuk, L. E. B., & Visser, M. E. (2009). Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. Proceedings of the Royal Society B: Biological Sciences, 276(1663), 1845–1854. https://doi.org/10.1098/rspb.2008.1937

Jones, C. V., Regan, C. E., Cole, E. F., Firth, J. A., & Sheldon, B. C. (2024). Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits. Evolution, qpae155. https://doi.org/10.1093/evolut/qpae155

Krebs, J. R. (1971). Territory and Breeding Density in the Great Tit, *(Parus Major L.)* Ecology, 52(1), 2–22. https://doi.org/10.2307/1934734

Lindén, M. (1988). Reproductive Trade-Off between First and Second Clutches in the Great Tit *(Parus major)*: An Experimental Study. Oikos, 51(3), 285–290. https://doi.org/10.2307/3565309

McCleery, R. H., Clobert, J., Julliard, R., & Perrins, C. M. (1996). Nest Predation and Delayed Cost of Reproduction in the Great Tit. Journal of Animal Ecology, 65(1), 96–104. https://doi.org/10.2307/5703

Perrins, C. M., & McCleery, R. H. (1985). The effect of age and pair bond on the breeding success of Great Tits *(Parus major)*. Ibis, 127(3), 306–315. https://doi.org/10.1111/j.1474-919X.1985.tb05072.x

Perrins, C. M., & McCleery, R. H. (1989). Laying Dates and Clutch Size in the Great Tit. The Wilson Bulletin, 101(2), 236–253.

Pyle, P., Sydeman, W. J., & Hester, M. (2001). Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. Journal of Animal Ecology, 70(6), 1088–1097. https://doi.org/10.1046/j.0021-8790.2001.00567.x

Rowley, I., Brooker, M., & Russell, E. (1991). The Breeding Biology of the Splendid Fairy-wren Malurus splendens: The Significance of Multiple Broods. Emu, 91(4), 197–221. https://doi.org/10.1071/mu9910197

Sæther, B.-E., & Bakke, Ø. (2000). Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. Ecology, 81(3), 642–653. https://doi.org/10.2307/177366

Schwartz, M. (2003). Phenology: An Integrative Environmental Science. Springer Science & Business Media.

Senécal, S., Mouchet, A., & Dingemanse, N. J. (2021). Life-history trade-offs, density, lay date—Not personality—Explain multibroodedness in great tits. Behavioral Ecology, 32(6), 1114–1126. https://doi.org/10.1093/beheco/arab068

Siracusa, E. R., Boutin, S., Dantzer, B., Lane, J. E., Coltman, D. W., & McAdam, A. G. (2021). Familiar Neighbors, but Not Relatives, Enhance Fitness in a Territorial Mammal. Current Biology: CB, 31(2), 438-445.e3. https://doi.org/10.1016/j.cub.2020.10.072

Stearns, S. C. (1976). Life-History Tactics: A Review of the Ideas. The Quarterly Review of Biology. https://doi.org/10.1086/409052

Tablado, Z., Revilla, E., & Palomares, F. (2009). Breeding like rabbits: Global patterns of variability and determinants of European wild rabbit reproduction. Ecography, 32(2), 310–320. https://doi.org/10.1111/j.1600-0587.2008.05532.x

Stearns, S. C. (1992). The Evolution of Life Histories. Oxford University Press. https://doi.org/10.1046/j.1420-9101.1993.6020304.x

Van Der Jeugd, H. P., & McCleery, R. (2002). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. Journal of Evolutionary Biology, 15(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

Verboven, N., Tinbergen, J. M., & Verhulst, S. (2001). Food, reproductive success and multiple breeding in the Great Tit *(Parus major)*. Ardea, 89(2), 387–406.

Verboven, N., & Verhulst, S. (1996). Seasonal Variation in the Incidence of Double Broods: The Date Hypothesis Fits Better than the Quality Hypothesis. The Journal of Animal Ecology, 65(3), 264. https://doi.org/10.2307/5873

Verhulst, S. (1998). Multiple breeding in the Great Tit, II. The costs of rearing a second clutch. Functional Ecology, 12(1), 132–140. https://doi.org/10.1046/j.1365-2435.1998.00165.x

Verhulst, S., & Nilsson, J. Å. (2008). The timing of birds' breeding seasons: A review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B: Biological Sciences, 363(1490), 399–410. https://doi.org/10.1098/rstb.2007.2146

Verhulst, S., & Tinbergen, J. M. (1991). Experimental Evidence for a Causal Relationship between Timing and Success of Reproduction in the Great Tit *(Parus m. Major)*. Journal of

Animal Ecology, 60(1), 269–282. https://doi.org/10.2307/5459

Verhulst, S., Tinbergen, J. M., & Daan, S. (1997). Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts? Functional Ecology, 11(6), 714–722. https://doi.org/10.1046/j.1365-2435.1997.00145.x

Vincent Arel-Bundock, Noah Greifer, & Andrew Heiss. (2024). How to Interpret Statistical Models Using marginaleffects for R and Python. Journal of Statistical Software, 111(9), 1–32. https://doi.org/10.18637/jss.v111.i09

Visser, M. E., Adriaensen, F., Van Balen, J. H., Blondel, J., Dhondt, A. A., Van Dongen, S., Du Feu, C., Ivankina, E. V., Kerimov, A. B., De Laet, J., Matthysen, E., McCleery, R., Orell, M., & Thomson, D. L. (2003). Variable responses to large-scale climate change in European Parus populations. Proceedings of the Royal Society B: Biological Sciences, 270(1513), 367–372. https://doi.org/10.1098/rspb.2002.2244

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2007). Edge effects in the great tit: Analyses of long-term data with GIS techniques. Conservation Biology, 21(5), 1207–1217. https://doi.org/10.1111/j.1523-1739.2007.00767.x

Woodman, J. P., Cole, E. F., Firth, J. A., Perrins, C. M., & Sheldon, B. C. (2023). Disentangling the causes of age-assortative mating in bird populations with contrasting life-history strategies. Journal of Animal Ecology, 92(5), 979–990. https://doi.org/10.1111/1365-2656.13851

Yasué, M., & Dearden, P. (2008). Replacement Nesting and Double-Brooding in Malaysian Plovers Charadrius peronii: Effects of Season and Food Availability. Ardea, 96(1), 59–72. https://doi.org/10.5253/078.096.0107

6

General Discussion

General Discussion

This thesis began with an interest in patterns of phenology within populations. Understanding what generates and maintains phenotypic variation is of key importance to understanding ecological and evolutionary processes. This is of particular importance for seasonal timing traits, which play a key role in fitness and population persistence. Phenological traits often serve as clear indicators of species' responses to climate change. To survive, species must be able to adjust their phenology to keep up with changing environments and shifts in seasons and seasonally variable resources (Cleland et al., 2007; Crick et al., 1997; Hetem et al., 2014). Therefore, understanding the drivers of variation in these traits and how they may evolve over time is essential for predicting species' ability to cope with environmental changes. We understand the decisions individuals make to be shaped by selection, leading to individuals timing arrival at a specific development stage with a particular aspect of their environment. Misalignment in this timing can have consequences not only at the individual level but also scale to the population level (Brook et al., 2015; Simmonds et al., 2020; Thomas et al., 2001). Therefore, understanding individual level patterns in phenology is crucial for understanding the population level patterns we see (Forrest and Miller-Rushing 2010). I focus in particular on the breeding timing of a wild bird population, where individuals are more successful when they time their egg laying so that the peak energy demand of chicks will align with the peak availability of food to maximise their survival.

Some of the key questions that arise are: how do we estimate the heritability of a seasonal timing trait well? How do we account for the environment at relevant scales for individuals making decisions about when to breed? What makes up the environment experienced by these individuals whilst they are making these decisions? Addressing these requires large datasets with detailed information on individuals' breeding behaviour over time and space. Such data are essential for identifying temporal shifts and disentangling the effects of intrinsic factors, such as genetics, from those driven by external environmental conditions. The long-term dataset of great tits in Wytham Woods provides an opportunity to delve deeper into these questions, by exploring phenological variation within a population, between individuals across time and space. With the wealth of data collected in Wytham across the years, the dataset offers a - sometimes dangerously - never-ending path of inquiry. I aimed overall to investigate the genetic, environmental and social drivers of breeding timing in this population of wild birds. In this final chapter, I discuss how this thesis contributes to our understanding of intraspecific variation in phenology.

My initial interest lay in disentangling genetic and environmental contributions to variation in breeding timing, whilst considering various assumptions and factors that could bias these estimates. For example, individuals experiencing more similar environments may also be more likely to show similarity in their timing traits. When individuals sharing similar environments are also genetically related, failing to account for these shared environments can lead to an overestimation of the variation attributed to genetic effects, when in reality it is driven by environmental factors (Kruuk & Hadfield, 2007). How, then, can we more comprehensively account for these shared environmental influences? This led me to dive into quantitative genetics, and became the first data chapter of my thesis. Using the extensive pedigree data and information on breeding locations from Wytham, I built on existing methods (e.g. Gervais et al., 2022; Regan et al., 2017; Rutschmann et al., 2020; Thomson et al., 2018) to account for shared environments beyond spatial proximity or space sharing. My findings emphasise the importance of incorporating shared environmental effects when estimating heritability, as failing to do so can inflate estimates (**Chapter 2**), and highlights the need to consider a species' life history and the structure of the environment they live in when attempting to estimate genetic contributions to phenotypic variation. An interesting next step which this work specifically highlighted is to look at the heritability of the environment itself, and how this may influence the heritability estimates of a trait. This is beginning to be considered e.g. (Munar-Delgado et al., 2024), and will provide to the field a more in depth understanding of genetic and nongenetic inheritance of environments, and how this can impact estimates of heritability.

Working on **Chapter 2** also made me think in more depth about this study system and timing traits more broadly, in particular about what constitutes an "environment" for an individual. Initially my focus was on simple measures of the physical environment, such as altitude, proximity to the edge of a habitat or breeding density, which was partly driven by what is known to impact laying date from previous research in this system and first hand experience in the field and partly by the relatively large amount of interest in such other factors in other systems (Wilkin et al., 2006; Wilkin, Garant, et al., 2007; Wilkin, Perrins, et al., 2007). However, it is likely that when a bird is beginning a clutch they will experience a far more complex environment, including factors such as the impact of social dynamics, age structure, and familiarity with conspecifics and surroundings.

Seasonal activities take place in social contexts. Social environments can be made up of interactions with other individuals through phenotypic plasticity or indirect genetic effects, and often play a role in determining individual behaviour (Charmantier et al., 2014). In birds, behaviours such as breeding timing can be transmitted both actively and inadvertently through social information from conspecifics (Helm, Piersma, and van der Jeugd 2006). This could vary due to the age or experience of individuals with each other and with their environments. As reported in previous work (Perrins & McCleery, 1985), I observe consistent differences in breeding timing with age, where juveniles tend to lay later than adults (**Chapter 3**) . How might the makeup of the age structure of an individual's neighbours influence their breeding timing? Understanding these dynamics provides insights into plasticity and the use of social cues.

Often the measure of breeding timing used in analysis is a year-centred laying date, which gives the laying date of an individual relative to the whole population within years (Jones et al., 2024; Van Der Jeugd & McCleery, 2002). This measure gives an overall picture of earlier or later dates but may not capture small scale variation or timing to local resource peaks, which may be more relevant to the local environment that individuals will experience themselves. As such I wanted to consider breeding timing when measured as mismatch from a local average (local breeding mismatch), to attempt to account for small scale variation spatially across the woodland. The local breeding mismatch measure was calculated relative to a nest box's average laying date over all study years. It may also be assumed that the average timing of breeding attempts in a given nest box will align somewhat with optimal timing for that location over years. Comparing these different measures of breeding timing measures could provide us with a better understanding of the scales at which these processes operate.

We found across **Chapter 3** and **Chapter 4** that there doesn't appear to be a shift towards the local average (with a decrease in local average mismatch), more that earlier year-centred laying date, also means earlier in relation to local average. It could be that mismatch at the laying stage is not critically important, as birds can adjust their timing later during egg laying or incubation, to ensure peak energy demand aligns with peak resource availability (Cresswell & McCleery, 2003). Or this might indicate that our measure of local breeding mismatch needs further investigation and refinement to better capture complexities of spatial variation in the woods. The assumption that a local breeding timing measure may represent the optimal timing for a specific location is supported by evidence that birds breeding around this local average time seem to maximise certain locally-determined measures of fitness. However, this relationship is complicated by findings that fitness is often maximised when birds are breeding earlier than the mean (Perrins & McCleery, 1989). There are current attempts to model this from an ecological stable state perspective, considering that what constitutes "optimal timing" may depend on the behavior of other individuals within the population. Overall, it is clear that it is important across systems to consider measures that are at the most relevant scale for what individuals are experiencing.

To consider how the social environment might shape phenology, in **Chapter 3** I explore the role of age-related social mechanisms and how the ages of individuals in the local neighborhood may influence a focal individual's phenology. I found that adult individuals breed earlier than juveniles even when accounting for local phenological variation. Further, adult birds surrounded by juveniles breed earlier than those surrounded by other adults, potentially due to competition or avoidance strategies. However juveniles do not appear to be affected by the age composition of their neighbourhood, maybe indicating that juveniles are less capable of using social cues or are forced to focus on other priorities i.e. finding a mate and establishing a territory. Separating the effects of the social and spatial environment is challenging because these factors often overlap. Individuals that interact socially are also likely to share physical space, making it difficult to disentangle these influences without large datasets of individuals or experimental work. However, this chapter makes a step forward towards providing a framework for understanding how social mechanisms influence reproductive timing in territorial breeding populations.

In **Chapter 4** I investigated the role of familiarity, both with partners and with a breeding site, on breeding timing, to consider how experience over time may drive when individuals are breeding. Previous research in this population showed familiarity plays a role in breeding success (Culina et al., 2020; Gokcekus et al., 2023). I extend this work here by exploring whether there is a relationship between familiarity and laying date local breeding mismatch, as well as incorporating familiarity with nest boxes. Familiarity with both partner and nest site was found to facilitate earlier breeding, for both year-centred laying date and local breeding mismatch. Birds remaining with the same partner were more likely to breed in the same nest box, but this was not always the case. It seems that partner familiarity was the main driver for earlier breeding, but individuals with an unfamiliar partner benefitted from having a familiar nest box and were able to lay almost as early. This suggests both forms of familiarity play complementary roles in influencing birds to time their reproduction. Future work could explore how these effects on laying date relate to fitness consequences, specifically experiments designed to isolate the effects of social familiarity (partner retention) from environmental familiarity (site fidelity) may help to clarify the mechanisms underlying these patterns. Furthermore, the measure of familiarity with a nest box could be extended to consider not just a specific location but, as in **Chapter 2**, using measures of the environment to compare environmental similarity between places a bird has nested over its lifetime; does a more familiar environment type mean earlier breeding too? When might birds choose to change nest boxes between seasons? And what environmental characteristics may they look for in a new nest box?

