Detecting context-dependence in the expression of demographic tradeoffs

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Abstract

Life history tradeoffs are one of the central tenets of evolutionary demography. Tradeoffs, depicting negative phenotypic or genetic covariances between individuals' demographic rates, arise from a finite amount of resources that each individual has to allocate in a zero-sum game between somatic and reproductive functions. While theory predicts that tradeoffs are ubiquitous, empirical studies have often failed to detect such negative covariances in wild populations. One way to improve the detection of tradeoffs is by accounting for the environmental context, as tradeoff expression may depend on environmental conditions. However, current methodologies usually search for fixed covariances between traits, thereby ignoring their context dependence. Here, we present a hierarchical multivariate 'covariance reaction norm' model, adapted to help detect context dependence in the expression of demographic tradeoffs. The method allows continuous variation in the phenotypic correlation between traits. We validate the model on simulated data for both intraindividual and intergenerational tradeoffs. We then apply it to empirical datasets of yellow-bellied marmots (*Marmota flaviventer*) and Soay sheep (*Ovis aries*) as a proof-of-concept showing that new insights can be gained by applying our methodology, such as detecting tradeoffs only in specific environments. We discuss its potential for application to many of the existing long-term demographic datasets and how it could improve our understanding of tradeoff expression in particular, and life-history theory in general.

Introduction

Demographic tradeoffs, which are characterized as negative covariances between fitness components such as somatic or reproductive traits, are central to life-history theory (Stearns, 1989), and are thought to drive much of the life-history diversity that exists (Bielby et al., 2007; Healy et al., 2019; Salguero-Gómez et al., 2016; Stearns, 1984). They originate from the basic fact that the total amount of resources or energy acquired by any one individual is limited, and has to be shared among several of the individual's fitness-related traits. In such a zero-sum game and in the absence of change in the total amount of resources acquired, any increase in the allocation of resources towards a specific fitness component will have to be at the expense of another fitness component. If tradeoffs did not exist, selection would maximize all fitness-related traits simultaneously and would lead to the impossible "darwinian demons" (Law, 1979). Therefore, demographic tradeoffs should be faced by all organisms and are, in theory, ubiquitous (Stearns, 1989, 1992; Williams, 1966). They can come in several forms (Stearns, 1989), being either intraindividual (traits involved relate to the fitness of the same individual) or intergenerational (traits involved relate to the fitness of a parent-offspring pair; e.g., offspring quantity-quality tradeoff). Despite their expected universality and being sought-after by evolutionary ecologists and biodemographers alike, life-history tradeoffs have been surprisingly hard to detect in wild populations (Metcalf, 2016), with successful probes too often confined to experimental approaches.

Several reasons could explain why tradeoffs are hard to detect in wild populations. First, while we often expect traits to covary in a simple bivariate manner by analyzing a single pair of demographic rates (note that demographic or vital rates, phenotypes, traits, fitness components can all be used interchangeably) at a time, tradeoff structures are often more complex. For instance, many more than two traits are likely to be involved in the resource allocation process (Cressler et al., 2017; de Jong, 1993; Pease & Bull, 1988), sometimes leading to complex hierarchical allocation trees, potentially resulting in some pairs of traits not covarying negatively (Gascoigne et al., 2022). Second, life-history traits can covary at different levels. While tradeoffs result from individuals' resource allocation processes, biodemographers often study tradeoffs as the temporal correlations among demographic rates at the population level (Compagnoni et al., 2016; Fay et al., 2020; Fay, Hamel, et al., 2022; van Tienderen, 1995). Tradeoffs can occasionally scale up to cause negative temporal covariances at the population level (van Tienderen, 1995), but in most cases these covariances are the results of environmental stochasticity and demographic reaction norms to shared ecological drivers (Fay, Hamel, et al., 2022; Knops et al., 2007; Paniw et al., 2020). Third, even though tradeoffs might be intrinsically present, individual heterogeneity can mask their presence among individuals. This specific ecological version of Simpson's paradox (Simpson, 1951) has been demonstrated by van Noordwijk and de Jong (1986): when the among-individual variance in resource acquisition is greater than the among-individual variance in resource allocation, the tradeoff is not expressed among individuals — even though it is theoretically present within individuals. In addition, expression of a tradeoff among individuals can also be influenced if the allocation and acquisition processes are not independent (Descamps et al., 2016; Fischer et al., 2009; Robinson & Beckerman, 2013). Altogether, this makes the detection of tradeoffs in wild populations difficult.

