

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 auto-correlation 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.

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

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).

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

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 ($V_{SPATIAL}$):

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

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 Material.

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).

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

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 ($V_{P \text{ within year}}$) assigned to additive genetic variance (V_A).

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

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 $V_{P \text{ within year}}$. 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% \pm 8.8% to 60.2% \pm 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% \pm 5.8%, nestbox model: 19.4% \pm 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% \pm 4.0% and 21.9% \pm 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% \pm 1.7% and the breeding environment model was slightly lower at 10.6% \pm 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% \pm 9.4% to 65.0% \pm 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 V_p	Est (SE)	Rel to V_p	Est (SE)	Rel to V_p	Est (SE)	Rel to 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	
$V_{p\text{-within year}}$	32.696		32.391		51.065		51.514	
$h^2_{\text{within year}}$	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	
$V_{p\text{-within year}}$	25.018		24.179		38.547		42.299	
$h^2_{\text{within year}}$	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, $V_{SPATIAL}$ = spatial proximity matrix, V_{NB} = nest box random effect, $V_{BREED\ ENV.}$ = breeding environment similarity matrix, V_R = residual variance, V_p = total phenotypic variance as sum of all variance components, $V_{p\text{-within year}}$ = total phenotypic variance as sum of all variance components excluding V_{BY} , $h^2_{\text{within year}}$ = within year heritability as proportion of V_A to $V_{p\text{-within year}}$.

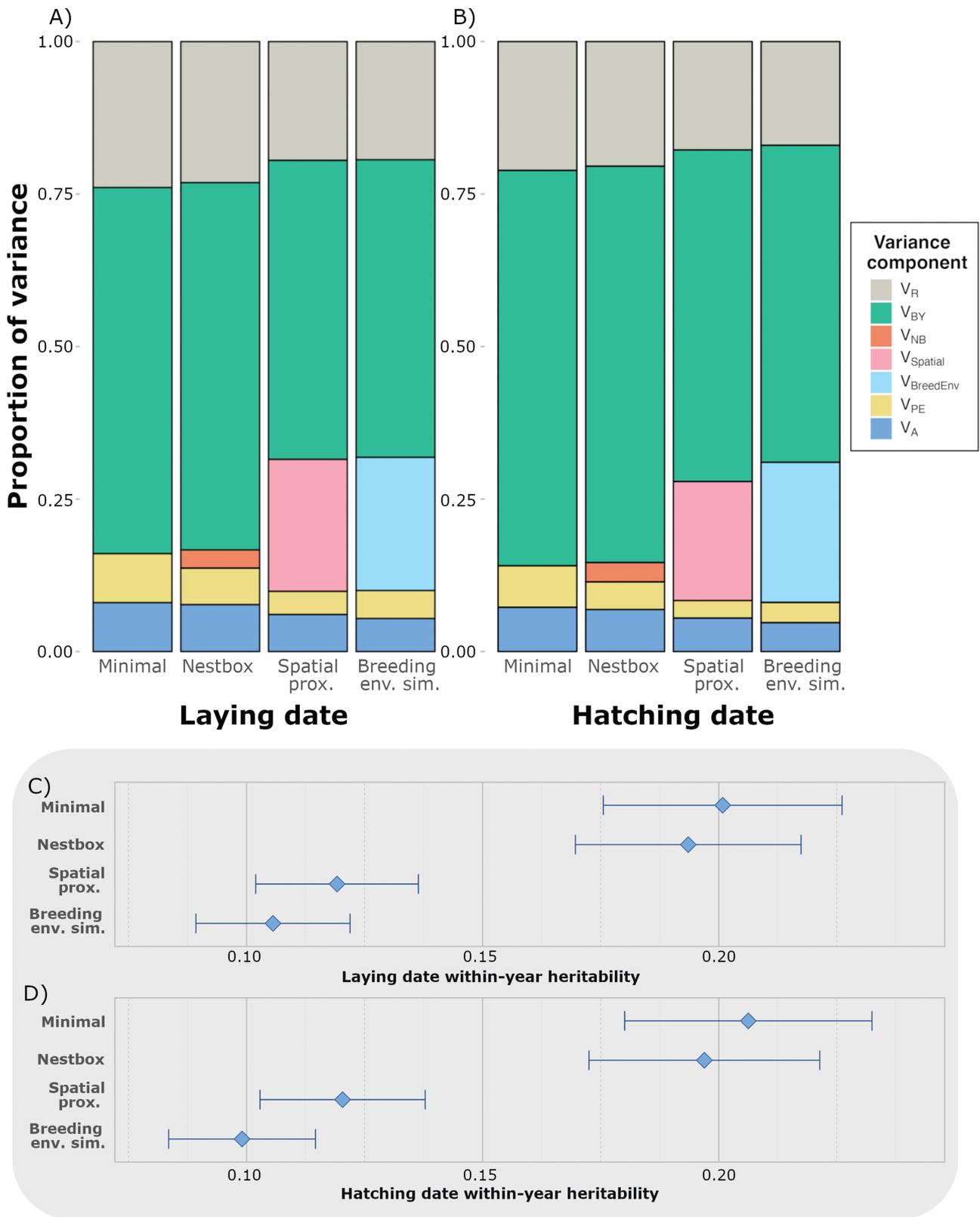


Figure 1. Proportion of variance assigned to each component for the 4 different models (specific information on all models in the methods), for (A) laying date and (B) hatching date. Colors correspond to each component. V_{BY} = breeding year, $V_{SPATIAL}$ = spatial proximity matrix, $V_{BREED ENV.}$ = 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 $V_{P-within year}$) 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 $3.2\% \pm 0.3\%$ of the variation. Within-year heritability only decreased slightly, from $20.6\% \pm 2.6\%$ in the minimal model to $19.7\% \pm 2.4\%$ 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 $19.5\% \pm 3.6\%$ of variation seen in hatching date, and the breeding environment similarity matrix explained $23.0\% \pm 3.7\%$. 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 ($17.8\% \pm 0.4\%$ and $17.0\% \pm 0.4\%$). 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.

Conclusion

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., & Vandekerckhove, 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., Béréanos, 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). Intra-specific 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., Petorelli, 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>