Ecological harshness mediates reproductive trade-offs in a great tit population

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Abstract

Lack's seminal work on bird clutch sizes has spurred expansive research on reproductive trade-offs, especially focusing on offspring quantity–quality trade-offs and the potential fitness consequences for the parents. The environment is a critical driver of the expression of individual reproductive traits, influencing them through plastic responses. However, the plasticity of reproductive trade-offs themselves across environments has seldom been studied, and these studies were often limited to experimental approaches and dichotomous environments. Using 58 years of detailed data from a great tit population, we employ the recently developed 'covariance reaction norm' (CRN) model to explore how continuous environmental variation influences the shape of reproductive trade-offs among individuals. Our analysis reveals that the offspring quantity–quality trade-off is predominantly stable across years, with minimal variation linked to ecological harshness during the breeding season. However, the CRN also demonstrated that the among-mother correlation between offspring mass and future offspring recruitment was positive, but only under harsh environmental conditions, suggesting that producing larger offspring provides fitness benefits when breeding conditions are suboptimal, which may reflect the importance of size for early-life competition. Altogether, this work highlights that there is temporal variation in some of the phenotypic correlations, mostly driven by environmental conditions, which shape the expression of offspring investment across breeding seasons. Our study shows the benefits of exploring old ecological questions in the light of new statistical methods, highlighting the importance of understanding how environmental variation shapes the expression of life history trade-offs and the evolution of plasticity in reproductive strategies.

Introduction

The offspring quantity–quality trade-off has been a central area of interest in life-history biology, with numerous studies exploring this long-standing topic, both theoretically (Williams, 1966; Smith & Fretwell, 1974; Fischer *et al.*, 2011), as well as empirically in various species (Lack, 1954; Sinervo & Licht, 1991; Einum & Fleming, 2000) including humans (Lawson & Mulder, 2016). All else being equal, selection should favor females producing more offspring, but these females also require enough resources to allocate to each offspring to ensure their survival, as larger offspring usually have better survival prospects (Sogard, 1997; Einum & Fleming, 2000; Marshall *et al.*, 2003; Fischer *et al.*, 2011). It was, therefore, initially proposed that each female has an inherent optimal brood size, such that it yields the highest possible recruitment, whereby any deviations from this brood size would lead to suboptimal offspring quality and thus lower overall recruitment (Lack, 1954). Overall, while some evidence agrees with Lack's initial hypothesis (Smith & Fretwell, 1974), with manipulated increases or decreases in clutch size leading to changes in offspring condition and suboptimal recruitment as a consequence (Pettifor *et al.*, 1988, 2001), most studies found that any increase in clutch size does not necessarily decrease offspring quality, and can even lead to higher recruitment (Perrins & Moss, 1975; Boyce & Perrins, 1987). Recent work has also shown how selection on offspring quality across breeding seasons can promote rather than constrain variability in females' clutch size in response to seasonal fluctuations (Westneat *et al.*, under review).

This potential lack of brood size optimization can have several causes. First, the offspring quantity–quality trade-off does not happen in isolation from other traits: females do not necessarily optimize the size of a single brood for highest possible recruitment, but rather balance it with their own survival and thus future reproductive opportunities, maximizing their lifetime reproductive success (Williams, 1966; Gustafsson & Sutherland, 1988; Dijkstra *et al.*, 1990). Second, it ignores the role of mating and bi-parental care present in many avian species, and thus overlooks factors such as mate quality and sexual conflicts over provisioning which can influence reproductive trade-offs (Smith & Härdling, 2000; Ratikainen *et al.*, 2018). Finally, models on optimal brood size have sometimes ignored the role played by the environment in mediating such reproductive trade-offs (Smith & Fretwell, 1974), as in many species, individuals adjust their offspring number and size via phenotypic plasticity (Fischer *et al.*, 2011).

The expression of trade-offs can change over time and and space due to phenotypic plasticity (Service & Rose, 1985; Björklund, 2004). These plastic changes in trait expression as a response to environmental variability can lead to changes in the variance and covariance between traits (de Jong, 1989; Martin, 2023), with the latter being determined by the relative amount of variance in resource acquisition vs. resource allocation between the given traits (van Noordwijk & de Jong, 1986). The environment influences the evolution of traits such as optimal offspring size, optimal clutch size, and their plasticity (Parker & Begon, 1986), which have since been widely studied (Braby, 1994; Fox & Czesak, 2000; Taborsky *et al.*, 2007; Allen *et al.*, 2008; Marshall *et al.*, 2008; Leips *et al.*, 2009). However, little is known about the influence of the environment on reproductive trade-offs themselves (i.e., on the correlation between traits) in wild populations, with most explorations limited to experimental approaches with discrete environments, or a dichotomization of the underlying continuous environmental variation (Messina & Slade, 1999; Czesak & Fox, 2003; Houslay *et al.*, 2018; Mitchell & Houslay, 2021). Discretizing continuous processes is rarely justifiable (MacCallum *et al.*, 2002; Beltran &

Tarwater, 2024). Historically this was done largely for practical reasons when studying trade-offs, as no modeling approach was available to easily study the influence of continuous environmental variation on genetic or phenotypic covariances (i.e., trade-offs) (Martin, 2023). However, it is likely that reproductive trade-offs in wild populations are influenced by the continuous environmental variation experienced by reproductive females. We, therefore, aim to use a new multivariate statistical approach that allows us to explore the role of continuous variation in environmental harshness on such reproductive trade-offs.

Here, we used one of the largest individual-based datasets of wild birds with the aim of applying a new statistical tool — the covariance reaction norm (CRN) model (Martin, 2023; Bliard *et al.*, 2024) — to revisit longstanding questions related to reproductive trade-offs faced by reproductive individuals in wild populations. The CRN model provides a novel framework to examine how continuous environmental variation influences the covariance between traits, allowing us to test longstanding hypotheses about trade-offs in a more ecologically realistic context (Martin, 2023; Bliard *et al.*, 2024). Here, we explored the dependence on key environmental variables of the among-individual (i.e., among-mother) correlations between three key traits: brood size, offspring mass, and offspring recruitment, with each trait viewed as a maternal character (i.e., analysed at the level of the brood). Overall, based on prior work, we hypothesized that we would find a trade-off (i.e., negative correlation) between brood size and offspring mass (Nur, 1984; Smith *et al.*, 1989), and that this correlation would become more negative in years of harsh ecological conditions (i.e., high density, low precipitation, low temperature, low beech mast), as trade-offs have often been shown to be stronger in poor conditions (Cohen *et al.*, 2020). We also hypothesized that the among-mother correlation between offspring mass and recruitment would be positive overall, as females producing larger offspring should have an improved recruitment, with more of these offspring surviving and reproducing in following years (Perrins & Moss, 1975; Nur, 1984). Importantly, we expected this correlation to be more positive under harsh ecological conditions, as in such conditions producing larger offspring might be key for their survival. When ecological conditions are milder or favorable (i.e., low density, high precipitation, high temperature, high beech mast), this correlation is expected to become null, as even smaller offspring might be as likely to survive in such conditions. Finally, we expected a slightly positive correlation between brood size and recruitment, as past studies have shown that mothers with the highest brood size had higher recruitment for this specific brood, even though it potentially leads to lower fitness across multiple broods (Boyce & Perrins, 1987). We also expected the correlation between brood size and recruitment to become more positive in breeding seasons with a low population density.

Methods

In this study, we explored whether the among-individual correlations between three main traits linked to reproduction depended on the environmental context. To this aim, we used 58 years of individual demographic and life-history data from the monitoring of a great tit population in Wytham Woods and applied a CRN model to brood size, offspring mass, and recruitment of offspring into the population in following years. In this model, we explored the role of ecological and environmental variables in governing the among-individual correlations between these traits.

Study system

The great tit is a common and widespread species across Eurasia, member of the Paridae family (Gosler *et al.*, 2020), and is one of the most widely studied passerines, that has become a model species for the study of behavioral and evolutionary ecology. It dwells in woodland and wooded farmland, as well as urban areas (Gosler *et al.*, 2020), and nests in tree cavities and artificial nest boxes. Great tits are annual breeders, forming pairs and breeding in the spring, usually producing a single clutch per year consisting of 5-12 eggs, even though second clutches later in the spring sometimes occur (Perrins, 1965). The study population is from Wytham Woods (Oxfordshire, United Kingdom, 51°77′N, 1°32′W), which has been monitored since 1947 (Perrins, 1965), and the monitoring has been standardized with a stable number of nest boxes since 1961 (Perrins, 1965; Perrins & McCleery, 1989). The curated and standardized data used in this study were accessed through SPI-Birds: study name "Wytham Woods", study ID "WYT", version 1.1.0 on October 16th 2023 (Culina *et al.*, 2021). As part of this long-term individual-based monitoring, individuals were fitted with unique metal rings to allow individual identification and followed throughout their lifespan (Lack, 1964). All breeding attempts were monitored until offspring fledged, and both parents and offspring were usually caught, identified, and individually measured (e.g., mass, tarsus length).

Individual and environmental variables

Using 58 years of individual-based monitoring data from 1961 to 2018, we analyzed three different traits. These were the response variables in our model (see "Data analysis" section) and include the size of the brood (number of nestlings), the mass of offspring (g), and the subsequent number of successful recruits from the brood. The mass of offspring was restricted to weight measurements of 14 days old offspring. Each brood size was recorded 14 days after hatching, and the fate of offspring from the brood was tracked, with recruitment defined as the number of offspring in a brood seen breeding within the population in subsequent years, a good measure of reproductive success that is often used as a proxy of parental fitness (McCleery & Clobert, 1990; Both & Visser, 2000; Wilkin *et al.*, 2006; but see Wolf & Wade, 2001 for a critical perspective). It is important to note that this measurement of offspring recruitment has often been used but is imperfect for many reasons, such as being confounded by natal dispersal. However, this bias is expected to be limited, as natal dispersal is limited in great tits, with many offspring dispersing short distances and therefore likely staying within the study population (Greenwood *et al.*, 1979; Verhulst *et al.*, 1997). In total, this yielded a final dataset encompassing 7287 broods from 5032 females across 58 years, with individual measures of mass and recruitment in the population in following years for 53753 offspring.