Chapter 5 addressed a question often overlooked in studies of breeding timing in birds; the occurrence of multiple breeding attempts within a season. Typical analyses will focus on first breeding attempts only, excluding second attempts (e.g. Cole et al., 2021; Jones et al., 2024; Van Der Jeugd & McCleery, 2002). This is the approach I followed in the earlier chapters too; however questions remained surrounding the prevalence of these second attempt, and what may drive their occurrence in this population. The non-random occurrence of these second breeding attempts in this population reported in this chapter highlights the importance of understanding what causes them. I hypothesise that second breeding attempts could be an important strategy for dealing with changing environments, possibly allowing individuals who may mistime their first breeding attempt, resulting in a failure, the opportunity to retry and raise a brood successfully within the same season instead of having to wait until the next year. This could be particularly important for short lived seasonally breeding birds because they often only have one season to breed and raise offspring, and so maximising the possibility for doing this successfully may be of greater importance than species that have a longer window of time over lifetime or within years (Sæther & Bakke, 2000).

This chapter provides a first look at the prevalence and predictors of second breeding attempts in the great tit population in Wytham, and provides the foundation to address further questions about the influences of second attempts on breeding success within years and over the lifetime of individuals. As well as raising important methodological considerations; most previous work has removed known second breeding attempts before carrying out analyses, but how might removing second breeding attempts from analyses affect the estimates and conclusions we draw from them?

Finally, this thesis opens the door to other particularly useful avenues of future research in Wytham. For example, to explore the influence of social effects further, particularly in the context of how social interactions during the non-breeding season affect the breeding season, there are extensive data on social networks of birds during their winter flocking period, from which could be mapped over the social interactions of individuals and their movements throughout the woods in the months leading up to the breeding season. There is also potential for this system to contribute to understanding how bird song relates to phenology on an individual level; specifically, there is 21,283 hours of male great tit song recorded at nest boxes during the breeding season. From first simple analyses we can see that there is a clear peak in a male's song activity around the date of first egg laying by his partner (Merino Recalde et al., 2024). These data could be used to explore potential markers that could be associated with social transmission of laying date via singing behaviour.

This thesis contributes to our understanding of the causes of variation in breeding timing by highlighting several key factors. I demonstrate the importance of accounting for environmental similarities experienced by related individuals when estimating the heritability of timing traits, and show how they may be biased without this consideration. Social influences are shown to affect breeding timing, with individuals' timing being linked to the age composition of their neighbours. Additionally familiarity with both breeding partners and nest boxes is found to advance breeding timing. Lastly, I show that second breeding attempts in this population are influenced by individual factors, and may represent an important reproductive strategy warranting further investigation.

Overall, I hope this thesis has provided interesting and valuable insights into the causes of variation in breeding timing, and provides a foundation for various streams of further work as outlined throughout the thesis. It is important to understand how these traits are shaped to inform our understanding of evolution, and to predict how phenological traits may respond to future environmental changes.

References

Brook, R. W., Leafloor, J. O., Abraham, K. F., & Douglas, D. C. (2015). Density dependence and phenological mismatch: Consequences for growth and survival of sub-arctic nesting Canada Geese. 10(1). https://doi.org/10.5751/ACE-00708-100101

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. Trends in Ecology and Evolution, 22(7), 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Cole, E. F., Regan, C. E., & Sheldon, B. C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. Nature Climate Change, 11(10), 872–878. https://doi.org/10.1038/s41558-021-01140-4

Cresswell, W., & McCleery, R. (2003). How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. Journal of Animal Ecology, 72(2), 356–366. https://doi.org/10.1046/j.1365-2656.2003.00701.x

Crick, H. Q. P., Dudley, C., Glue, D. E., & Thomson, D. L. (1997). UK birds are laying eggs earlier. Nature, 388, 526–527.

Culina, A., Firth, J. A., & Hinde, C. A. (2020). Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population: Pairs that meet earlier do better. Proceedings of the Royal Society B: Biological Sciences, 287(1941). https://doi.org/10.1098/rspb.2020.1554rspb20201554

Gervais, L., Morellet, N., David, I., Hewison, A. J. M., Réale, D., Goulard, M., Chaval, Y., Lourtet, B., Cargnelutti, B., Merlet, J., Quéméré, E., & Pujol, B. (2022). Quantifying heritability and estimating evolutionary potential in the wild when individuals that share genes also share environments. Journal of Animal Ecology, 0–2. https://doi.org/10.1111/1365-2656.13677

Gokcekus, S., Firth, J. A., Regan, C., Cole, E. F., Sheldon, B. C., & Albery, G. F. (2023). Social Familiarity and Spatially Variable Environments Independently Determine Reproductive Fitness in a Wild Bird. The American Naturalist, 201(6), 813–824. https://doi.org/10.1086/724382

Hetem, R. S., Fuller, A., Maloney, S. K., & Mitchell, D. (2014). Responses of large mammals to climate change. Temperature, 1(2), 115–127. https://doi.org/10.4161/temp.29651

Jones, C. V., Regan, C. E., Cole, E. F., Firth, J. A., & Sheldon, B. C. (2024). Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits. Evolution, qpae155. https://doi.org/10.1093/evolut/qpae155

Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. Journal of Evolutionary Biology, 20(5), 1890–1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Merino Recalde, N., Estandía, A., Pichot, L., Vansse, A., Cole, E. F., & Sheldon, B. C. (2024). A densely sampled and richly annotated acoustic data set from a wild bird population. Animal Behaviour, 211, 111–122. https://doi.org/10.1016/j.anbehav.2024.02.008

Munar-Delgado, G., Nicolaus, M., Both, C., & Edelaar, P. (2024). Quantifying heritability of the environment using animal models: A case study. https://ecoevorxiv.org/repository/view/6483/

Perrins, C. M., & McCleery, R. H. (1985). The effect of age and pair bond on the breeding success of Great Tits *(Parus major)*. Ibis, 127(3), 306–315. https://doi.org/10.1111/j.1474-919X.1985.tb05072.x

Perrins, C. M., & McCleery, R. H. (1989). Laying Dates and Clutch Size in the Great Tit. The Wilson Bulletin, 101(2), 236–253.

Regan, C. E., Pilkington, J. G., Bérénos, C., Pemberton, J. M., Smiseth, P. T., & Wilson, A. J. (2017). Accounting for female space sharing in St. Kilda Soay sheep (Ovis aries) results in little change in heritability estimates. Journal of Evolutionary Biology, 30(1), 96–111. https://doi.org/10.1111/jeb.12990

Rutschmann, A., de Villemereuil, P., Brekke, P., Ewen, J. G., Anderson, N., & Santure, A. W. (2020). Consequences of space sharing on individual phenotypes in the New Zealand hihi. Evolutionary Ecology, 34(5), 821–839. https://doi.org/10.1007/s10682-020-10063-z

Sæther, B.-E., & Bakke, Ø. (2000). Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. Ecology, 81(3), 642–653. https://doi.org/10.2307/177366

Simmonds, E. G., Cole, E. F., Sheldon, B. C., & Coulson, T. (2020). Testing the effect of quantitative genetic inheritance in structured models on projections of population dynamics. Oikos, 129(4), 559–571. https://doi.org/10.1111/oik.06985

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M., & Speakman, J. R. (2001). Energetic and Fitness Costs of

Mismatching Resource Supply and Demand in Seasonally Breeding Birds. Science, 291(5513), 2598–2600. https://doi.org/10.1126/science.1057487

Thomson, C. E., Winney, I. S., Salles, O. C., & Pujol, B. (2018). A guide to using a multiple-matrix animal model to disentangle genetic and nongenetic causes of phenotypic variance. PLOS ONE, 13(10), e0197720. https://doi.org/10.1371/journal.pone.0197720

Van Der Jeugd, H. P., & McCleery, R. (2002). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. Journal of Evolutionary Biology, 15(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2006). Density effects on life-history traits in a wild population of the great tit *(Parus major)*: Analyses of long-term data with GIS techniques. Journal of Animal Ecology, 75(2), 604–615. https://doi.org/10.1111/j.1365-2656.2006.01078.x

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2007). Edge effects in the great tit: Analyses of long-term data with GIS techniques. Conservation Biology, 21(5), 1207–1217. https://doi.org/10.1111/j.1523-1739.2007.00767.x

Wilkin, T. A., Perrins, C. M., & Sheldon, B. C. (2007). The use of GIS in estimating spatial variation in habitat quality: A case study of lay-date in the Great Tit *(Parus major)*. Ibis, 149(SUPPL. 2), 110–118. https://doi.org/10.1111/j.1474-919X.2007.00757.x

A

Supporting Information Chapter 2

Supplementary Information for paper:

Shared environmental similarity between relatives influences heritability of reproductive timing in wild great tits

Table of Contents

Section 1 - Regression analysis

Repeating analysis from Van der Jeugd & McCleery 2002 with additional data.

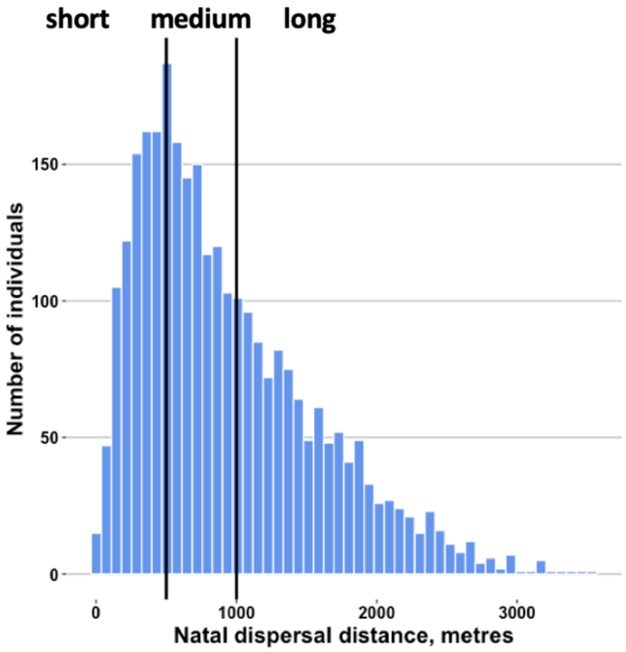
Parent-offspring regressions use phenotypic similarity between related individuals to estimate heritability (Lynch & Walsh, 1998). For single parent-offspring regression, the coefficient estimate from a linear regression of mother's mean phenotype against daughter's mean phenotype is multiplied by the inverse proportion of expected genes shared to estimate the heritability; hence in this case it is multiplied by two as the offspring share, on average, half their genes with the parent (Boag & van Noordwijk, 1987). The parent-offspring regressions were calculated for laying and hatching date, and then based on previous analysis of this population by (Van Der Jeugd & McCleery, 2002a) the analysis was repeated by forming groups of relatives with different dispersal distances, to emphasis the effect of shared environments. We present this updating of the initial analysis of van der Jeugd and McCleery (2002) for two reasons: (1) It was an early attempt to estimate formally the effect of shared environments on heritability of timing and we consider it interesting to repeat with a substantially larger data set; (2) it provides a simple visual interpretation of the effect of increased spatial distance on heritability.

Parent-offspring regressions

Parent-offspring regressions use phenotypic similarity between related individuals to estimate heritability (Lynch & Walsh, 1998). Using just female birds, from the pedigree there were 3,371 relationships where both a daughter and mother had recorded first egg lay dates; 95% (N = 3,187) of those pairings also had a recorded hatch date (the decrease in number of hatch dates compared to laying dates is due to abandoned nests before or during incubation). Overall, this includes 4,604 unique birds (some daughters will also be included as mothers, and some mothers will have multiple daughters). Due to significant differences in mean laying and hatching date between years and age classes all dates were standardised by year and age. The age of all birds was known to good degree of certainty, either from records of their birth, or from aging from plumage when caught. If an individual had multiple recorded laying or hatching dates (46% of individuals included in this study) their lifetime mean was taken. If a mother had multiple recorded daughters who bred, the mother was included once for each mother-daughter pairing.

Accounting for dispersal distance

Natal dispersal distance was defined as the distance moved by an individual between their natal box (the nest box they were born in), to the box where they first breed (most commonly at age 1). The median natal dispersal for females was 786m, with 62% breeding within 1km of where they were born (Supplementary Figure 1). Natal dispersal distance is a straightforward way to begin to account for the shared environment between mothers and daughters. The environment in Wytham is heterogenous over small scales; for example across the 385ha woodland altitude varies by 100m (Wilkin, Perrins, et al., 2007). So, we may expect offspring that disperse shorter distances to end up in a more similar environment to their parents.



Supplementary Figure 1 – Natal dispersal distance – Natal dispersal distance of females in population. Vertical black lines show where the data was split to create the short, medium and long dispersal groups, labelled above the plot. Further details about dispersal groupings in Table 1, n = 3371. The median natal dispersal distance is 786m.

Natal dispersal distance was calculated for all daughters. To replicate the analysis from (Van Der Jeugd & McCleery, 2002b) we then split the mother-daughter pairings into three distance groups: 'short' (0-500m), 'medium' (500-1000m) and 'long' (>1000m) dispersers. The number of pairs and mean dispersal distance within each group are shown in Supplementary Table 1, and a histogram showing the range in dispersal distances overall, with lines indicating where the groups are split, is shown in Supplementary Figure 1 – note that the groupings are artificial, but that these distance classes do split the data into three approximately equal sized groups. The parent-offspring regressions were recalculated for each of these dispersal groupings, and heritability estimated for each.

Supplementary Table 1 – Dispersal distance groupings – The data were split into 3 groups, short, medium and long dispersers, depending on the distance daughters moved from their natal to first breeding box. The table shows the number of mother-daughter pairings in each group (N), and the distance range and mean distance dispersed within each group.