How much individuals vary in acquisition and allocation of resources determines if a tradeoff is detected among individuals (Metcalf, 2016; Reznick et al., 2000; van Noordwijk & de

Jong, 1986). Part of this variance might be fixed, stemming from genetic, developmental, or consistent behavioral differences that constrain how much resources are acquired and allocated to somatic vs. reproductive functions (Réale et al., 2007; Wilson & Nussey, 2010). The remaining variance is likely to be plastic (Spigler & Woodard, 2019), where investment in acquisition vs. allocation likely depends on the environmental context (Cohen et al., 2020; Sgrò & Hoffmann, 2004; Stearns et al., 1991). For instance, in several species, no tradeoffs were found among captive animals fed *ad libitum* (Kengeri et al., 2013; Landes et al., 2019; Ricklefs & Cadena, 2007). Similarly, controlled laboratory experiments on several species have shown that tradeoffs detection and strength were dependent on resource abundance (Gebhardt & Stearns, 1988; Messina & Fry, 2003; Messina & Slade, 1999; Spigler & Woodard, 2019). However, despite evidence that tradeoff expression depends on the environmental context, statistical methods to detect this context dependence in wild populations have, to date, rarely been applied.

Multivariate models are commonly employed to detect tradeoffs in wild populations (Cam et al. 2002, 2013; Hamel et al. 2018; Paterson et al. 2018; Fay et al. 2022a). In quantitative genetics, such models allow for the simultaneous analysis of multiple dependent variables like fecundity, growth, and survival (Kruuk et al. 2008; Wilson et al. 2010). These variables each have their own predictors, and the models estimate the correlated residual variances unaccounted for by the primary predictors. These models can be used to study residual correlations between traits at different levels, such as among-year or among-individual correlations. For example, after accounting for primary predictors, such models quantify whether years with high survival in a population are also years with high recruitment; or whether individuals with higher fecundity have lower or higher growth rates. However, these correlations among residual variances are estimated as fixed. Estimating fixed correlations might not necessarily be problematic in the case of experimental work, in which environmental conditions can be held constant within each treatment. However, wild populations are unlikely to experience fixed conditions, as the environmental context will vary in a continuous fashion, hence influencing the expression of tradeoffs. Therefore, there is a need to analyse and predict continuous variation of phenotypic correlations.

Here, we repurpose a hierarchical multivariate ‘covariance reaction norm’ (hereafter CRN) model recently developed by Martin (2023), which allows the incorporation of continuous predictors directly on the covariance matrix, for application to sampling designs typical in population ecology, enabling the study of the context-dependent expression of tradeoffs. As a proof-of-concept, we first validate this model on two simulated datasets, respectively focusing on an intergenerational tradeoff and an intraindividual tradeoff. We then apply our model on two empirical datasets of wild populations of yellow-bellied marmots *Marmota flaviventer* and Soay sheep *Ovis aries*. Prior studies have explored tradeoffs between demographic rates in both species (Kroeger et al., 2020; Tavecchia et al., 2005). For instance, in yellow-bellied marmots, a quality-quantity tradeoff in offspring has been observed for older mothers. In Soay sheep, the costs of reproduction have been particularly evident for breeding ewes in high-density populations or following harsh winters. However, the environmental context-dependence of these tradeoffs has yet to be studied explicitly. In the marmots, which inhabit high-altitude, highly seasonal environments, and the sheep, which face severe winter storms and fluctuating population densities, we hypothesize that tradeoffs are more likely to manifest under unfavorable ecological conditions (Cohen et al., 2020; Sgrò & Hoffmann, 2004).