The explanatory variables in our model included both individual and environmental variables. The individual variables were the mass of the mother (g) of each brood, as well as the breeding age of the mother, which has an influence on reproductive success (Bouwhuis *et al.*, 2009). All breeding individuals were aged as first year breeders (1 year old) or older breeders (>1 year old), and this categorisation was based on plumage characteristics during captures when the exact age was not known from the ring number (Crates *et al.*, 2016; Simmonds *et al.*, 2020).

The environmental variables were spring temperature, spring precipitation, population density, beech mast index, and synchrony of laying dates with the caterpillar peak, which are all known to be important for great tit reproduction. These predictors were chosen because they directly influence resource availability, breeding timing, or parental effort in great tits. For instance, lower spring temperatures and precipitation may limit caterpillar abundance, a key food source, increasing the cost of brood provisioning, while population density may reflect competition for resources. Spring temperature and precipitation were obtained from the nearby Radcliffe Meteorological Station (Burt & Burt, 2019). Spring precipitation was defined as the sum of precipitation from April 1st to May 31st, the period when offspring are in the nest (Simmonds *et al.*, 2020). Following Simmonds et al. (2020) analysis of climatic windows critical for great tits (Bailey & Pol, 2016; van de Pol *et al.*, 2016; Simmonds *et al.*, 2020), spring temperature was defined as the daily mean temperature from March 1st to May 9th. As usually estimated in this system, population density in a given year was calculated as the number of females hatching at least one egg (Simmonds *et al.*, 2020). Beech mast index has been routinely collected in Wytham Woods and across Europe (Lack, 1964; Perdeck *et al.*, 2000; Grøtan *et al.*, 2009), and is scored as an ordinal variable of increasing beech mast ranging from 0 to 2. Years of high beech mast are expected to be beneficial for fledgling survival in the fall and over winter by providing abundant food resources, and is therefore an important factor for offspring recruitment. Finally, synchrony is an individual's measure of phenological timing in relation to an annual, population-wide, measure of caterpillar abundance. More precisely, we calculated it as the difference between the half-fall date, which is the median date of capture of 5th instar caterpillars of the of winter moth *Opheroptera brumata* larvae, which indexes the timing of peak abundance of this species (Van Noordwijk *et al.*, 1995; Hinks *et al.*, 2015), and the female's laying date.

Missing data imputation

The final datasets contained missing data for some variables. More specifically, out of a total of 7287 broods, the mass of the mother was missing for 1147 observations (15.7%), while the breeding age was not known for 210 observations (2.9%). Regarding the environmental variables across the 58 years of monitoring, 14 years had an unknown half fall date (24.1%) and 5 years had a missing beech mast index (8.6%). We imputed these missing data points using predictive mean matching with the R package *mice* (Buuren & Groothuis-Oudshoorn, 2011; Buuren *et al.*, 2023). To account for imputation uncertainty, we generated 20 alternative imputed datasets using this method, and each of these datasets was then analyzed and subsequently combined, successfully propagating imputation uncertainty in the results throughout the analysis.

Data analysis

We aim to explore the ecological correlates of phenotypic correlations between maternal traits linked to reproduction in great tits, more precisely the phenotypic correlations between brood size and offspring quality (using mass as a proxy), and between offspring quality and offspring recruitment in the population in following years. To this aim, we used a multivariate Covariance Reaction Norm (CRN) model, which is a recently developed model (Martin, 2023) that we have previously tailored to routinely collected demographic data (Bliard *et al.*, 2024), allowing phenotypic covariances to vary through time or space in response to environmental variation. We apply this method on the three traits of interest in this study: brood size, offspring mass, and offspring recruitment (all treated as maternal traits, analysed at the level of the brood).

We first modeled offspring mass at day 14 with a Gaussian distribution (equation 1), as a function of $\mathbf{X_1}$ (a N x P matrix of N measurements of P predictors, including an intercept), with predictors being spring temperature, spring precipitation, population density, beech mast index, synchrony and its quadratic effect, the mass of the mother and the age of the mother. All the continuous variables were standardized. In addition, we included a year random effect $\boldsymbol{\delta_1}$ and a nestbox random effect $\boldsymbol{\gamma_1}$. The year random effect accounts for inter-annual variability in environmental conditions, while the nestbox random effect controls for potential variation in territory quality or non-random selection of specific nestboxes by reproductive individuals. These random effects ensure that observed phenotypic correlations are not biased by unmeasured temporal or spatial factors. We also added a year-specific mother random effect $\boldsymbol{\alpha_{1(Y)}}$ structured across repeated measurements by **W** (a N x J matrix of J mothers), which as explained further below could vary in response to year-specific ecological conditions. Finally, σ is the residual variation describing the within-brood variance.

$$\begin{gathered}\boldsymbol{\mu_1} = \boldsymbol{X_1\beta_1} + \boldsymbol{\delta_1} + \boldsymbol{\gamma_1} + \boldsymbol{W\alpha_{1(Y)}} \\ \boldsymbol{offspring\ mass} \sim Normal(\boldsymbol{\mu_1}, \sigma_{\mu_1})\end{gathered} \tag{1}$$

As our second trait, brood size, is underdispersed relative to a Poisson distribution, we modeled it using an ordinal regression (also called cumulative logistic regression; equation 2), as a function of $\mathbf{X_2}$, with covariates being the same as in $\mathbf{X_1}$, but not containing an intercept and differing in the number of observations. Similarly, we also included a year random effect $\boldsymbol{\delta_2}$ and a nestbox random effect $\boldsymbol{\gamma_2}$. In the absence of repeated measurement for each mother in a given year (a single brood per female in a breeding season), as indicated by the exclusion of **W**, we included a year-specific observation-level random effect $\boldsymbol{o_{2(Y)}}$. Here, the cumulative probability of having at most *i* offspring is given as a function of the thresholds θ_i and the matrix of covariates $\mathbf{X_2}$, as well as the random effects.

$$\mathrm{logit}\left(\Pr\left(\boldsymbol{N_{offspring}} \leq i\right)\right) = \theta_i - \left(\boldsymbol{X_2}\boldsymbol{\beta_2} + \boldsymbol{\delta_2} + \boldsymbol{\gamma_2} + \boldsymbol{o}_{\boldsymbol{2}(Y)}\right) \tag{2}$$

We modeled the third trait, offspring recruitment, describing the number of offspring from a given brood found breeding in the population in following years, with a zero-inflated Poisson distribution (equation 3). Recruitment data were expected to be heavily zero-inflated because many broods produced no recruits, due to factors such as brood predation and low offspring survival. The zero-inflation term ψ was included because posterior predictive checks with a simpler Poisson model without zero inflation highlighted an over-representation of zeros, causing the model to fit poorly to the data. The probability of observing a given number of offspring recruited into the population in following years was modeled as a function of $\mathbf{X_3}$, which is similar to $\mathbf{X_2}$ with the addition of an intercept. Year $\boldsymbol{\delta_3}$ and nestbox $\boldsymbol{\gamma_3}$ random effects were included as well. Since offspring recruitment was analyzed at the level of the brood (one measure of recruitment per brood), we did not have repeated measurements in a given year for mothers, and therefore included a year-specific observation-level random effect $\boldsymbol{o}_{3(Y)}$.

$$\log(\boldsymbol{\mu_3}) = \boldsymbol{X_3}\boldsymbol{\beta_3} + \boldsymbol{\delta_3} + \boldsymbol{\gamma_3} + \boldsymbol{o}_{\boldsymbol{3}(Y)} \tag{3}$$

$$p(\boldsymbol{N_{recruits}} \mid \psi, \boldsymbol{\mu_3}) = \begin{cases} \psi + (1-\psi)Poisson(0 \mid \boldsymbol{\mu_3}), & \text{if } N_{recruits} = 0 \\ (1-\psi)Poisson(\boldsymbol{N_{recruits}} \mid \boldsymbol{\mu_3}), & \text{if } N_{recruits} > 0 \end{cases}$$

We also tried an alternative modeling approach by using a binomial distribution to estimate the probability of offspring recruiting in the population, but unfortunately this model suffered from convergence issues that could not be resolved.