Trait & Group	*N*	*Distance range*	*Median distance*
Laying Date			
short	986	0-500m	315m
medium	1095	500-1000m	718m
long	1290	>1000m	1480m
Hatching Date			
short	946	0-500m	318m
medium	1032	500-1000m	720m
long	1209	>1000m	1482m

Regressions results

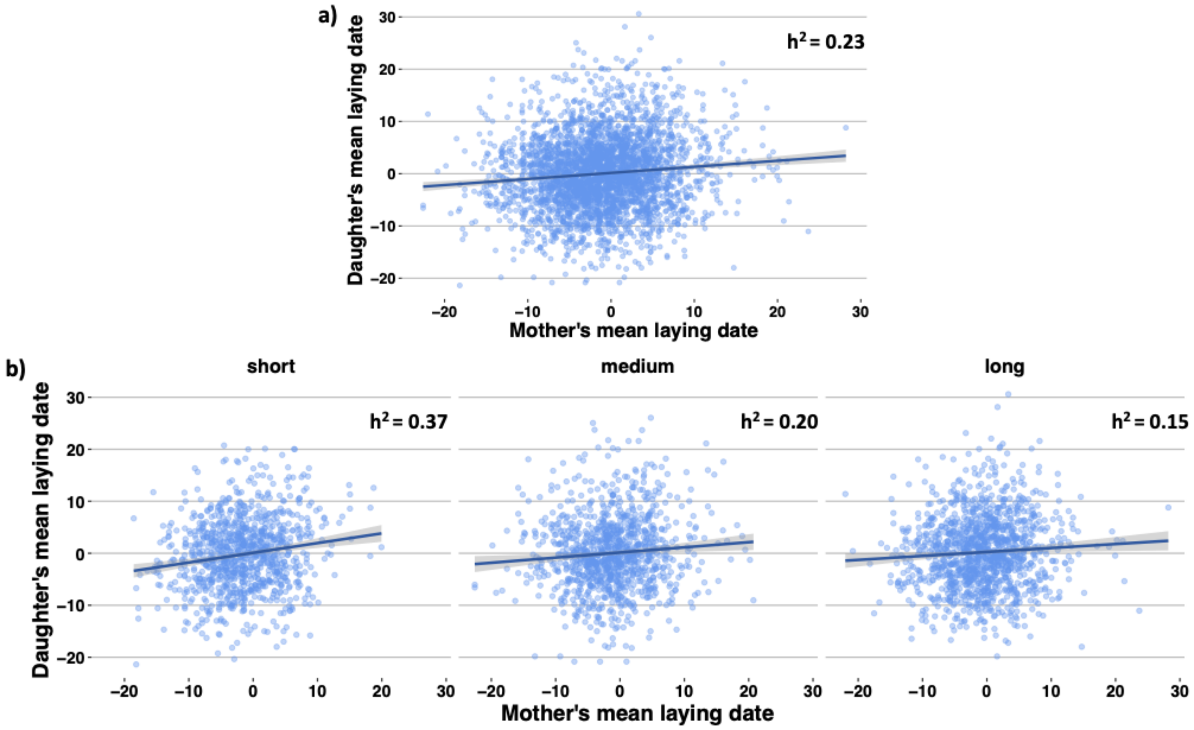
Results are shown in Supplementary Table 2, alongside the estimates of heritability for laying date from (Van Der Jeugd & McCleery, 2002b).

Supplementary Table 2 – Regression model output – (1) is results from (Van Der Jeugd & McCleery, 2002b) and (2) are from this study. Hatching date vs laying date. h^2 is the within-year heritability, as the ratio of V_A to $V_{P\text{-within years}}$, SE is the standard error of heritability. N is the number of pairings of mothers and daughters used in each analysis.

	short			***medium***			***long***			***overall***		
	h^2	*SE*	*N*	h^2	*SE*	*N*	h^2	*SE*	*N*	h^2	*SE*	*N*
Laying date(1)	0.40	0.10	399	0.25	0.09	458	0.07	0.10	476	0.24	0.06	1332
Laying date(2)	0.37	0.07	986	0.20	0.07	1095	0.15	0.06	1290	0.23	0.04	3371
Hatching date(2)	0.35	0.07	946	0.18	0.07	1032	0.16	0.04	1209	0.24	0.04	3187

Laying date

The regressions using all data gave a heritability estimate of 23 ± 4% (Supplementary Figure 2a). When data was split by dispersal distance groups, there was a 2.5-fold difference in heritability estimates between short and long dispersers (Supplementary Figure 2b). The analysis of short dispersers gives a heritability estimate of 37 ± 7%, whilst the analysis of long dispersers yielded an estimate of 15 ± 6%.



Supplementary Figure 2 – Heritability split by dispersal. Simple linear parent-offspring regressions for laying date. a) regression with all individuals, b) shows regressions of 3 dispersal distance groups, short, medium and long. h^2 is heritability calculated as twice the estimates coefficient, in the case of single-parent offspring regressions.

Hatching date

Heritability estimates for hatching date were strikingly similar to those for laying date. The overall parent-offspring regression analysis yield an estimated heritability of hatching date as 24 ± 4%. When the data was split up the short disperser's heritability was estimated to be 2.2 times that of the long dispersers' heritability (35 ± 7% compared to 16 ± 4%).

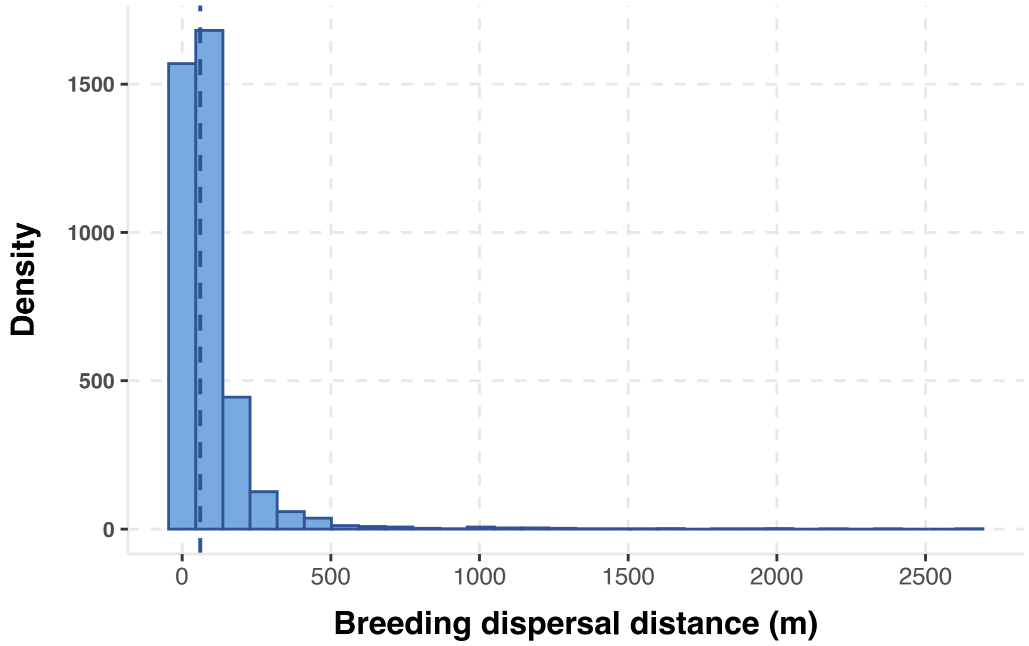
Summary

It is striking that the heritability estimates calculated using parent-offspring regressions with the updated data are very similar results to those found in earlier estimates by Van der Jeugd and McCleery (2002), despite being estimated with more than twice the quantity of data. Heritability estimates declined with increasing dispersal distance of daughters, clearly demonstrating the effect of a common environment on similarity in timing of breeding, with offspring that nest closer to where their parents did also breeding at a more similar time. However, we know parent-offspring regressions do not utilise the full extent of data we have available and often overestimate heritability. In our analysis, heritability estimated using the animal model gave lower estimates in all models compared to the overall parent-offspring regressions, agreeing with previous work (Evans et al., 2020; Kruuk & Hadfield, 2007; Merilä & Sheldon, 2000; Postma & Charmantier, 2007; Sheldon et al., 2003; van Noordwijk, 1984).

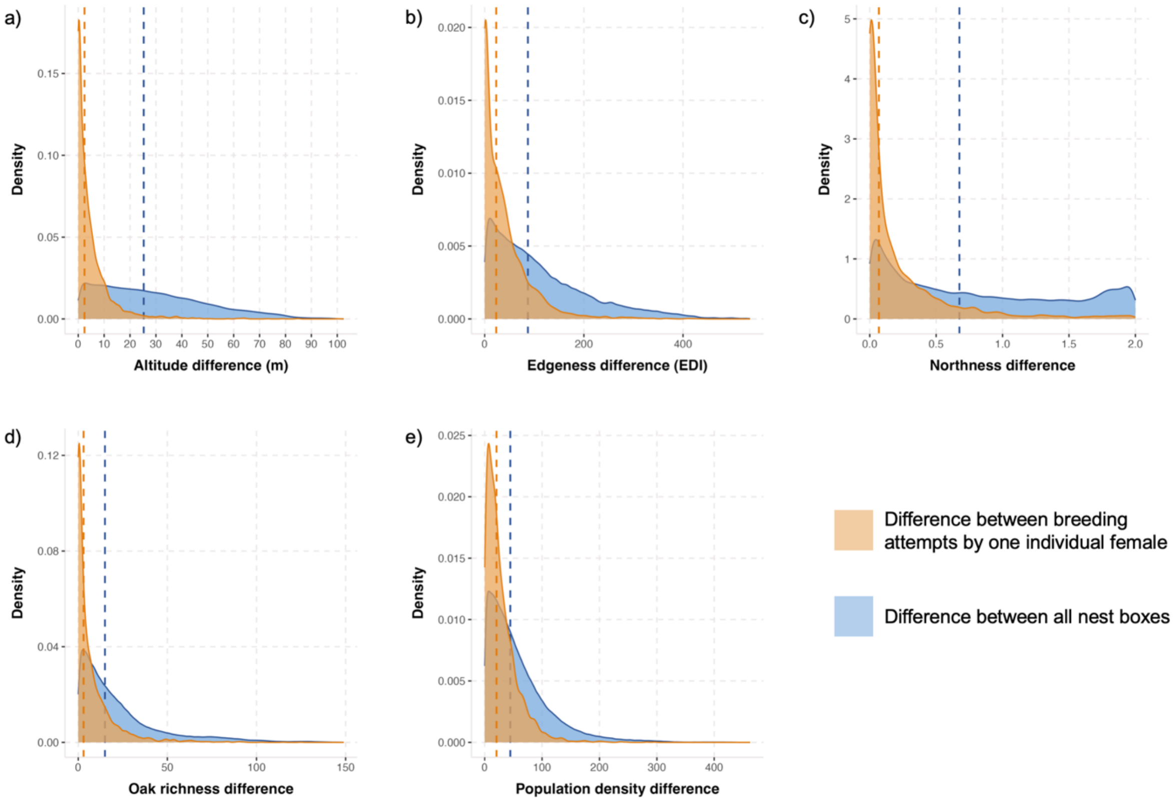
Section 2 - Methods and Results

Supplementary Table 3 – Chick hatch weights - When unsure of hatch day, chicks can be weighed to estimate day of hatching. Newly hatched chicks are clearly identifiable by eye, but chicks slightly older are more difficult to judge. Weighing 2 or 3 of the largest chicks and taking an average weight can help estimate the day of hatching using the table below.

Day	**Great tit**
1 (hatch day)	0-2g
2	2-3
3	3-4.3
4	4.3-6.0
5	6.0-7.7
6	7.7-9.4
7	9.4-11.2
8	11.2-13.0
9	13.0-14.6
10	14.6+



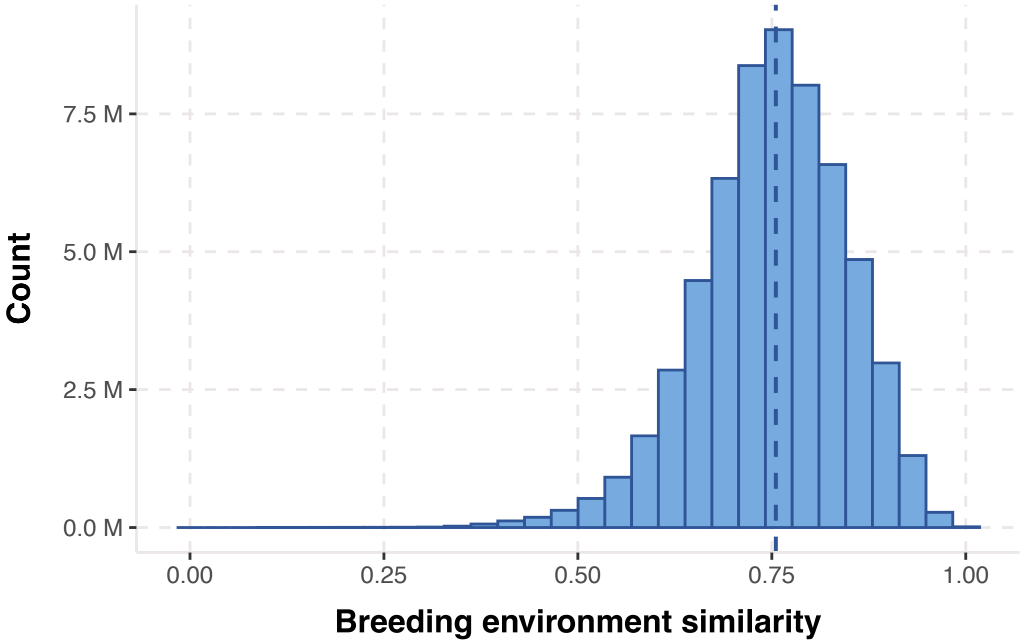
Supplementary Figure 3 – Breeding dispersal. Histogram of the distances moved in metres between nest boxes by females who were recorded breeding in multiple years (n = 2589 females, 954 females were recorded breeding in more than 2 years (max 8 years), and 958 (14.6%) breeding dispersal movements were 0m i.e. a female re-nesting in the same box in consecutive years). Breeding dispersal has a median of 60.75m, considerably less than natal dispersal which has a median of 786m.