To investigate context dependence of the phenotypic correlations between these three traits, the year-specific among-individual random effect $\boldsymbol{\alpha}_{1(Y)}$ and observation-level random effects $\boldsymbol{o}_{2(Y)}$ and $\boldsymbol{o}_{3(Y)}$ were drawn from a multivariate normal distribution governed by year-specific covariance matrices $\boldsymbol{P}_{(Y)}$ (equation 4). The year-specific covariance matrices can then be decomposed in their primary elements, i.e., the year-specific phenotypic correlations between the three traits (r_{12},r_{13},r_{23}) and their variances ($\sigma_{\alpha 1}{}^2$, $\sigma_{o2}{}^2$, $\sigma_{o3}{}^2$), given that a covariance is just the product of the correlation between traits and the square roots of the variances. We then model the year-specific phenotypic correlations ($r_{(Y)}$), as well as the year specific variances ($\sigma^2{}_{(Y)}$), as a function of a subset of the environmental covariates contained in $\mathbf{X_4}$ (equation 4). The covariates are spring temperature, spring precipitation, population density, and beech mast index.

$$\left[\boldsymbol{\alpha}_{\mathbf{1}(Y)}, \boldsymbol{o}_{\mathbf{2}(Y)}, \boldsymbol{o}_{\mathbf{3}(Y)}\right] \sim Multivariate\ Normal\left(\mathbf{0}, \boldsymbol{P}_{(Y)}\right) \tag{4}$$

$$\boldsymbol{P}_{(Y)} = \begin{bmatrix} \sigma^2_{\alpha_1(Y)} & r_{12(Y)}\ \sigma_{\alpha_1(Y)}\sigma_{o_2(Y)} & r_{13(Y)}\ \sigma_{\alpha_1(Y)}\sigma_{o_3(Y)} \\ r_{12(Y)}\ \sigma_{\alpha_1(Y)}\sigma_{o_2(Y)} & \sigma^2_{o_2(Y)} & r_{23(Y)}\ \sigma_{o_2(Y)}\sigma_{o_3(Y)} \\ r_{13(Y)}\ \sigma_{\alpha_1(Y)}\sigma_{o_3(Y)} & r_{23(Y)}\ \sigma_{o_2(Y)}\sigma_{o_3(Y)} & \sigma^2_{o_3(Y)} \end{bmatrix}$$

$$\operatorname{atanh}\left(\boldsymbol{r}_{(Y)}\right) = \boldsymbol{X_4\beta_4}$$

$$\exp\left(\sigma_{(Y)}\right) = \boldsymbol{X_4\beta_5}$$

Regarding the choice of priors, we used a standard flat prior for the zero-inflation coefficient ψ (equation 5), which is a default prior for this parameter in most statistical software.

$$\psi \sim Beta(1,1) \tag{5}$$

We specified regularizing priors for all the $\boldsymbol{\beta}$ slope coefficients (equation 6) to reduce our risk of false positive and increase the robustness and generalizability of our findings (see Lemoine, 2019 for discussion). Narrower priors were used for $\boldsymbol{\beta_4}$ to avoid putting to much weight on extreme correlations.

$$\boldsymbol{\beta_1}, \boldsymbol{\beta_2}, \boldsymbol{\beta_3}, \boldsymbol{\beta_5} \sim Normal(0,1) \tag{6}$$

$$\boldsymbol{\beta_4} \sim Normal(0, 0.5)$$

For the year-specific among-individual σ_α and year-specific observation-level σ_o standard deviations, as well as for the within-brood variance σ, we used exponential priors (equation 7).

$$\sigma_{\mu_1} \sim Exponential(2) \tag{7}$$

We specified the year random effects $\boldsymbol{\delta}$ on the three traits studied by drawing them from univariate (i.e. non-correlated) normal distributions, also using exponential distributions for the variance terms λ (equation 8).

$$\begin{gathered} \boldsymbol{\delta_1} \sim Normal(0, \lambda_1) \\ \boldsymbol{\delta_2} \sim Normal(0, \lambda_2) \\ \boldsymbol{\delta_3} \sim Normal(0, \lambda_3) \\ \lambda_1, \lambda_2, \lambda_3 \sim Exponential(2) \end{gathered} \tag{8}$$

Finally, since breeding individuals sample nest boxes non-randomly, the nextbox random effects $\boldsymbol{\gamma}$ were specified as multivariate, thus estimating the among-nestbox covariances, as not accounting for this correlation could potentially lead to biasing the estimation of the context-dependent among-individual correlations we aimed to detect. We therefore drew the γ vectors from a multivariate normal distribution with covariance matrix **Σ**. The covariance matrix **Σ** is decomposed into its standard deviation matrix **S**, with exponential priors for each standard deviation parameter ω, and its correlation matrix **R**, which is specified with a Lewandowski-Kurowicka-Joe prior distribution (equation 9; see Martin 2023 for further details on the LKJ prior).

$$[\boldsymbol{\gamma_1}, \boldsymbol{\gamma_2}, \boldsymbol{\gamma_3}] \sim Multivariate\ Normal(\boldsymbol{\Sigma}) \tag{9}$$

$$\boldsymbol{\Sigma} = \mathbf{SRS}$$

$$\mathbf{S} = \begin{bmatrix} \omega_1 & 0 & 0 \\ 0 & \omega_2 & 0 \\ 0 & 0 & \omega_3 \end{bmatrix}$$

$$\omega_1, \omega_2, \omega_3 \sim Exponential(2)$$

$$\mathbf{R} \sim LKJ(\mathbf{2})$$

Model implementation

The multivariate CRN model (Martin, 2023; Bliard *et al.*, 2024) described above was implemented in a Bayesian framework using the statistical programming language Stan (Carpenter *et al.*, 2017), which uses an extended and cutting-edge Hamiltonian Monte Carlo algorithm (Hoffman & Gelman, 2014). We ran the model through R version 4.3 (R Core Team, 2023), using the R package CmdStanR version 0.8.1 (Gabry & Češnovar, 2020). As detailed in the previous methods section, weakly informative regularizing priors were used for all parameters. We performed 20 alternative models, one for each of the imputed dataset, to ensure that imputation uncertainty was propagated through the analysis. Each model ran on 3 chains with a warm-up period of 1000 iterations, and sampled for 1000 iterations per chain, keeping all the iterations (Link & Eaton, 2012), thus totalling 3000 saved posterior samples per alternative model. We ensured that convergence was reached for each model by obtaining R-hat values below 1.01 for all parameters (Gelman & Rubin, 1992), and by visually inspecting trace plots. We then merged the posterior distributions of all the 20 alternative models, thus obtaining a single posterior distribution made of 60000 posterior samples (3000 x 20) for the combined model accounting for imputation uncertainty. Throughout the results, we report the posterior median effect sizes, alongside credible intervals. We provide the Stan code on GitHub (https://github.com/lbiard/tradeoffs_parus_major) and will archive it on Zenodo upon acceptance of the manuscript.

Results

Our results reveal that the offspring quantity–quality trade-off remains expressed across all environmental contexts, with slight relaxation under favourable conditions. In contrast, the phenotypic correlation between offspring mass and recruitment is strongly context-dependent, becoming null under favourable conditions such as low density but persisting in harsher years. Contrary to our hypothesis, we found no correlation between brood size and recruitment.

We expected the offspring quantity–quality trade-off to be highly constrained, whereby mothers producing larger broods would also produce smaller offspring. The results of our model confirm this expectation, as the among-mother correlation between brood size and offspring mass was found to be negative across all environmental contexts (Figure 1). The negative correlation between brood size and offspring mass was slightly relaxed in years of high precipitation, and, to a lesser extent, in years of low population density, although these effects were small and are associated with high uncertainties (Figure 1).

The among-mother correlation between the mass of offspring produced and their recruitment in subsequent years tended to be positive overall (Figure 2), such that mothers producing larger offspring tend to have higher offspring recruitment. This follows expectations that larger offspring are more likely to survive, thus being more likely to be present as breeders in following years. However, we found rather strong effects of the environmental context on this correlation. Following our expectations, under favorable conditions such as low population density, high spring temperature, or high spring precipitation, this correlation tended to be null, such that the mass of offspring was not clearly associated with their recruitment (Figure 2). While we expected the same for beech mast index, we found the opposite result, with the correlation becoming null in years of low beech mast (Figure 2).

Contrary to our hypothesis, we found no correlation between brood size and recruitment, and this correlation was invariant across environmental contexts (Figure 3). We discuss below whether this null correlation could be the result of either biological or statistical constraints.

The among-nestbox correlations between brood size and offspring mass (median = 0.033 [10-90% intervals = -0.519; 0.563]) and between brood size and recruitment (0.032 [-0.525; 0.575]) were found to be close to zero. However, we found an overall positive correlation among nest boxes between offspring mass and recruitment (0.387 [-0.249; 0.776]), which could reflect some degree of spatial variation in nestbox or overall territory quality.

Estimated effects of all the covariates on the three among-individual correlations highlight that the uncertainty around the median estimated effects is fairly large despite the high sample size used (Figure 4). Environmental covariates are also found to influence trait variances in various ways (Figure S3, S4, S5, S6). Overall, covariate effects on the primary traits (Figure S1, S2) align with previous studies: population density negatively affected reproductive traits, while beech mast index and maternal breeding age had positive effects across all traits. In addition, posterior predictive checks highlight a good fit of the model to the data (Figure S7).

Discussion

We used individual-based data from one of the longest individual-based monitoring of a great tit population, together with a newly developed hierarchical “covariance reaction norm” model (Martin, 2023) tailored for demographic data lacking repeated measurements within years for some traits (Bliard *et al.*, 2024). Despite some uncertainty in the results, we found evidence that the phenotypic correlations between brood size and offspring mass, and especially between offspring mass and offspring recruitment, are temporally variable and dependent on the environmental conditions experienced during the breeding season. Overall, harsher conditions lead females who lay larger broods to have smaller offspring, and the propensity for these smaller offspring to recruit is lower. Interestingly, these relationships are weakened during favorable breeding seasons. Yet, regardless of the environment, the fitness outcome for mothers does not seem to be influenced by the size of their brood, as it is not ultimately associated with offspring recruitment, though offspring recruitment is not always a reliable fitness proxy for mothers (Wolf & Wade, 2001). We discuss these findings and potential limitations of our modeling approach that could blur some of the biological associations studied here.

The trade-off between offspring quantity and offspring quality was found to be strong and highly constrained in this population of great tit. Regardless of the environmental conditions experienced during the breeding seasons, the among-females correlation between brood size and the size of their offspring was close to -1, thus highlighting a strong trade-off. We only found a weak influence of the environmental context, with the expression of the trade-off being slightly stronger under harsh conditions (e.g. high population density). Convincing evidence of context-dependence between offspring number and size has been found in studies on human fertility, whereby such trade-off is absent in favorable socio-economic classes while being found under poorer socio-economic conditions (Gillespie *et al.*, 2008; Meij *et al.*, 2009; Lawson & Mulder, 2016). Similarly, laboratory studies on invertebrates found phenotypic and genetic correlations between offspring number and size to depend on the degree of food availability (Messina & Slade, 1999; Czesak & Fox, 2003; Messina & Fry, 2003). However, we found that the trade-off is expressed across all environments in great tits, and a potential explanation could be that little variance in quality or resource acquisition remains among females once accounting for primary predictors such as mother's mass and age. For instance, the study of Ebert (1993) on *Daphnia* has shown that the offspring number and size trade-off is initially found to be influenced by food availability, but the genetic correlations all became negative once accounting for mother's condition. Similarly, negative phenotypic correlations between offspring quantity and quality were found after adjusting for maternal size in a meta-analysis across animal species (Lim *et al.*, 2014). Therefore, if our primary covariates accounted well for maternal heterogeneity in this great tit population, it could result in such a strongly negative correlation.

We found that the correlation between offspring mass and recruitment is overall positive (Figure 2), such that larger offspring are better quality offspring, thus being more likely to recruit in the population in following years. This is in line with numerous other past results in great tits, wherein offspring mass or size are usually found to be associated with future outcomes, from survival to recruitment (Both *et al.*, 1999; Monrós *et al.*, 2002; Garant *et al.*, 2004; Wilkin *et al.*, 2006; Bouwhuis *et al.*, 2015; Rodríguez *et al.*, 2016), while being independent of their laying date (Wilkin *et al.*, 2006). However, our study also explores the dependence of this association on environmental conditions experienced during the breeding season. Interestingly, we found that this association was stronger under harsh conditions, whereby producing small offspring might be particularly detrimental as they would not fare well due to poor climatic conditions (e.g., dry and cold springs; Figure 2) or stronger competition from a higher population density (Both *et al.*, 1999). However, during favorable breeding seasons, the correlation between offspring mass and recruitment becomes null, with mild conditions and low competition allowing even frail offspring to survive and recruit in following seasons, thus highlighting that phenotypic selection for offspring body mass is likely variable and its temporal dynamics are potentially mediated by environmental conditions (Braby, 1994; Grant & Grant, 2002; Siepielski *et al.*, 2009). This echoes findings from Bouwhuis *et al.* (2015), where broods with heavier offspring experienced a better recruitment probability, with this relationship being stronger during warmer springs. Such fluctuating selection is expected to promote the evolution of adaptive plasticity in reproductive behavior (de Jong, 1995). Despite most results following our expectations, the estimated effect for the beech mast index goes opposite to our predictions, with theoretically better years (i.e., higher beech mast index) associated with a stronger, more positive correlation. Although speculative, one possible explanation could be that females do an anticipatory adjustment of brood size based on future resource availability, whereby they would adjust brood size based on some external cues that correlate with beech seed production in the autumn following the breeding season. For instance, these anticipatory effects in relation to masting events have been found in red squirrels *Tamiasciurus hudsonicus* and *Sciurus vulgaris* (Boutin *et al.*, 2006). In great tits, this might lead to increased brood size at the population level during years of high beech mast (Figure S1), which in turn is likely to increase nestling and fledgling abundance in the population. This increase in the abundance of great tits and potentially other bird species might lead to a decrease in individual perceived predation risk (e.g., through dilution effects), thus making it less detrimental for nestlings to put on weight (Gentle & Gosler, 2001; Macleod *et al.*, 2005). Though the estimated effect is rather modest in size and somewhat uncertain (Figure 4), warranting caution with biological interpretation, this highlights the need for further exploration of the indirect effects of environmental variables on reproductive trade-offs.

Overall, we found a lack of correlation between brood size and subsequent successful recruitment, together with no evidence of a dependence on the environmental context. Several non-mutually exclusive reasons, both biological and statistical, could explain this invariant and null correlation. First, the lack of association could just reflect that after accounting for primary predictors on both traits, there is just no biological association between residual brood size and recruitment and no environmental effects, which would mean that regardless of environmental conditions, producing a small brood of big nestlings or a large brood of small nestlings is likely leading to the same fitness outcome for females. Second, brood size and recruitment are both non-repeated measures within a given year (i.e., context). Thus, even though we are interested in the among-individual correlation between the traits, by not having several measures per individual in a given year, within- and among-individual covariances cannot be properly disentangled. Such observation-level correlation reflects the among-individual correlation only if traits repeatabilities are high (Bliard *et al.*, 2024). The repeatability of clutch size in great tit is usually medium to high (e.g., 0.51 in Perrins and Jones (1974)). However, if the repeatability of females' offspring recruitment is low, our estimate may mostly reflect the within-individual correlation between both traits (Searle, 1961; Dingemanse & Dochtermann, 2013; Bliard *et al.*, 2024). Given that brood size is in part optimized following Lack's principle (Williams, 1966), such that any large deviation is likely leading to reduced recruitment (Gustafsson & Sutherland, 1988;

Pettifor *et al.*, 1988; but see Westneat *et al.*, under review), the within-individual correlation could be expected to be close to null, which might explain our results. Third, recruitment of offspring into the population in following years is an imperfect measure of fitness. As previously noted, because offspring effects on recruitment may be independent of maternal traits, it might thus be a poor proxy of females' fitness per se (Wolf & Wade, 2001). It is necessarily an underestimate due to imperfect detection, being confounded with long distance (i.e., outside the study area) natal dispersal (Gimenez *et al.*, 2008). Dispersal events could themselves be linked to the environmental context experienced by the nestlings (McCaslin *et al.*, 2020). For instance, it had been argued that social dominance, which could hypothetically be related to the size of the brood an offspring was reared in, could in turn influence the natal dispersal distance of offspring (Nilsson & Smith, 1985; Smith & Nilsson, 1987; Smith *et al.*, 1989). Such a limitation could potentially obscure any association between brood size and recruitment (Gimenez *et al.*, 2008). Finally, it could also be possible that the lack of association and lack of environmental effects result from interaction effects between environmental variables that were not accounted for, even though we did not have specific biologically motivated interaction to include.

Altogether, we found that, although the brood size – offspring mass trade-off was highly constrained, the among-individual correlation between offspring mass and recruitment was strongly dependent on changes in population density and harshness of the environment during the breeding season, with females producing larger offspring experiencing higher recruitment only during harsh breeding seasons. This study demonstrates that in this great tit population, among-individual covariances respond to continuous environmental change and temporal variation in population density, a phenomenon that has mostly been neglected up to now, which highlights that knowledge about life-history theory and trade-offs can be improved through the incorporation of context dependence. Future studies could extend this approach to other populations or species (Culina *et al.*, 2021), to further understand how environmental variation shapes trade-offs and life-history evolution (Chantepie *et al.*, 2024). Overall, such a framework allows us to revisit old ecological questions related to patterns of selection in fluctuating density-dependent environments through the lens of new multivariate statistical methods, and therefore expand from an often univariate view on the topic to studying multivariate patterns of trait (co)expression (Wright *et al.*, 2019; Martin, 2023).

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Authors contributions

LB conceived the study and analyzed the data, using an initial modeling framework developed by JSM. EC and BS collected and curated the data. LB wrote the first draft. All authors contributed to the editing of the manuscript.

Data and code availability

The formatted data, as well as the R and Stan code necessary to reproduce the results are available on GitHub https://github.com/lbiard/tradeoffs_parus_major and will be archived on Zenodo. The raw datasets analyzed in the current study are available in the SPI-Birds Database (study name: Wytham Woods, study ID: WYT, version: 1.0.0, data custodian: Ben Sheldon).

Figures

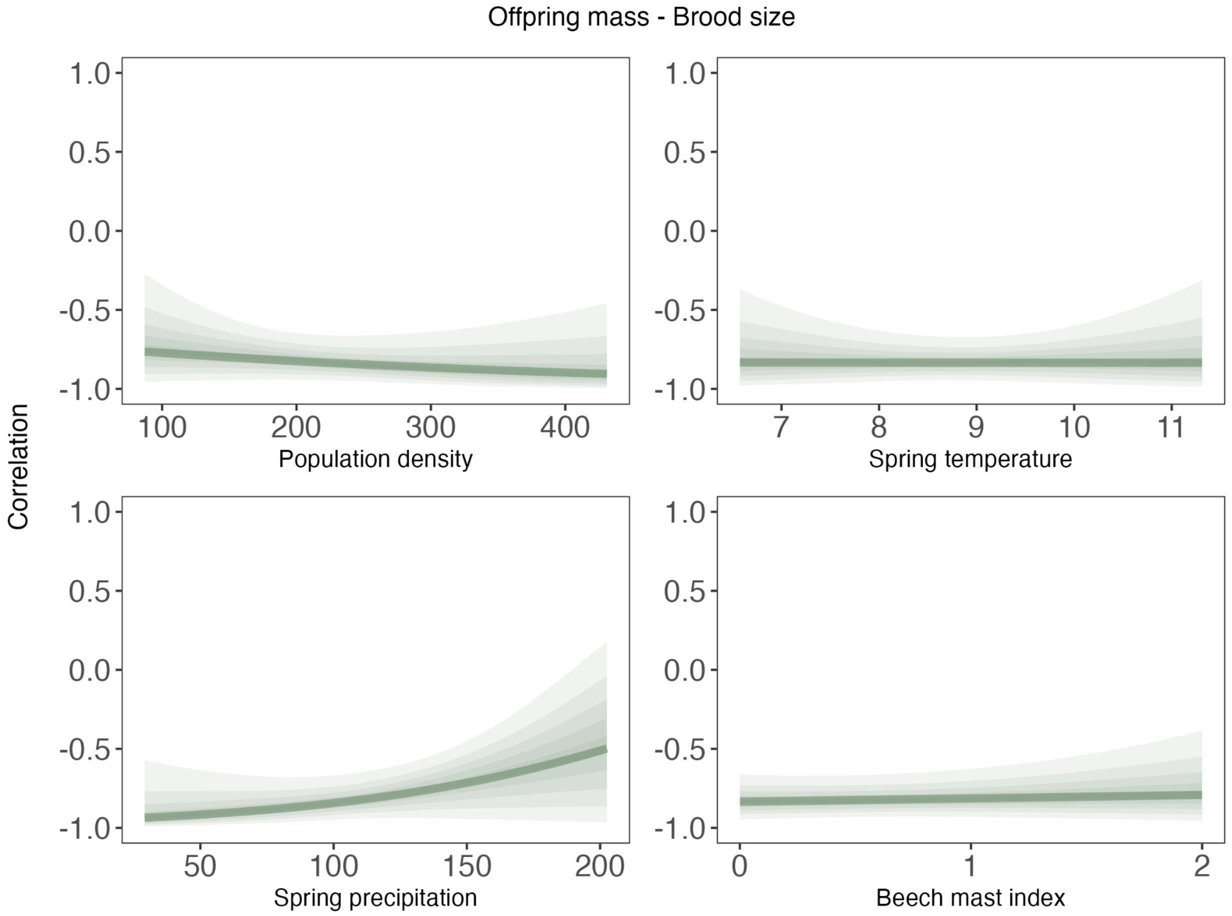

Figure 1: Estimated phenotypic correlations between offspring mass and brood size as a function of population size (top left panel), spring temperature (top right panel), spring precipitation (bottom left panel), and beech mast index (bottom right panel). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