Supplementary Figure 4 – Environmental differences between boxes used by one female. Smoothed histograms using kernel density estimates showing the distribution of differences between nest boxes in the measured environmental factors (a) altitude, b) edge distance index, c) northness, d) oak richness within 75m and e) population density. In blue is the difference between all possible combinations of the 1019 nest boxes throughout the woodland (n = 1,023,132), in orange is the differences between nest boxes used by a female who is recorded breeding in multiple years (n = 6568), and so illustrate the distribution of differences in the environmental factors due to breeding dispersal. The vertical dashed lines indicate the median.

Construction of the environmental similarity matrix

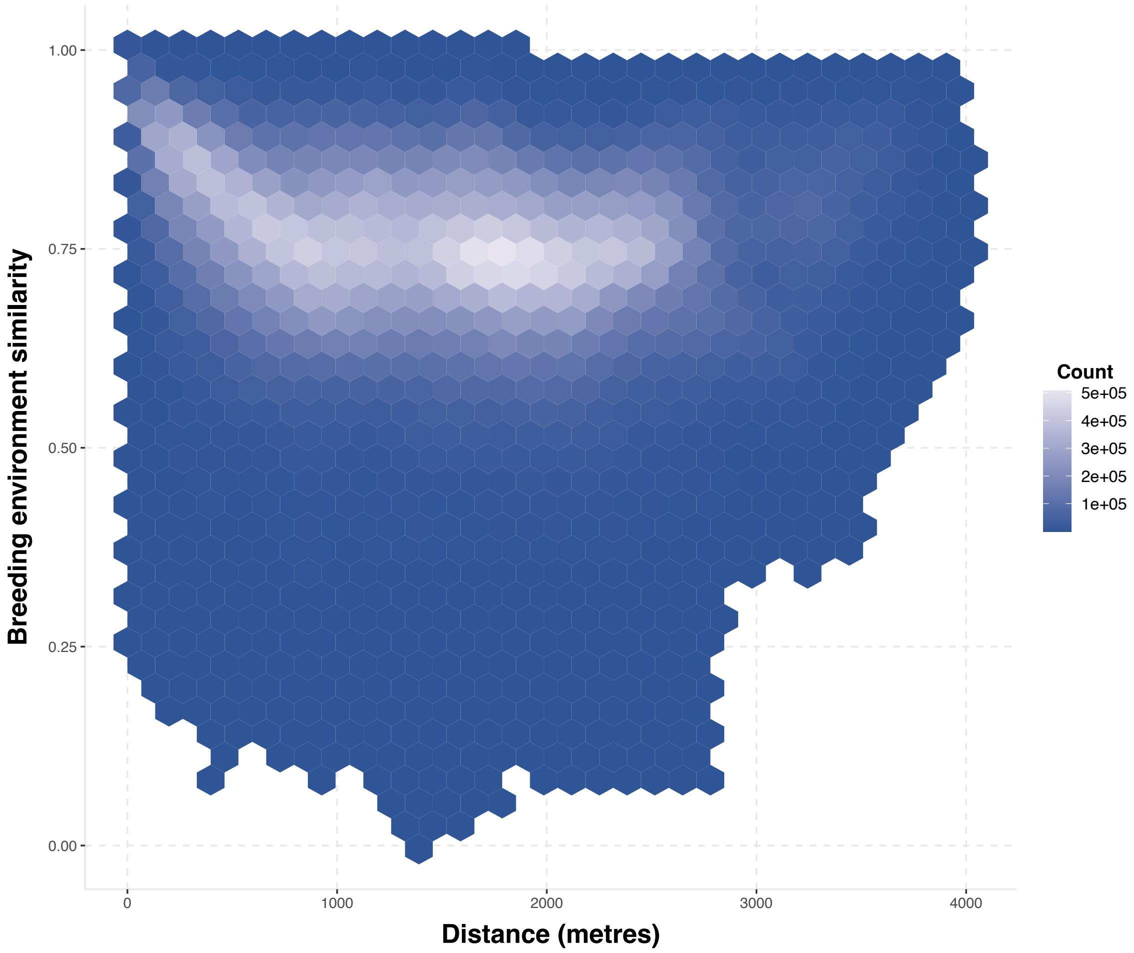
In order to construct the environmental similarity matrix, we included the following factors: altitude, edge distance index, northness, oak-richness within 75m, and population density (expressed as the square root of territory size). A value for each factor is assigned to every nest box throughout the woods: altitude, edge distance index and northness are point estimates from the nestbox location. The woodland is surrounded by farmland, and so the measure of edge distance index is calculated by multiplying a nest boxes edge distance (>0) by the proportion of woodland habitat within its 1.75-ha buffer. Thus, nest boxes farther than 75 m from the woodland edge were assigned an EDI value equal to their edge distance, whereas nest boxes within 75 m of the wood land edge were assigned an EDI value in proportion to the incidence of woodland within their 1.75-ha buffers (Wilkin, Garant, et al., 2007). The woodland is surrounded by farmland, and so the measure of edge distance index is calculated by multiplying a nest boxes edge distance (>0) by the proportion of woodland habitat within its 1.75-ha buffer. Thus, nest boxes farther than 75 m from the woodland edge were assigned an EDI value equal to their edge distance, whereas nest boxes within 75 m of the wood land edge were assigned an EDI value in proportion to the incidence of woodland within their 1.75-ha buffers (Wilkin, Garant, et al., 2007). Oak-richness within 75m is the number of oak trees within a 75m radius of each nestbox, and population density is estimated using Thiessen polygons (Wilkin, Perrins, et al., 2007), to give the territory size for each breeding attempt in each box (so it will vary between years depending on breeding population density), the square root is taken.



Supplementary Figure 5 – Breeding environment similarity measure histogram. Pairwise environmental similarity measure calculated between every pair of birds across all years, using the Euclidean distance of 5 measures of the birds breeding environment (detailed in methods). n = 58,974,720. Median breeding environmental similarity is 0.76.

Supplementary Table 4 – Mantel correlation values. Mantel correlations from comparing the environmental factors used to make up the environmental similarity matrix. As well as mantel correlations between each environmental factor and the environmental similarity matrix and the spatial proximity matrix.

	Breeding env. matrix	*Spatial matrix*	*Population density*	*Oak richness*	*Northness*	*Edge distance index*
Altitude	0.357	0.113	0.066	-0.011	-0.007	-0.004
Edge distance index	0.406	0.043	0.102	0.017	0.001	
Northness	0.429	0.166	0.009	0.118		
Oak richness	0.518	0.102	-0.001			
Population density	0.501	0.005				
Spatial matrix	**0.192**					



Supplementary Figure 6 – Breeding environment similarity vs spatial matrix correlation. Coefficients Relationship between raw distance and breeding environment similarity between all pairwise comparisons of birds (n = 58,974,720). The breeding environment similarity values are calculated by taking a combination of 5 factors of the environment we know to have a relationship with breeding timing, and using Euclidean distance measure in multivariate space between all individuals with every other individual to give one value of similarity for all pairwise comparisons. The final similarity values were again scaled to give a value of 1 along the diagonal, with 0 as the distance between birds in the most dissimilar environments. Mantel tests show a correlation of 0.1923 between the matrix of spatial distance and the matrix of breeding environment similarity.

Supplementary Table 5 - Fixed effects Coefficients and standard errors of fixed effects for four models for both traits. Models all include breeding year, additive genetic, permanent environment effects. Nestbox model includes nestbox ID random effect. Spatial models include matrix of spatial proximity random effect and environmental model includes breeding environment similarity matrix random effect.

Model	*Trait*	*Fixed effect*	*Level*	*Coefficient*	*Standard Error*
Minimal model	Laying Date	Female age	Adult	0.000	NA
			Juvenile	2.386	0.100
	Hatching Date	Female age	Adult	0.000	NA
			Juvenile	1.540	0.023
Nestbox model	Laying Date	Female age	Adult	0.000	NA
			Juvenile	2.387	0.099
	Hatching Date	Female age	Adult	0.000	NA
			Juvenile	1.536	0.023
Spatial model	Laying Date	Female age	Adult	0.000	NA
			Juvenile	2.368	0.097
	Hatching Date	Female age	Adult	0.000	
			Juvenile	1.510	0.023
Breed. env. model	Laying Date	Female age	Adult	0.000	NA
			Juvenile	2.360	0.098
	Hatching Date	Female age	Adult	0.000	NA
			Juvenile	1.513	0.023

References

Boag, P. T., & van Noordwijk, A. J. (1987). Quantitative Genetics. In *Avian Genetics*. https://doi.org/10.1016/b978-0-12-187571-8.50009-5

Evans, S. R., Postma, E., & Sheldon, B. C. (2020). It takes two: Heritable male effects on reproductive timing but not clutch size in a wild bird population*. *Evolution*, *74*(10), 2320–2331. https://doi.org/10.1111/evo.13980

Kruuk, L. E. B., & Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives. *Journal of Evolutionary Biology*, *20*(5), 1890–1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Lynch, M., & Walsh, B. (1998). *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Inc.

Merilä, J., & Sheldon, B. C. (2000). Lifetime reproductive success and heritability in nature. *American Naturalist*, *155*(3), 307–310. https://doi.org/10.1086/303330

Postma, E., & Charmantier, A. (2007). What “animal models” can and cannot tell ornithologists about the genetics of wild populations. *Journal of Ornithology*, *148*(SUPLL. 2), 633–642. https://doi.org/10.1007/s10336-007-0191-8

Sheldon, B. C., Kruuk, L. E. B., & Merilä, J. (2003). Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution*, *57*(2), 406–420. https://doi.org/10.1111/j.0014-3820.2003.tb00274.x

Van Der Jeugd, H. P., & McCleery, R. (2002a). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *Journal of Evolutionary Biology*, *15*(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

Van Der Jeugd, H. P., & McCleery, R. (2002b). Effects of spatial autocorrelation, natal philopatry and phenotypic plasticity on the heritability of laying date. *Journal of Evolutionary Biology*, *15*(3), 380–387. https://doi.org/10.1046/j.1420-9101.2002.00411.x

van Noordwijk, A. J. (1984). Problems in the Analysis of Dispersal and a Critique on its ` Heritability ' in the Great Tit. *Journal of Animal Ecology*, *53*(2), 533–544.

Wilkin, T. A., Garant, D., Gosler, A. G., & Sheldon, B. C. (2007). Edge effects in the great tit: Analyses of long-term data with GIS techniques. *Conservation Biology*, *21*(5), 1207–1217. https://doi.org/10.1111/j.1523-1739.2007.00767.x

Wilkin, T. A., Perrins, C. M., & Sheldon, B. C. (2007). The use of GIS in estimating spatial variation in habitat quality: A case study of lay-date in the Great Tit Parus major. *Ibis*, *149*(SUPPL. 2), 110–118. https://doi.org/10.1111/j.1474-919X.2007.00757.x

B

Supporting Information Chapter 3

The influence of age and social interactions on plasticity in breeding phenology in a wild bird population - SUPPORTING INFORMATION

Carys V. Jones*, Joe P. Woodman*, Josh A. Firth & Ben C. Sheldon

Contents

1 Supplementary methods

In addition to calculating average lay date given local phenological variation by taking the median lay date at the box-level, we additionally defined local average breeding timing by taking the median of all year-centred lay dates 1965–2023 associated with all nest-boxes found within 75m of (and including) the focal nest-box. The foraging range of breeding great tits is estimated as 75m (Barnes 1975; Naef-Daenzer 2000; Wilkin et al. 2007). As such, within any year, there are unoccupied boxes in areas of high nest-box density which are largely associated with the same local environment when occupied in the long-term. Calculating average local breeding timing through this method, in addition to the individual box-level, therefore corrects for potential biases that are obtained at the box-level since boxes in areas of higher density are occupied less (Woodman et al. 2024), but retains local environmental differences in tree bud-burst phenology which are positively correlated within distances less than 100m (Hinks et al. 2015; Table S2 for all results; Fig. S5).

As well as modelling absolute lay date and breeding timing mismatch depending on the age type of a focal individual's neighbourhood (all juvenile, all adult, mixed, or no neighbours), we also constructed models to estimate the marginal effects of local age structure on breeding timing defined by the proportion of adult neighbours. We suggest that the methods used in the main text are more biologically meaningful in that it allows us to include focal individuals with no neighbours in the same model (whereas in this case, such individuals are removed, such that they are note treated the same as individuals with only juvenile neighbours, i.e. 0% adult neighbours; Table S3 for results; Fig. S6).

2 Supplementary tables

Table S1 – Model structure for predicting age-specific breeding timing depending on the age structure of a local breeding neighbourhood as used in the main text.

Response variable	**Fixed effect**	**Interaction term**	**Random effects**
(1) Absolute breeding timing	Neighbourhood age type (all juvenile, all adult, mixed, or no neighbours)	Age of focal female (juvenile/adult)	Year, nest-box ID, female ID
(2) Breeding timing compared to average of focal nest-box ('local breeding timing mismatch')	Neighbourhood age type (all juvenile, all adult, mixed, or no neighbours)	Age of focal female (juvenile/adult)	Year, nest-box ID, female ID

Table S2 - Posterior predictions from Bayesian regression models modelling breeding timing (either absolute breeding timing; local breeding timing mismatch at the box-level; or local breeding timing mismatch at the 75m radius level) by neighbourhood age structure (either all juveniles; all adults; mixed age-cohorts; or no neighbours) depending on focal female age (either juvenile or adult). We report the posterior median with 95% credible intervals.