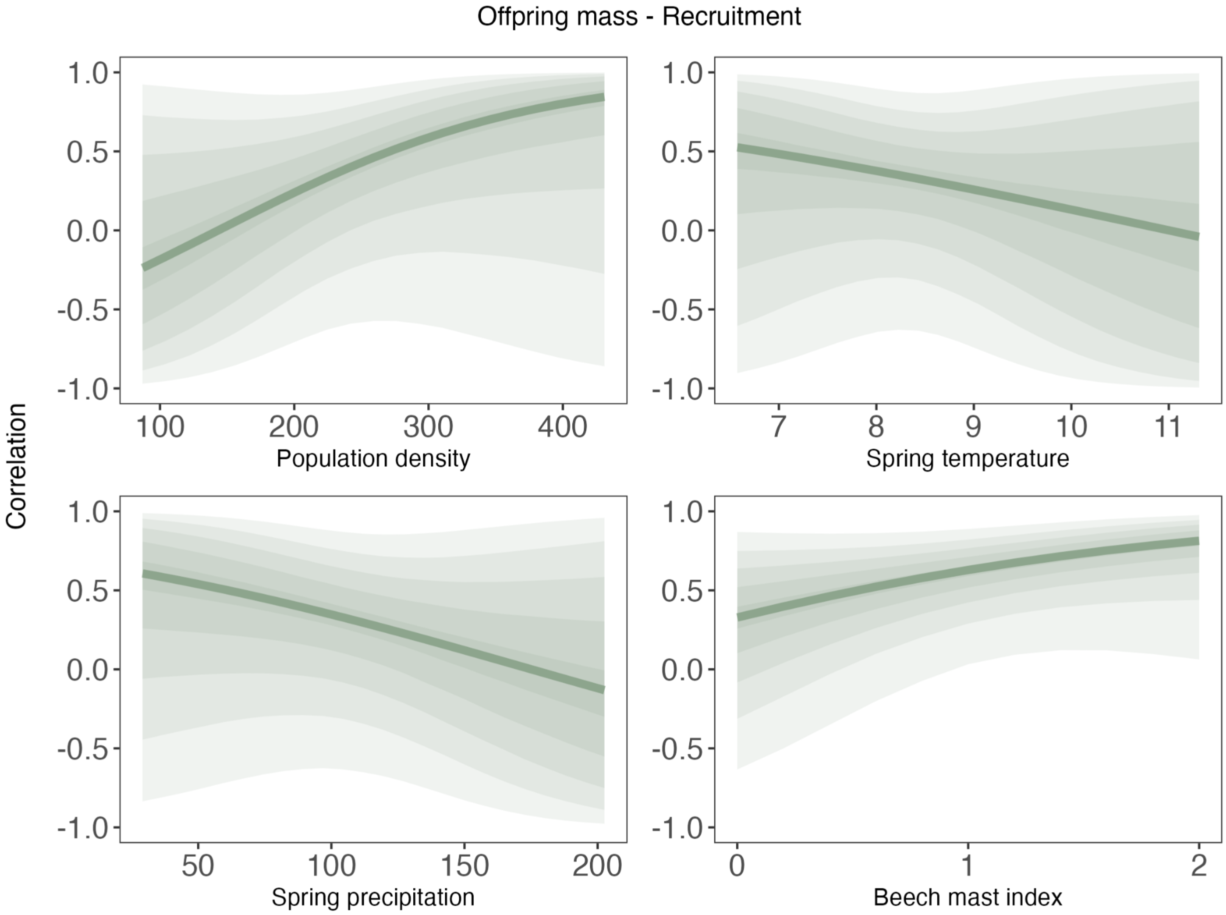

Figure 2: Estimated phenotypic correlations between offspring mass and recruitment as a function of population size (top left panel), spring temperature (top right panel), spring precipitation (bottom left panel), and beech mast index (bottom right panel). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

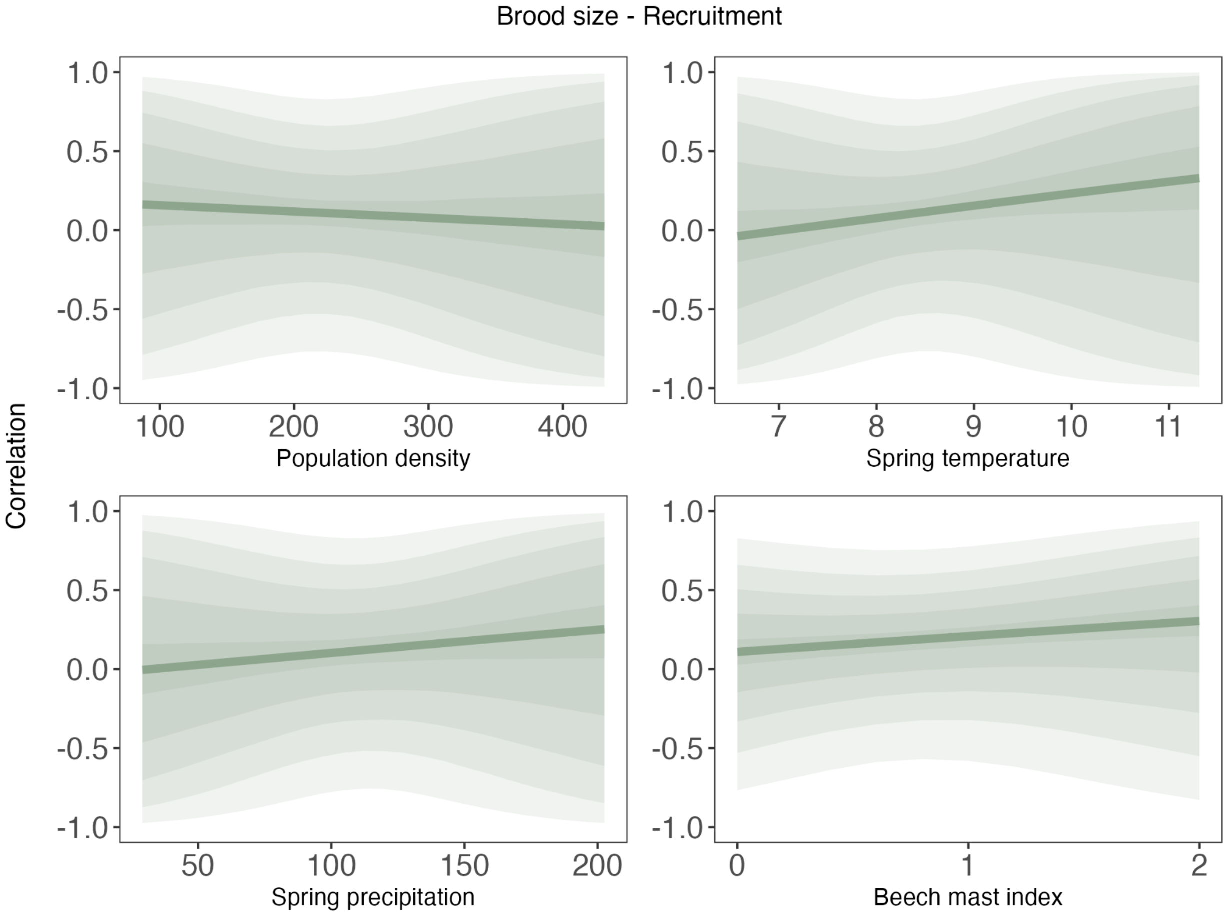

Figure 3: Estimated phenotypic correlations between brood size and recruitment as a function of population size (top left panel), spring temperature (top right panel), spring precipitation (bottom left panel), and beech mast index (bottom right panel). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

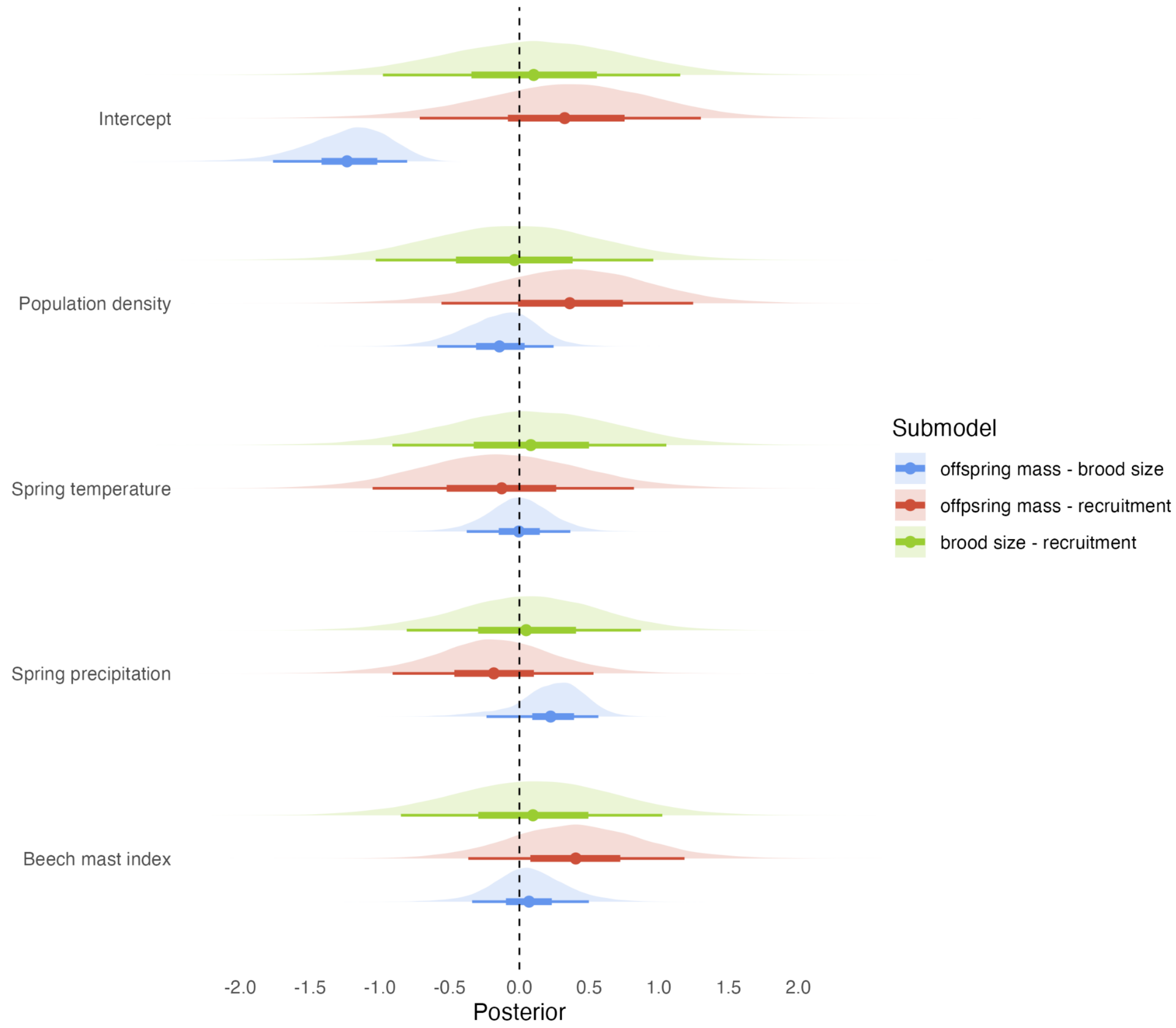

Figure 4: Estimated effects of standardized predictors on the phenotypic correlations between offspring mass and brood size (blue), offspring mass and recruitment (red), and brood size and recruitment (green).

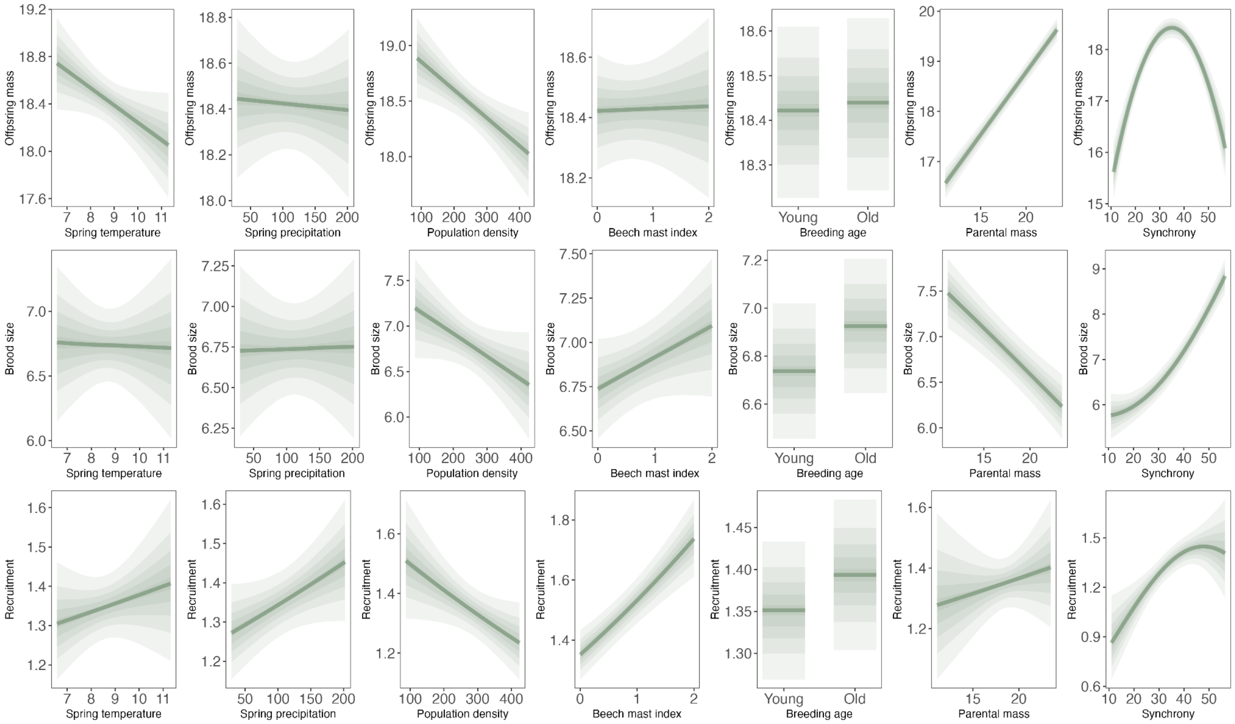

Figure S1: Associations estimated by the model between spring temperature, spring precipitation, population density, beech mast index, breeding age, parental mass, and laying date synchrony (panels from left to right) with offspring mass (top row), brood size (middle row), and recruitment (bottom row). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

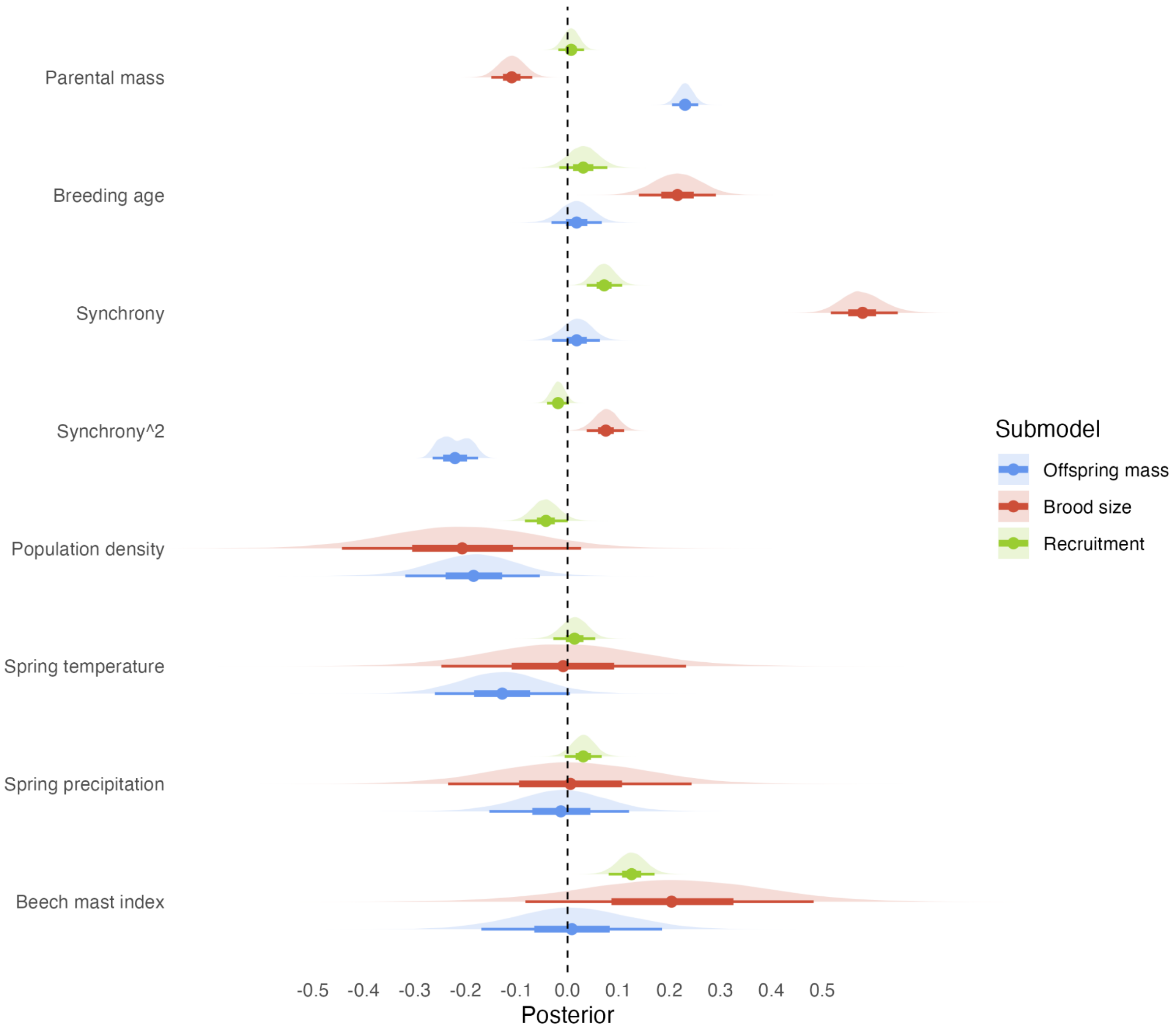

Figure S2: Estimated effects of standardized predictors on primary traits: offspring mass (blue), brood size (red), and recruitment (green).