Model	**Focal female age**	**Neighbourhood age structure**	**Posterior median**	**95% credible intervals**
Absolute breeding timing	Adult	All adult	-1.213	[-1.495, -0.926]
		All juvenile	-1.802	[-2.078, -1.526]
		Mixed	-1.951	[-2.283, -1.612]
		No neighbours	-1.353	[-1.578, -1.126]
	Juvenile	All adult	0.929	[0.638, 1.213]
		All juvenile	0.668	[0.402, 0.924]
		Mixed	0.481	[0.160, 0.797]
		No neighbours	0.780	[0.569, 0.986]
Local breeding timing mismatch (box-level)	Adult	All adult	-0.331	[-0.628, -0.004]
		All juvenile	-0.831	[-1.118, -0.536
		Mixed	-0.667	[-1.008, -0.335]
		No neighbours	-0.629	[-0.857, 0.407]
	Juvenile	All adult	1.723	[1.429, 2.019]
		All juvenile	1.450	[1.1183, 1.718]
		Mixed	1.477	[1.146, 1.800]
		No neighbours	1.308	[1.089, 1.520]
Local breeding timing mismatch (75m radius level)	Adult	All adult	-0.283	[-0.576, 0.004]
		All juvenile	-0.890	[-1.171, -0.609]
		Mixed	-0.675	[-1.013, 0.344]
		No neighbours	-0.644	[-0.875, -0.415]
	Juvenile	All adult	1.864	[1.564, 2.170]
		All juvenile	1.508	[1.261, 1.774]
		Mixed	1.593	[1.277, 1.917]
		No neighbours	1.327	[1.110, 1.540]

Table S3 – Marginal effects from Bayesian regression models modelling breeding timing (either absolute breeding timing; local breeding timing mismatch at the box-level; or local breeding timing mismatch at the 75m radius level) by the proportion of adult neighbours depending on focal female age (either juvenile or adult. We report the posterior median with 95% credible intervals.

Model	Focal female age	Marginal effect	95% credible intervals
Absolute breeding timing	Adult	0.464	[0.006, 0.919]
	Juvenile	0.294	[-0.163, 0.757]
Local breeding timing mismatch (box-level)	Adult	0.428	[-0.008, 0.877]
	Juvenile	0.292	[-0.155, 0.741]
Local breeding timing mismatch (box-level)	Adult	0.521	[0.052, 0.980]
	Juvenile	0.380	[-0.080, 0.820]

3 Supplementary figures

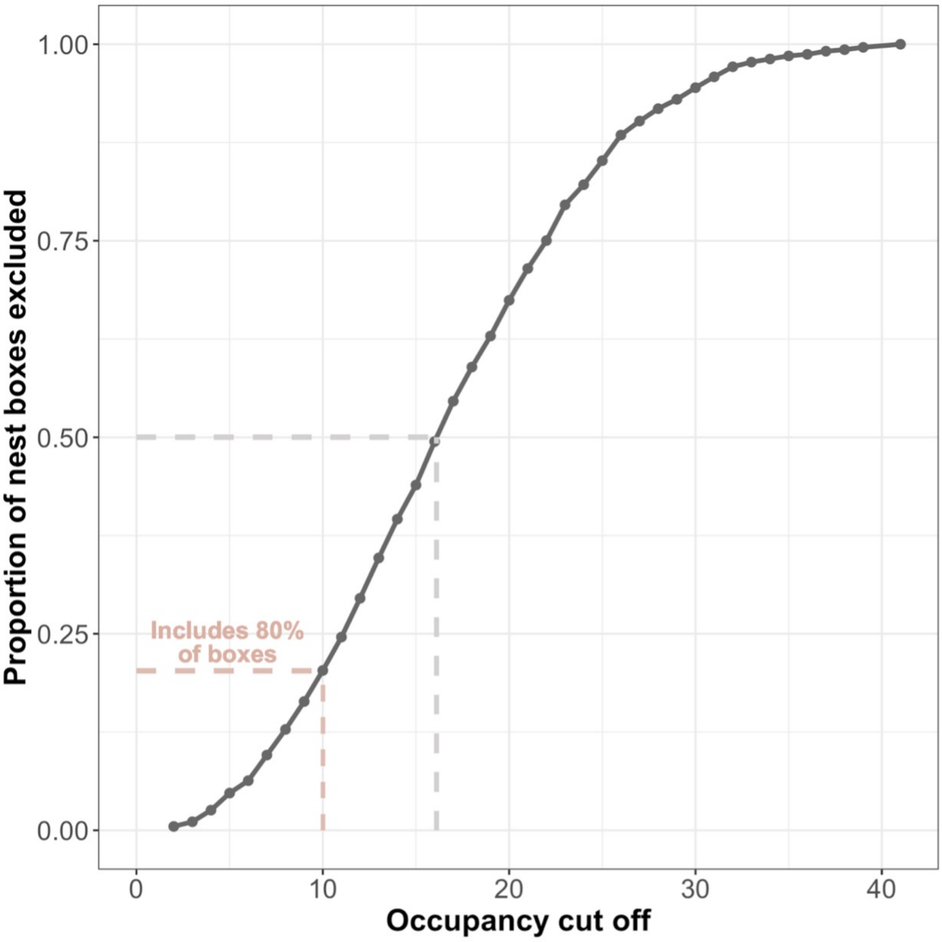


Fig. S1 - The proportion of boxes that would be excluded from our dataset if increasingly stricter occupancy cut off points are used. The grey dashed line indicates an occupancy cut off of 16 times which would exclude 50% of boxes. We decided to use a cut off of 10 times, indicated by the pink line, which leads to the exclusion of 20% of boxes, leaving 80% of the total boxes left to include in the analysis.

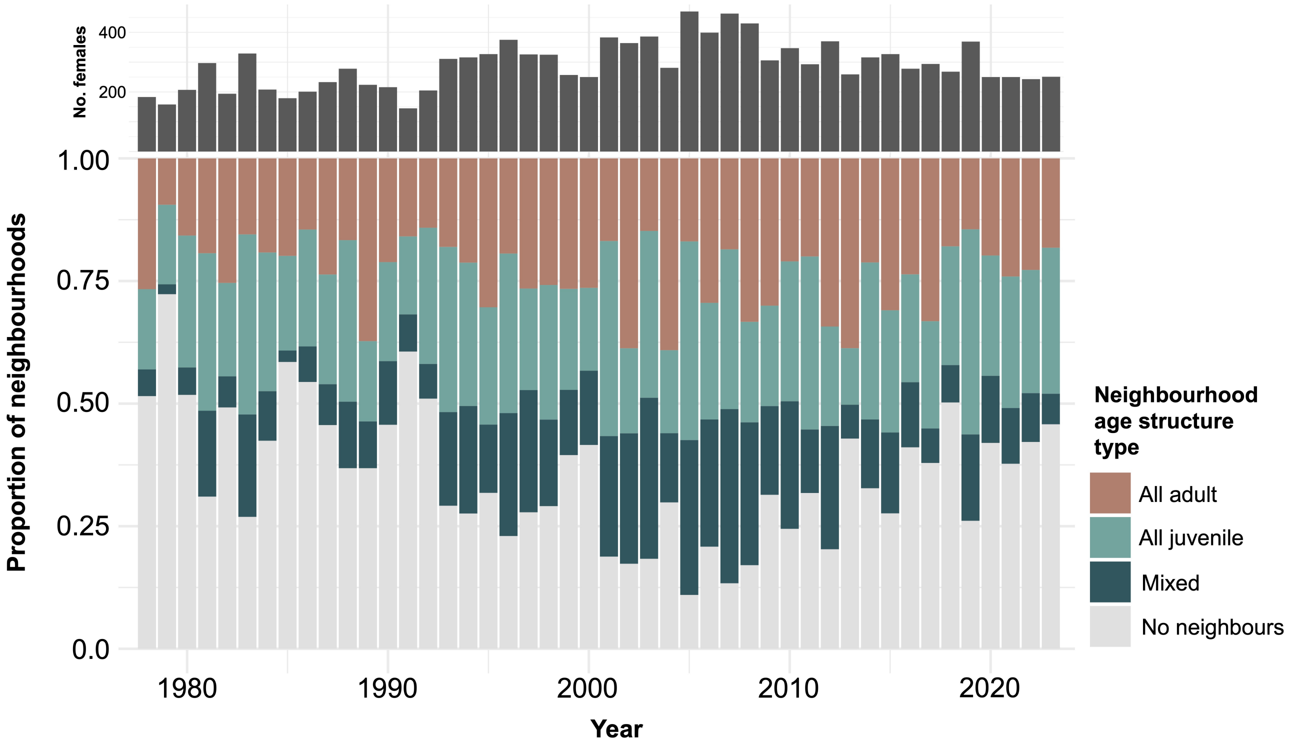


Fig. S2 - The proportion of each annual breeding population consisting of different neighbourhood types and female population size 1978–2023.

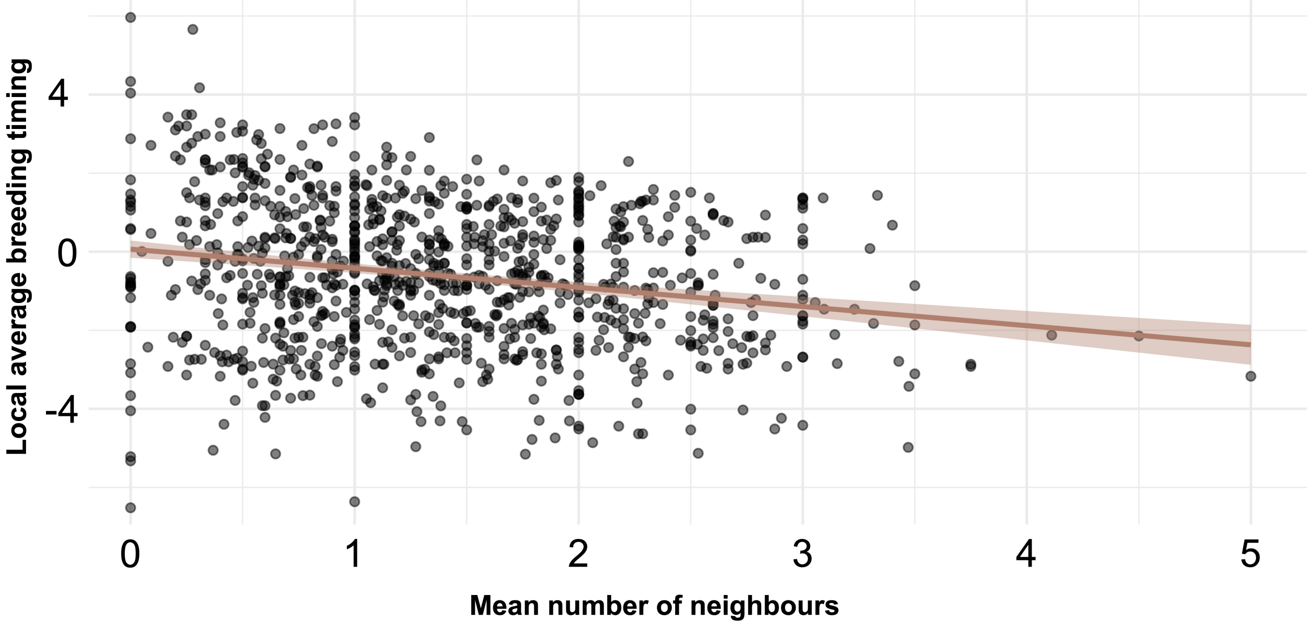


Fig. S3 - Relationship between the mean number of neighbours (individuals found breeding within 75m) and the local average breeding timing for each nest-box. There is a weak negative relationship between these two variables (Spearman's correlation: r = -0.119, p $<$ 0.01).

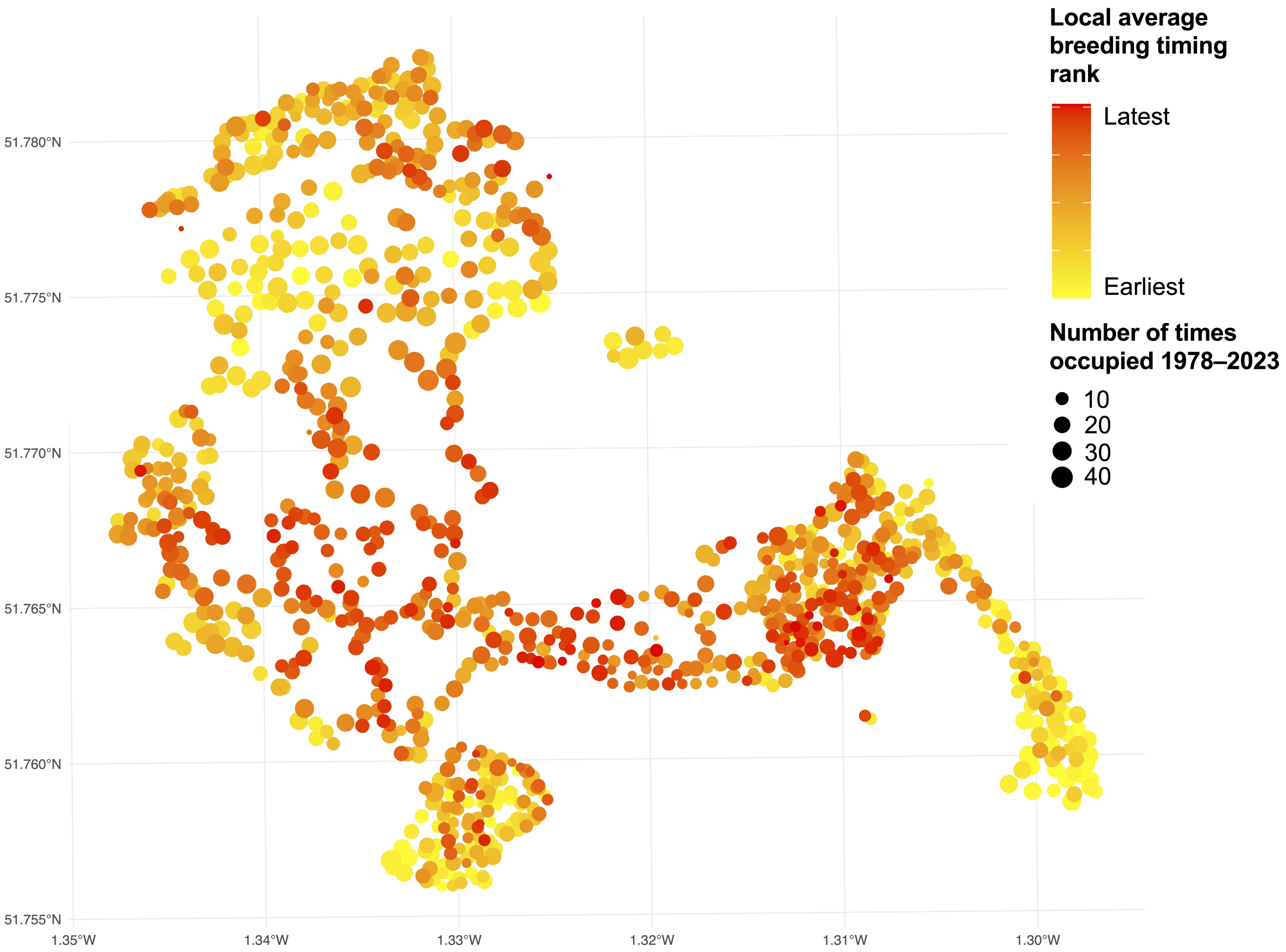


Fig. S4 - Map of nest-boxes across Wytham Woods, with colour on a scale of yellow–red representing the average timing of each nest-box from earliest to latest (i.e. median year-centred lay date of each nest-box), and point size relative to the number of times it has been occupied. As seen, there are regions of the study site where nest-box density relates to the local average timing, due to habitat heterogeneity across the woods. For example, the south-east corner has high box density, but also has early average breeding timing due to lower altitude and being closer to the woodland edge. In contrast, the central south region of the woods has later average timings due to being higher altitude and further from the edge, and this region also has lower than average nest-box density.

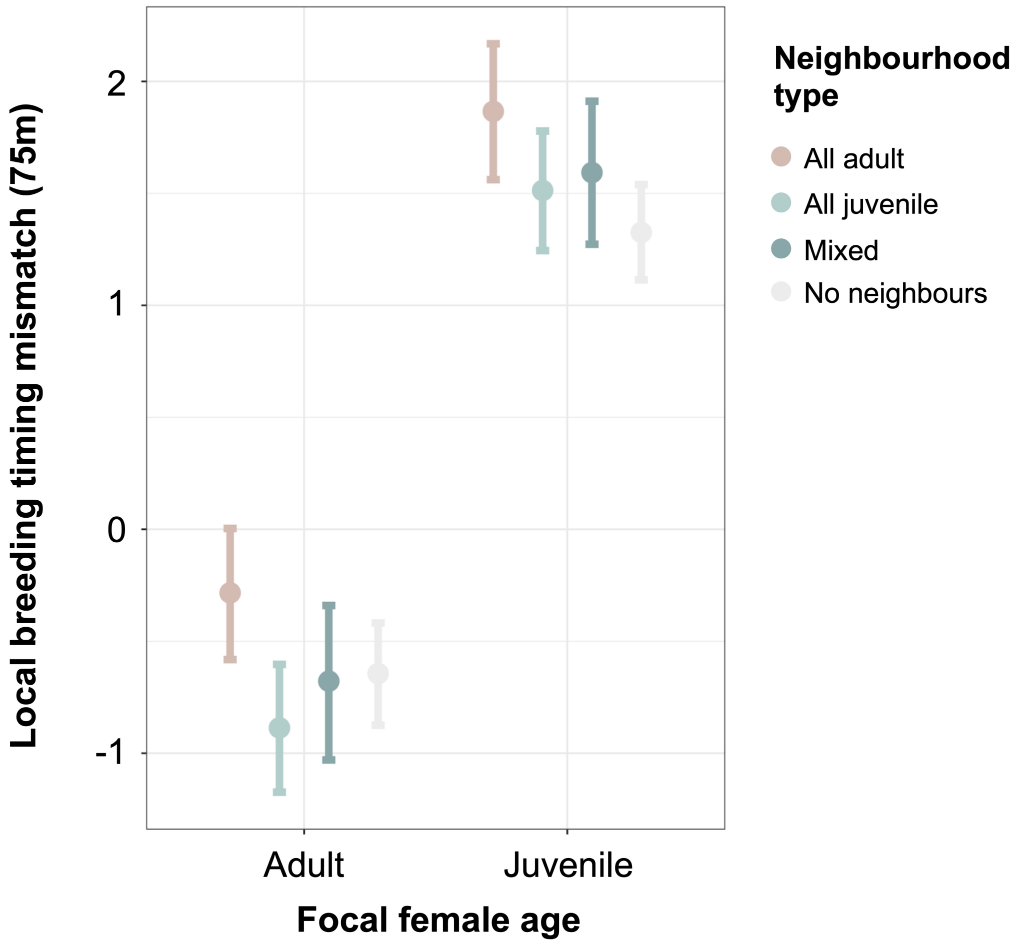


Fig. S5 - Marginal predictions from models using local breeding timing mismatch defined using a 75m radius as opposed to at the box-level. This model shows very similar results to the model that uses box-level mismatch, where adults breed on average 2 days earlier than juveniles. Adults with all adult neighbours slightly later breeding and a reduced mismatch (closer to 0) compared to adults with all juvenile neighbours, with those with a mixed age neighbourhood spanning across these two categories. Juveniles did not show much difference in local breeding timing mismatch depending on the age structure of their neighbourhood.

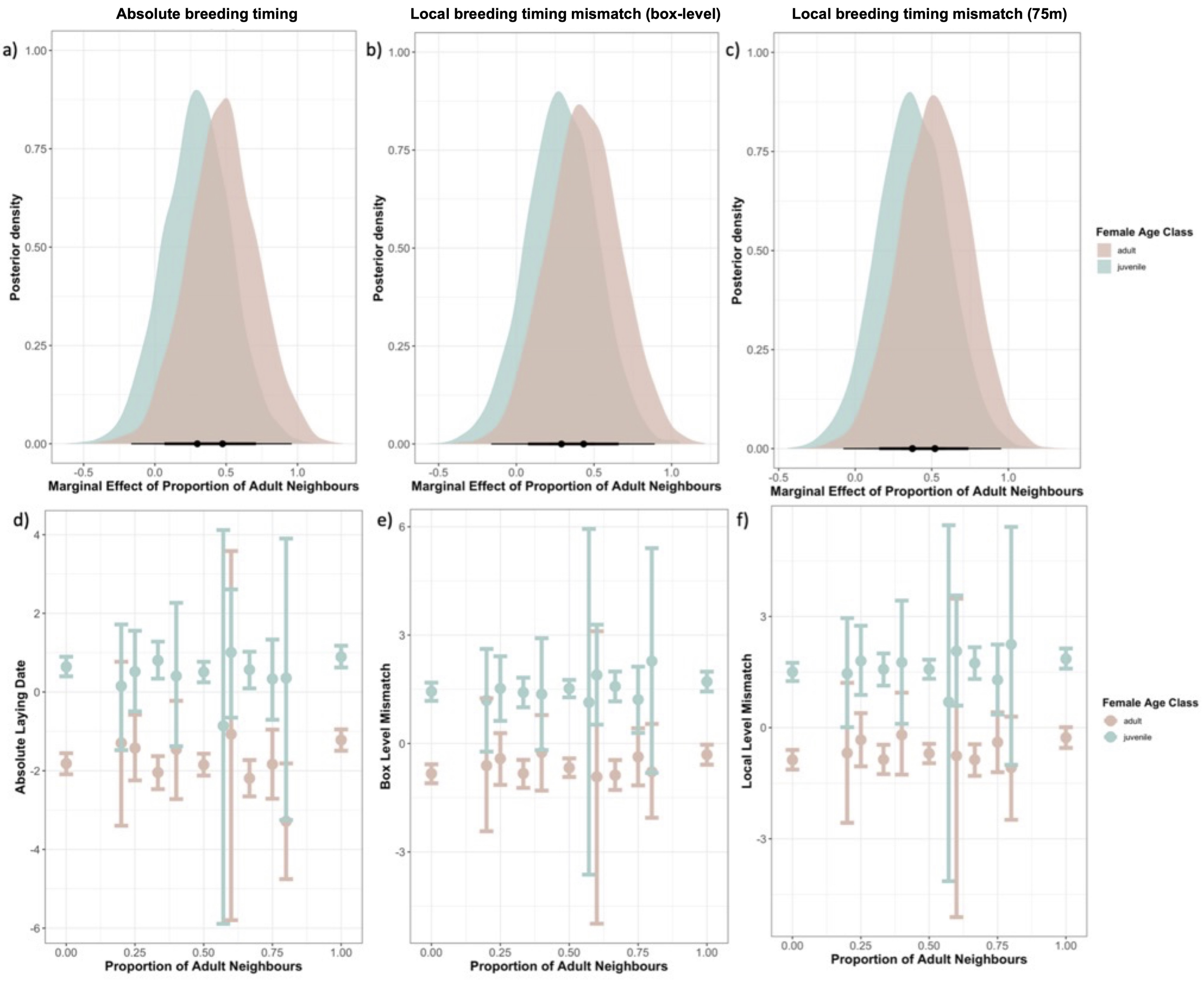


Fig. S6 - The top row of plots shows the marginal effects posterior density of the proportion of adult neighbours on breeding timing as a) absolute breeding timing, b) local breeding timing mismatch calculated at the box-level and c) local breeding timing mismatch calculated at the 75m radius level. The bottom row of plots shows a binned representation of the marginal predictions from the same models as the top row, d) absolute breeding timing, e) local breeding timing mismatch calculated at the box-level and f) local breeding timing mismatch calculated at the 75m radius level.

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4 References

Barnes, J.A.G. (1975). The titmice of the British Isles. David & Charles.

Hinks, A.E., Cole, E.F., Daniels, K.J., Wilkin, T.A., Nakagawa, S. & Sheldon, B.C. (2015). Scale-dependent phenological synchrony between songbirds and their caterpillar food source. American Naturalist, 186, 84–97.

Naef-Daenzer, B. (2000). Patch time allocation and patch sampling by foraging great and blue tits. Anim Behav, 59, 989–999.

Wilkin, T.A., Perrins, C.M. & Sheldon, B.C. (2007). The use of GIS in estimating spatial variation in habitat quality: A case study of lay-date in the Great Tit Parus major. Ibis, 149, 110–118.

Woodman, J.P., Cole, E.F., Firth, J.A. & Sheldon, B.C. (2024). Age-specificity in territory quality and spatial structure in a wild bird population. bioRxiv.

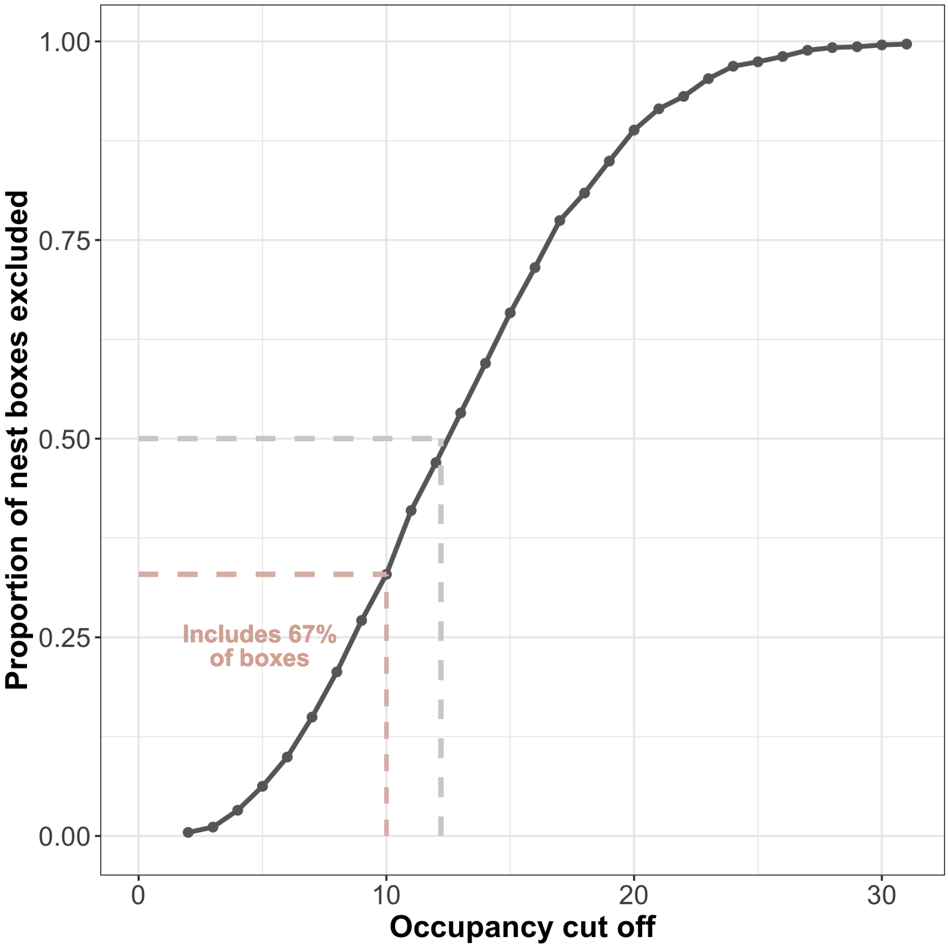
C

Supporting Information Chapter 4

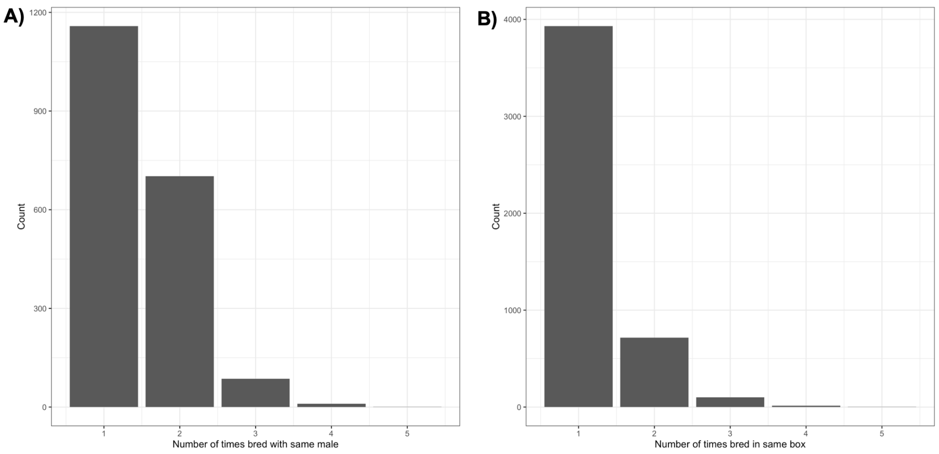
Pair fidelity and site familiarity effects on the timing of breeding in wild great tits -