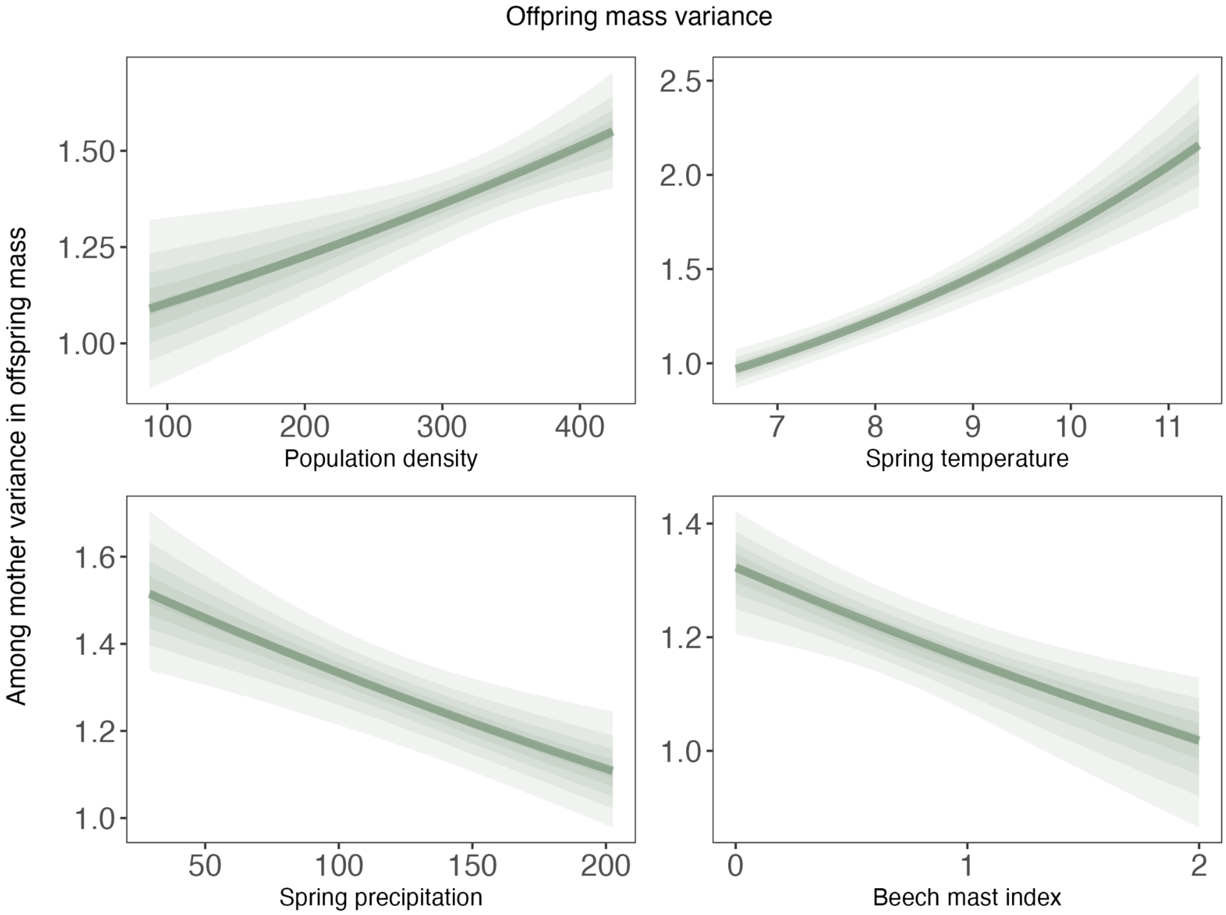

Figure S3: Estimated among-mother variance in offspring mass as a function of population size (top left panel), spring temperature (top right panel), spring precipitation (bottom left panel), and beech mast index (bottom right panel). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

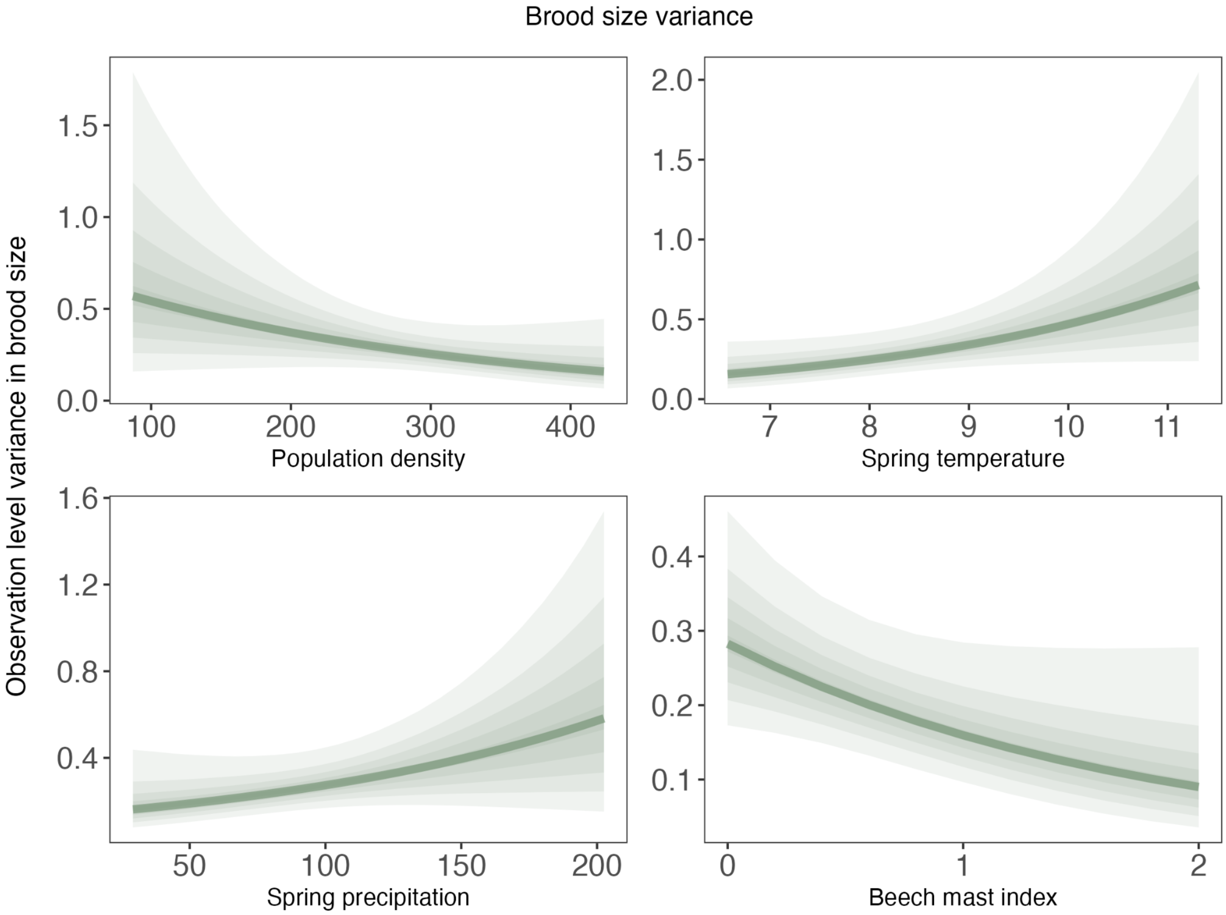

Figure S4: Estimated observation-level variance in brood size as a function of population size (top left panel), spring temperature (top right panel), spring precipitation (bottom left panel), and beech mast index (bottom right panel). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