SUPPORTING INFORMATION

Carys V. Jones*, Charlotte E. Regan, Josh A. Firth & Ben C. Sheldon



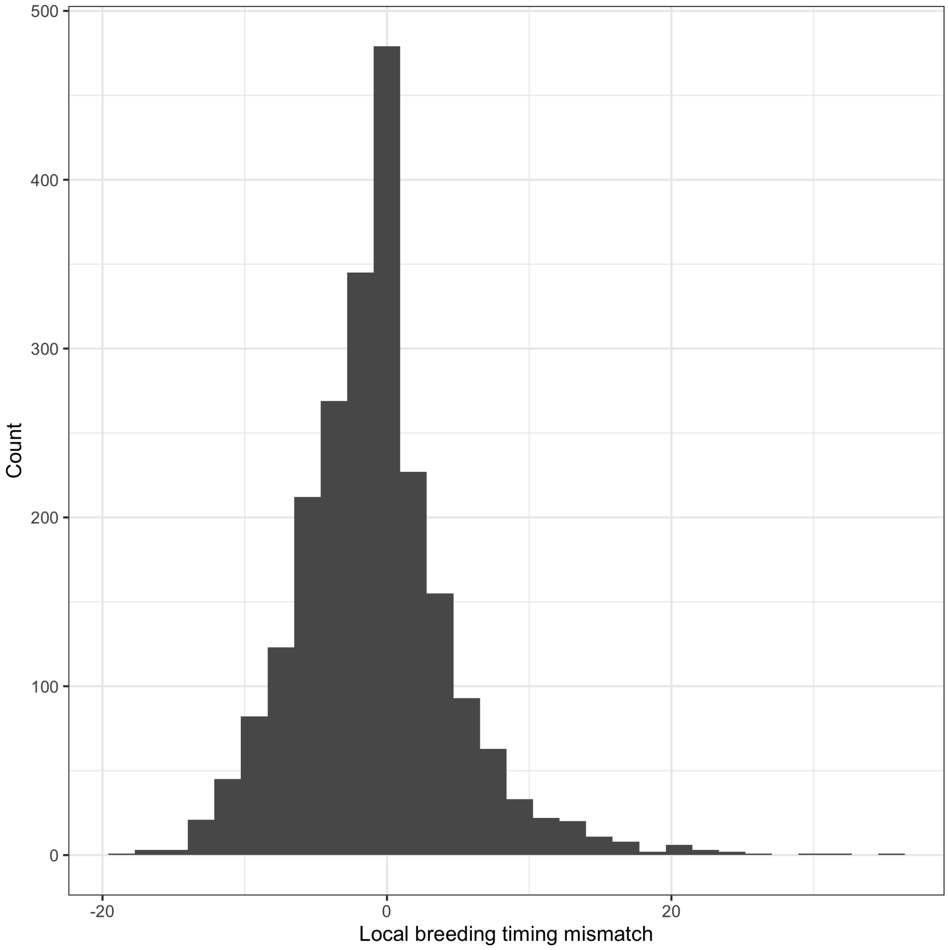
Supplementary Figure 1. The proportion of boxes that would be excluded from our dataset if increasingly stricter occupancy cut off points are used. The grey dashed line indicates an occupancy cut off of 16 times which would exclude 50% of boxes. We decided to use a cut off of 10 times, indicated by the pink line, which leads to the exclusion of 20% of boxes, leaving 80% of the total boxes left to include in the analysis.



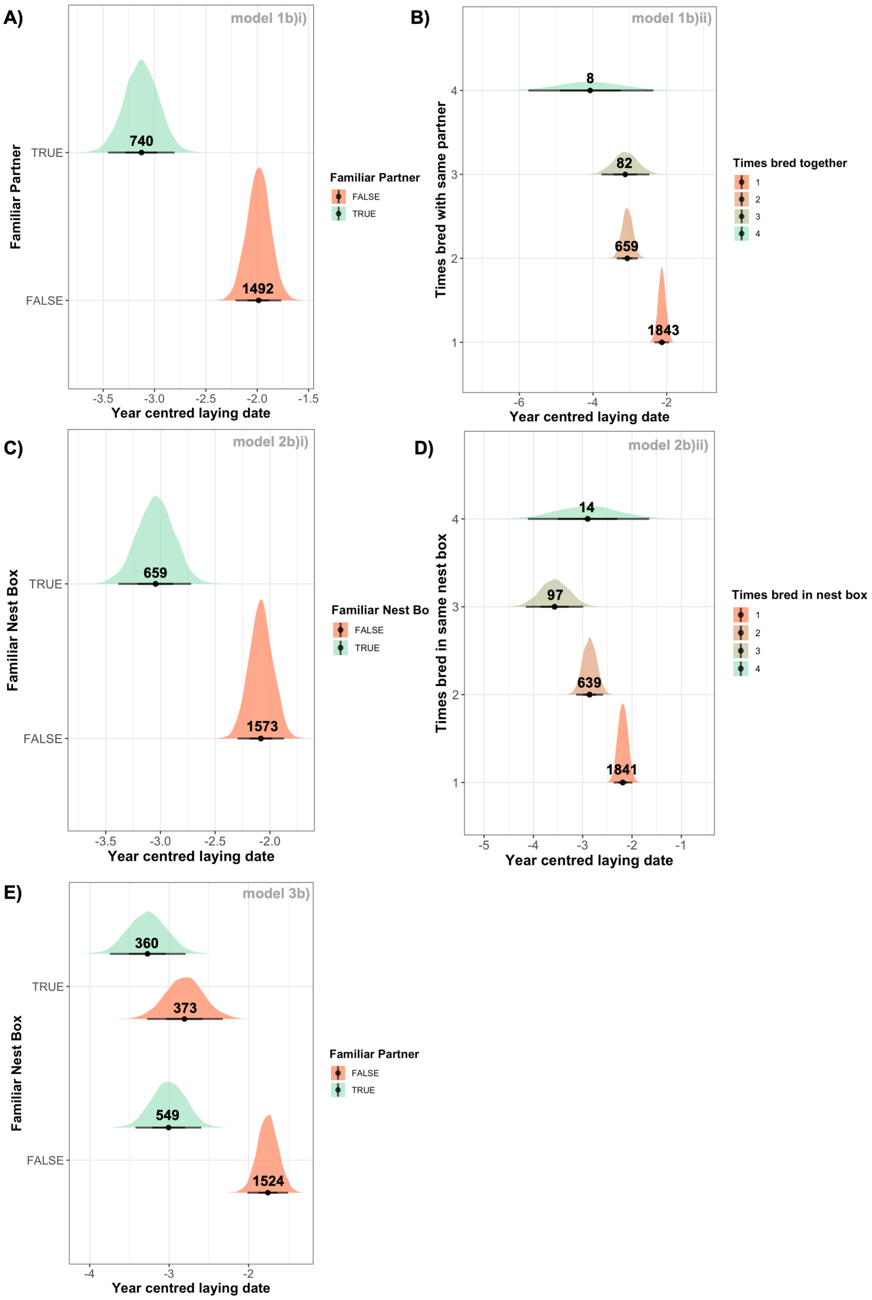
Supplementary Figure 2. For each of the unique 1,957 females in this subset A) a count of number of times they bred with the same male. B) a count of number of times they bred in the same nest box

Supplementary Table 1. Model structure for predicting breeding timing (as local breeding timing mismatch and year-centred laying date) depending on an individual females familiarity with partner and nest box.

Model name	**Response**	**Fixed effects**	**Random effects**
1a)i)	Local breeding timing mismatch	Familiarity with male (binary) Age at breeding	Mother ID Nest box ID Year
1b)i)	Year-centred laying date	Familiarity with male (binary) Age at breeding	Mother ID Nest box ID Year
1a)ii)	Local breeding timing mismatch	Familiarity with male (continuous) Age at breeding	Mother ID Nest box ID Year
1b)ii)	Year-centred laying date	Familiarity with male (continuous) Age at breeding	Mother ID Nest box ID Year
2a)i)	Local breeding timing mismatch	Familiarity with nest box (binary) Age at breeding	Mother ID Nest box ID Year
2b)i)	Year-centred laying date	Familiarity with nest box (binary) Age at breeding	Mother ID Nest box ID Year
2a)ii)	Local breeding timing mismatch	Familiarity with nest box (continuous) Age at breeding	Mother ID Nest box ID Year
2b)ii)	Year-centred laying date	Familiarity with nest box (continuous) Age at breeding	Mother ID Nest box ID Year
3a)i)	Local breeding timing mismatch	Familiarity with nest box (binary) Familiarity with male (binary) Age at breeding	Mother ID Nest box ID Year
3b)i)	Year-centred laying date	Familiarity with nest box (binary) Familiarity with male (binary) Age at breeding	Mother ID Nest box ID Year



Supplementary Figure 3. Distribution of local breeding timing mismatch over 2,232 breeding attempts. The range is -18.27 days to 35.87 days, with a median of -0.88 days.



Supplementary Figure 4. Marginal posterior predictions of year-centred laying date for each of the models run (models labelled in top right corner of each plot correspond to model structures in Supplementary Table 1. Response variables for each model: **A)** binary partner familiarity **B)** partner familiarity count (with 5 times removed, as there is only 1 instance) **C)** binary nest box familiarity **D)** nest box familiarity count (with 5 times removed as there is only 2 instances) **E)** binary partner familiarity and interaction with nest box familiarity.

Supplementary Table 2. Posterior predictions from Bayesian regression models modelling breeding timing (either local breeding mismatch or year-centred-laying dates) depending on familiarity with partner and/or nest box (either binary TRUE or FALSE or a count of times together). We report the posterior median with 95% credible intervals. Model structures can be found in Supplementary Table 1.

Model name	Familiar partner	Familiar nest box	Estimate	95% CI
1a)i)	FALSE		-0.58	[-0.82, -0.33]
1a)i)	TRUE		-1.36	[-1.73, -0.99]
1b)i)	FALSE		-2.12	[-2.55, -1.72]
1b)i)	TRUE		-2.98	[-3.50, -2.48]
2a)i)		FALSE	-0.64	[-0.86, -0.42]
2a)i)		TRUE	-1.31	[-1.66, -0.98]
2b)i)		FALSE	-2.08	[-2.29, -1.87]
2b)i)		TRUE	-3.04	[-3.39, -2.72]
3a)i)	FALSE	FALSE	-0.35	[-0.61, -0.09]
3a)i)	TRUE	FALSE	-1.46	[-1.93, -1.02]
3a)i)	FALSE	TRUE	-1.14	[-1.64, -0.64]
3a)i)	TRUE	TRUE	-1.48	[-1.96, -1.00]
3b)i)	FALSE	FALSE	-1.76	[-2.01, -1.50]
3b)i)	TRUE	FALSE	-3.01	[-3.42, -2.60]
3b)i)	FALSE	TRUE	-2.81	[-3.28, -2.32]
3b)i)	TRUE	TRUE	-3.27	[-3.74, -2.79]

Model name	Breeding attempts with partner	Breeding attempts with nest box	Estimate	95% CI
1a)ii)	1		-0.68	[-0.88, -0.47]
1a)ii)	2		-1.40	[-1.69, -1.11]
1a)ii)	3		-1.51	[-2.15, -0.87]
1a)ii)	4		-1.81	[-3.40, -0.25]
1a)ii)	5		-1.82	[-5.50, 1.94]
1b)ii)	1		-2.13	[-2.33, -1.93]
1b)ii)	2		-3.07	[-3.35, -2.78]
1b)ii)	3		-3.13	[-3.77, -2.47]
1b)ii)	4		-4.08	[-5.76, -2.36]
1b)ii)	5		-5.80	[-9.82, -1.98]
2a)ii)		1	-0.74	[-0.94, -0.54]
2a)ii)		2	-1.22	[-1.50, -0.94]
2a)ii)		3	-1.56	[-2.16, -0.95]
2a)ii)		4	-1.25	[-2.49, 0.01]
2a)ii)		5	-1.07	[-3.67, 1.56]
2b)ii)		1	-2.19	[-2.37, -1.99]
2b)ii)		2	-2.86	[-3.13, -2.59]
2b)ii)		3	-3.57	[-4.15, -2.99]
2b)ii)		4	-2.90	[-4.11, -1.65]
2b)ii)		5	-2.32	[-5.03, 0.36]

Supplementary Table 3. Marginal effects of exact age at breeding of females from Bayesian regression models modelling breeding timing (either local breeding mismatch or year-centred laying date) by the familiarity with partner and/or nest box (either binary TRUE or FALSE or a count of times together). We report the posterior median with 95% credible intervals. Model structures can be found in Supplementary Table 1. median with 95

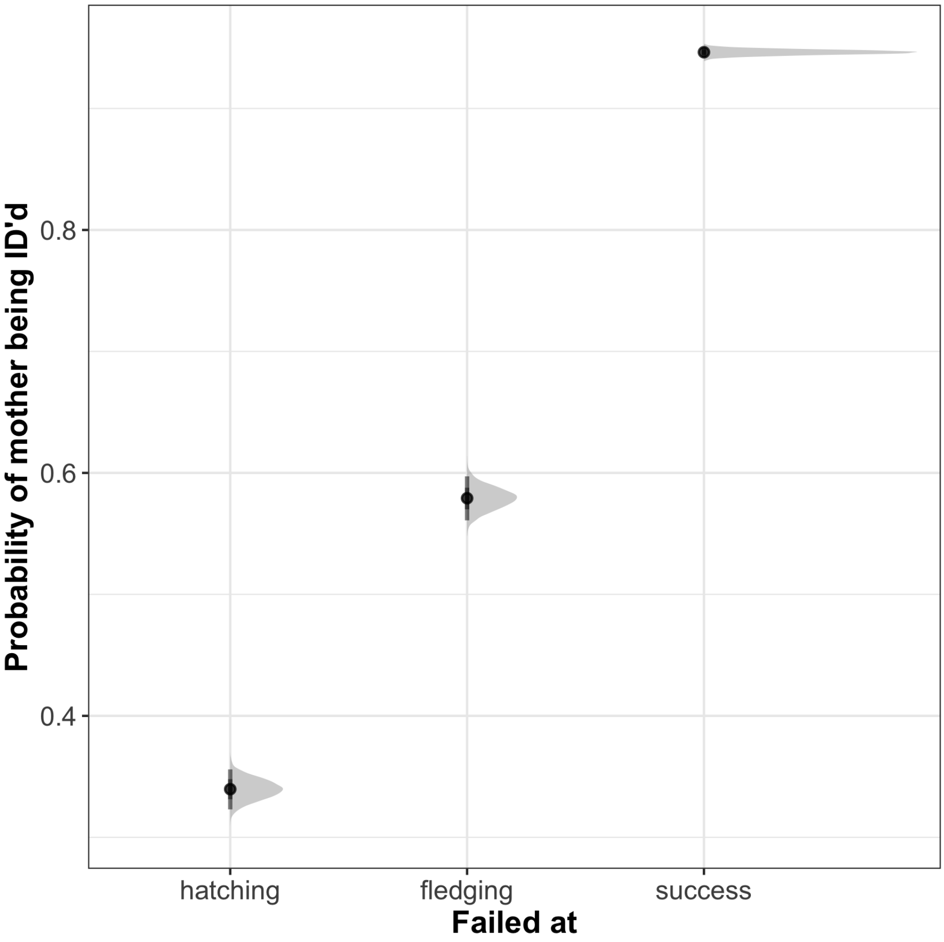
Model name	**Marginal effect**	**95% CI**
1a)i)	0.230 days per year	[0.016, 0.449]
1b)i)	0.193 days per year	[-0.032, 0.419]
1a)ii)	0.297 days per year	[0.097, 0.493]
1b)ii)	0.268 days per year	[0.064, 0.478]
2a)i)	0.237 days per year	[0.022, 0.458]
2b)i)	0.212 days per year	[-0.006, 0.435]
2a)ii)	0.319 days per year	[0.118, 0.521]
2b)ii)	0.310 days per year	[0.094, 0.530]
3a)i)	0.226 days per year	[0.004, 0.435]
3b)i)	0.195 days per year	[-0.031, 0.413]