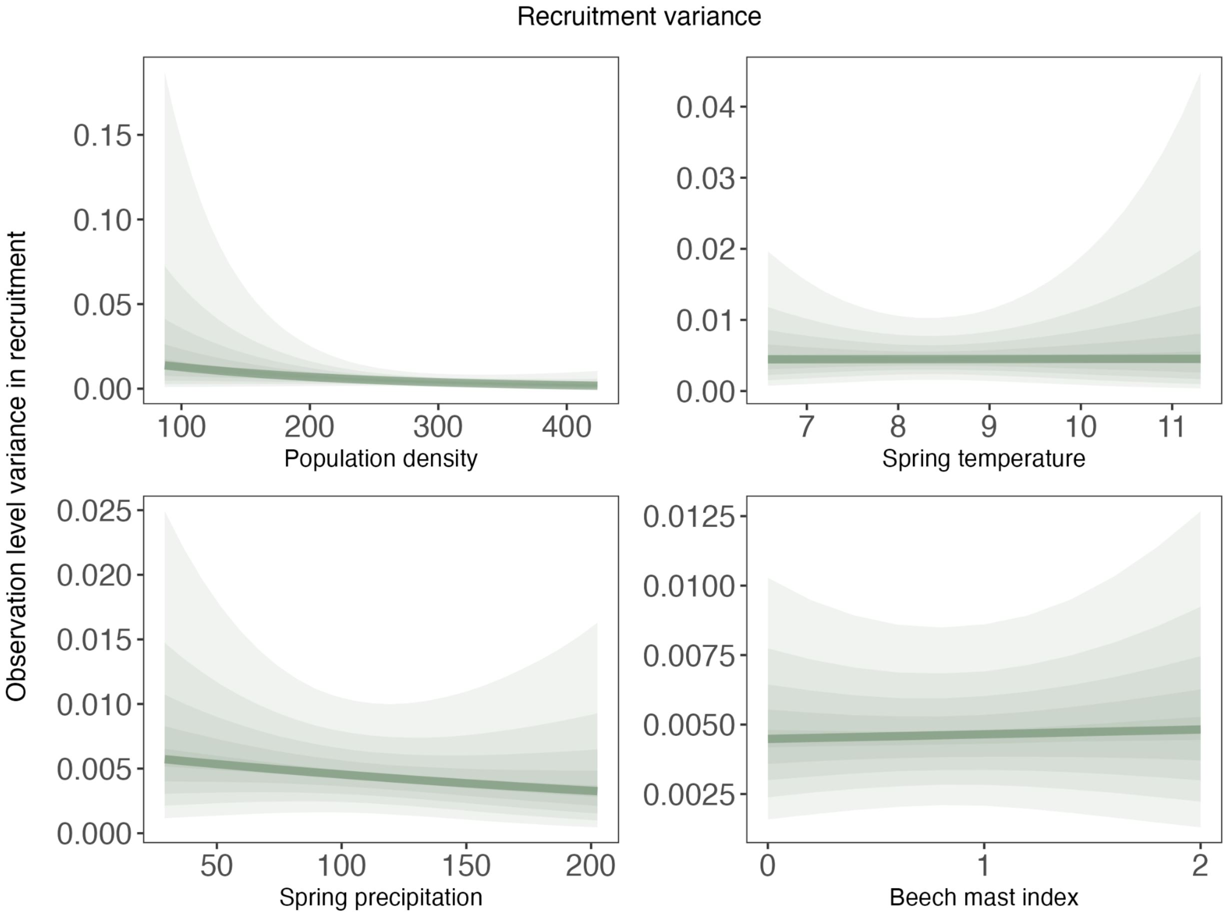

Figure S5: Estimated observation-level variance in offspring recruitment as a function of population size (top left panel), spring temperature (top right panel), spring precipitation (bottom left panel), and beech mast index (bottom right panel). Posterior median effect sizes are represented by the darker lines, and 10% to 90% credible intervals are represented by the shaded bands.

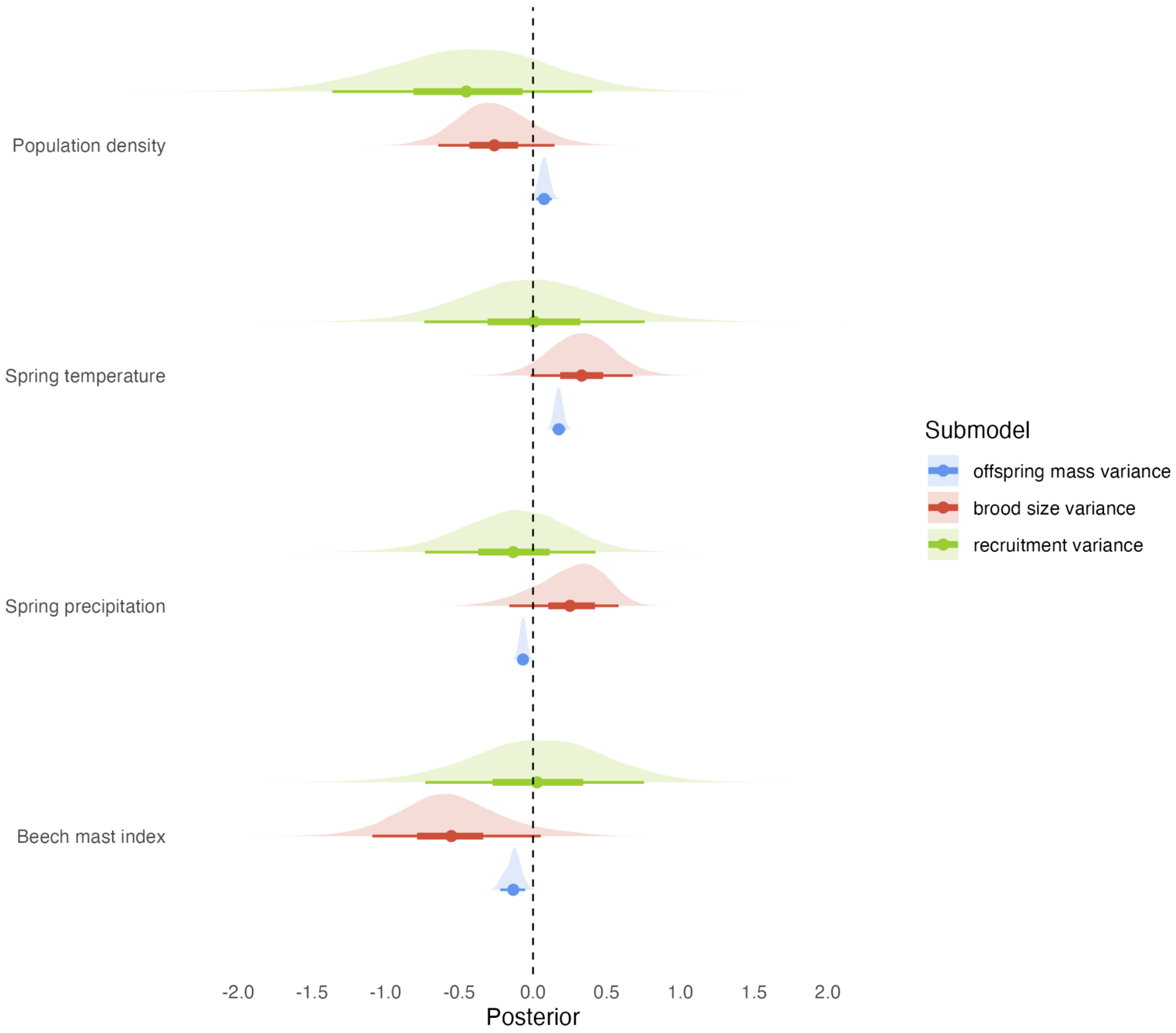

Figure S6: Estimated effects of standardized predictors on the among-mother variance in offspring mass (blue), observation-level variance in brood size (red), and observation-level variance in offspring recruitment (green).

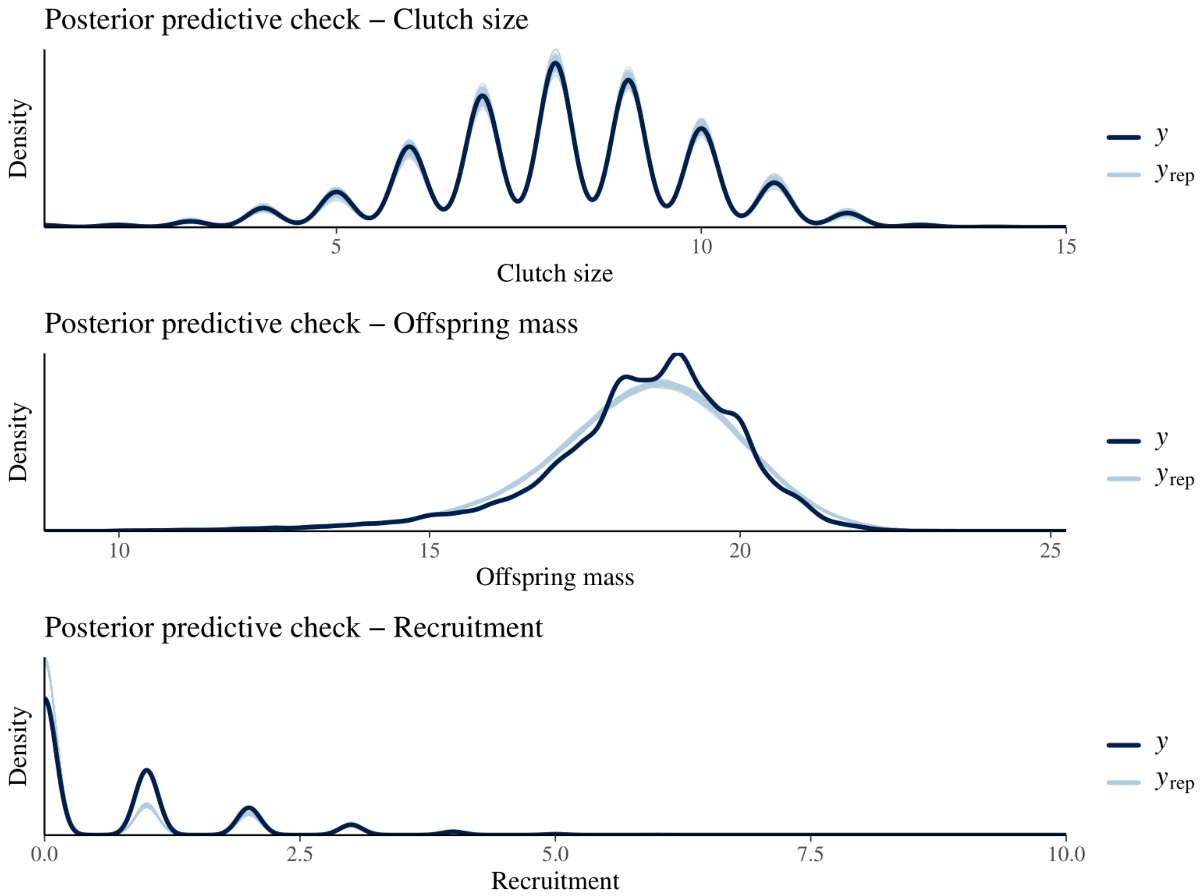

Figure S7: Posterior predictive checks showing the concordance between the distribution of the data (y) and the distribution of data generated under the statistical model (y_{rep}), for brood size (top panel), offspring mass (middle panel), and offspring recruitment (bottom panel). This highlights a decent fit of the models, but a small overestimation of zeros in recruitment.

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