D

Supporting Information Chapter 5

Predictors of second breeding attempts in a predominantly single brooded bird population - SUPPORTING INFORMATION

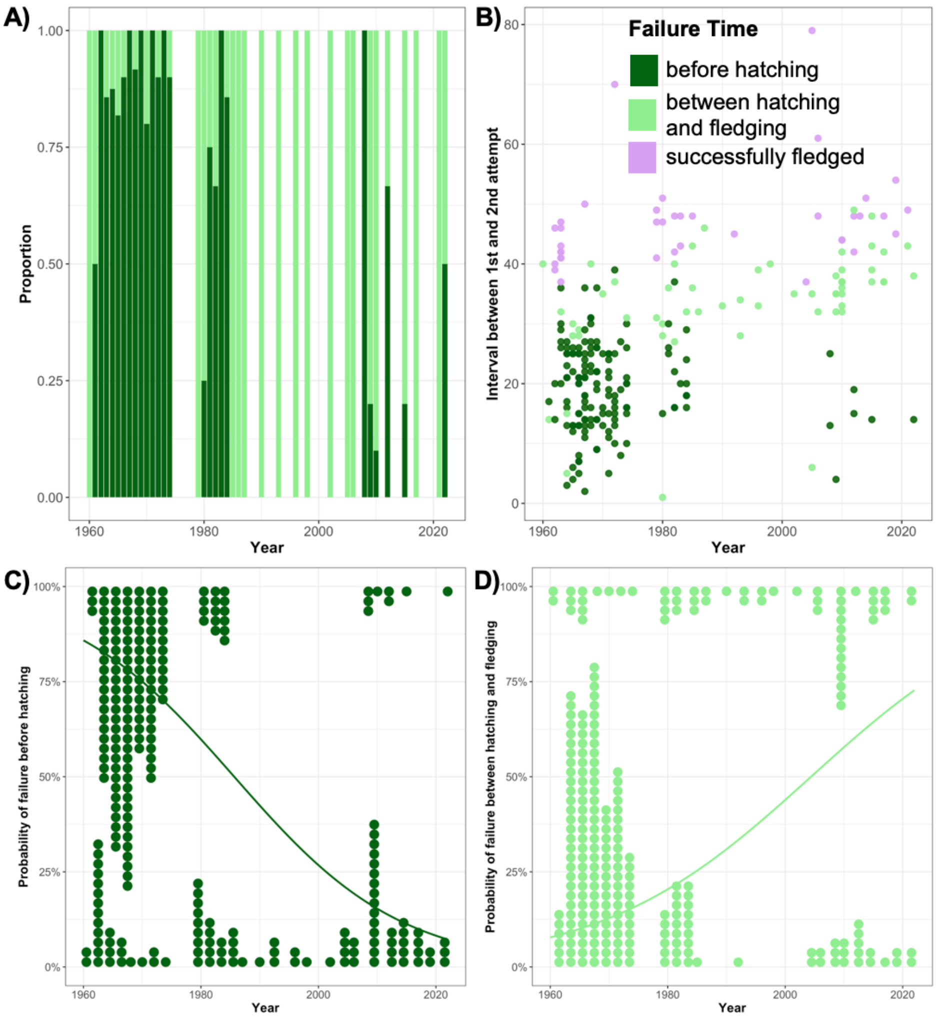
Carys V. Jones*, Charlotte E. Regan, Josh A. Firth & Ben C. Sheldon



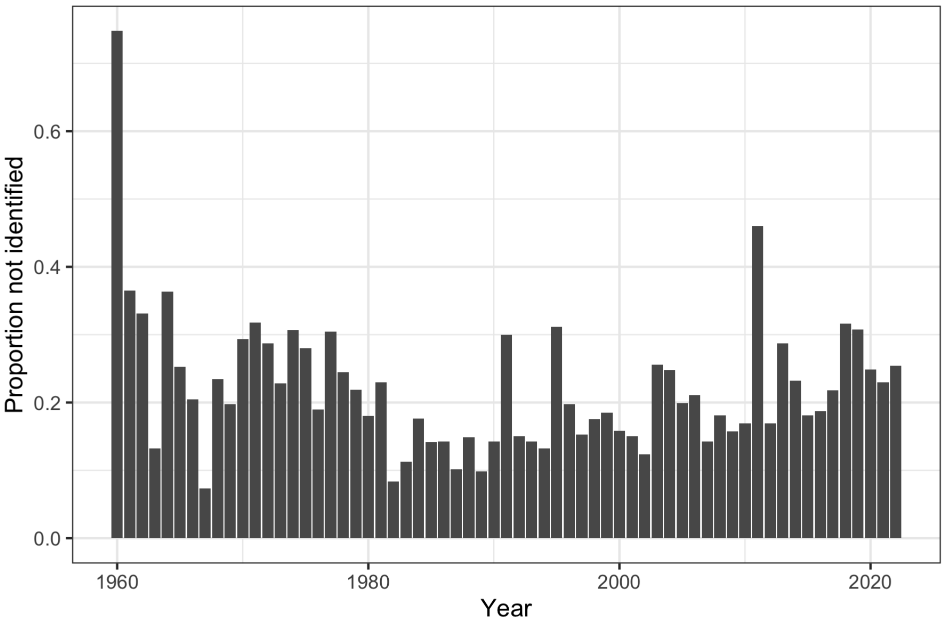
Supplementary Figure 1. Probability of breeding female being identified depending on the outcome of the breeding attempt. Broods that fail earlier on are less likely to have parents identified. Tested using Bayesian gaussian mixed effects model, with random effect of year. Plot shows marginal predictions for proportion of females identified depending on what the outcome of her nest was, 'hatching' = failure before hatching, 'fledging' = failure between hatching a fledging, and 'success' = successfully raised brood to fledging. Probability of being identified increased between mothers failing before hatching to those failing between hatching and fledging. And then even more so for those that successfully fledge a brood.

Supplementary Table 1. Model structures for all models specified in main text. Breeding age group = juvenile (1 year old) or adult (older than 1 year old). Age continuous = individuals exact age at breeding. Failure time = before hatching or between hatching and fledging.

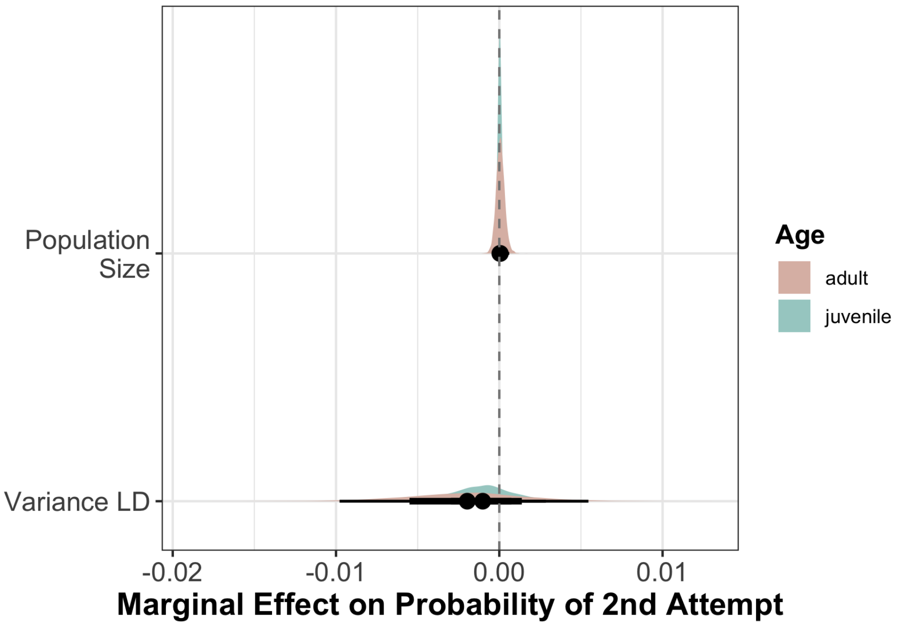
Model name	Response	Fixed effects	Random effects
1	April lay date	Breeding attempt number Year Breeding age group	Mother ID Nest box ID
2	First lay date scaled within years	Has second attempt (0 or 1) Breeding age group (interaction term)	Mother ID Nest box ID Year
3a)	Had a second attempt (0 or 1)	Breeding age group First lay date scaled within years Failure time	Mother ID Nest box ID Year
3b)	Had a second attempt (0 or 1)	Continuous age First lay date scaled within years Failure time	Mother ID Nest box ID Year
4	Had a second attempt (0 or 1)	Median lay date of year Variance in lay date within year Population size Age structure of neighbourhood	Mother ID Nest box ID Year



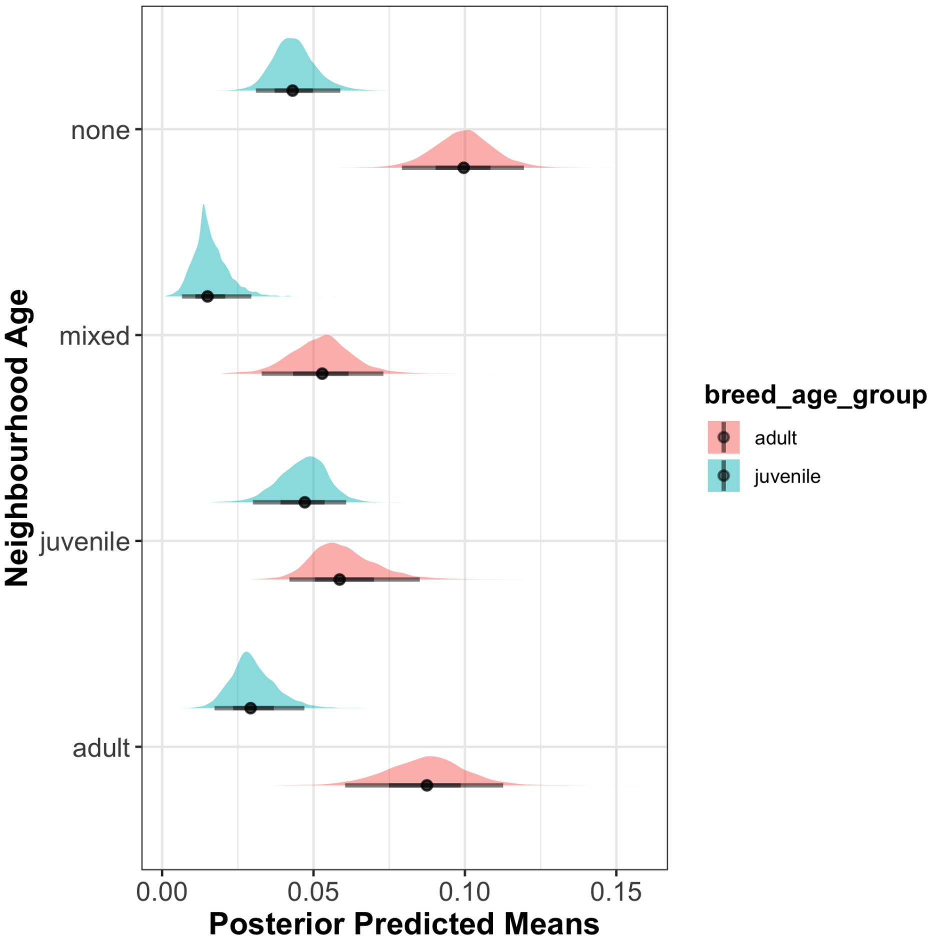
Supplementary Figure 2. **A)** Types of failures over time, split to hatching = failure before hatching, and fledging = failure between hatching and fledgling. **B)** Interval between first and second breeding attempts by timing of failure. Interval is greater when failure is happening between hatching and fledgling, vs before hatching and vs those that have a successful first brood (raise chicks to fledge) Models run to look at change in probability of failure at different points over time of study, using Bayesian logistic regression model with Bernoulli likelihood to see how binary response variable of whether the probability of a breeding attempt failing **C)** before hatching or **D)** between hatching and fledging changed over study years. Probability of failure before hatching decreases by -1.22 [-1.41, -1.01] percentage points per year and the probability of failing between hatching and fledging increases 0.79 [0.61, 0.94] percentage points per year.



Supplementary Figure 3. Proportion of breeding females not identified over years of the study.



Supplementary Figure 4. Posterior distribution of marginal effect of population size, and within year laying date variance on probability of females whose first breeding attempt fails having a second attempt, split by the female's age at breeding (juvenile = 1 year old, adult = 2+ years old). Population density and variance in laying date appear to have no effect on probability of second breeding attempts (model 4).



Supplementary Figure 5. Posterior marginal predictions of the probability of having a second attempt after a failure, split by neighbourhood age group and age of breeding female (model 4).