Methods

The model

In this study, we employ a newly introduced CRN model (Martin, 2023), which has been initially developed to predict continuous changes in trait associations when genetic data or repeated individual measurements are available. A key assumption of multivariate models thus far has been that phenotypic correlations caused by demographic tradeoffs are fixed through time or space (Cam et al., 2002; Hamel et al., 2018). The CRN approach provides a solution to this general challenge, by allowing for phenotypic covariances to vary in response to variation in the environment. In the present study, we extend application of this general CRN approach to the detection of context-dependent demographic tradeoffs between life-history traits, with special consideration to sampling conditions typical of long-term field research in population ecology. Specifically, we examine the use of bivariate CRN models to test for the presence of tradeoffs when genetic data or repeated individual measurements are lacking in a given environmental context (e.g., during a specific sampling event such as a breeding season or a year). These are typical situations in field research that motivate further refinement of the quantitative genetic models proposed by Martin (2023).

Consider a CRN model investigating how environmental contexts **X** (an N x P matrix of *N* measurements of *P* predictors) affect the phenotypic means of β_μ and among-individual correlations β_r between two Gaussian life history trait measures $\mathbf{z_1}$ and $\mathbf{z_2}$ with repeated individual measurements in each environmental context. We begin by focusing on linear models to simplify notation and aid comprehension, with generalized models for non-Gaussian distributions discussed further below. Following Martin (2023) in the absence of genetic data, our bivariate phenotypic model is given by

$$\begin{aligned} \boldsymbol{z_1} &= \boldsymbol{X}\,\boldsymbol{\beta_{\mu 1}} + \boldsymbol{Y}\boldsymbol{\alpha_{1(X)}} + \boldsymbol{\epsilon_{1(X)}} \\ \boldsymbol{z_2} &= \boldsymbol{X}\,\boldsymbol{\beta_{\mu 2}} + \boldsymbol{Y}\boldsymbol{\alpha_{2(X)}} + \boldsymbol{\epsilon_{2(X)}} \end{aligned} \tag{1.1}$$

$$\left[\boldsymbol{\alpha_{1(X)}}, \boldsymbol{\alpha_{2(X)}}\right] \sim \boldsymbol{N}\left(\boldsymbol{0}, \boldsymbol{P}_{(\boldsymbol{X})}\right)$$
$$\left[\boldsymbol{\epsilon_1}, \boldsymbol{\epsilon_2}\right] \sim \boldsymbol{N}\left(\boldsymbol{0}, \boldsymbol{\Sigma}_{(\boldsymbol{X})}\right)$$

Trait values are expressed as a function of the average effects $\beta_{\mu\mathbf{1}}$ and $\beta_{\mu\mathbf{2}}$ of **X** on each phenotype, as well as among-individual effects $\alpha_{\mathbf{1}(\boldsymbol{X})}$ and $\alpha_{\mathbf{2}(\boldsymbol{X})}$ that are repeatable across measurements and within-individual effects $\epsilon_{1(X)}$ and $\epsilon_{\mathbf{2}(\boldsymbol{X})}$ that are stochastic across measurements. The model matrix **Y** (an N x J matrix for *J* subjects) structures the among-individual effects $\alpha_{(\boldsymbol{X})}$ across repeated measurements. (Co)variances between independent among- and within-individual effects are respectively described by **P** and **Σ** covariance matrices. To detect context-dependent tradeoff expression, we use environmental information in **X** to predict the among-individual trait covariance matrix $\mathbf{P}_{(X)}$.

$$\boldsymbol{P}_{(\boldsymbol{X})} = \begin{bmatrix} \sigma^2_{\alpha_1(X)} & r_{\alpha(X)}\,\sigma_{\alpha_1(X)}\sigma_{\alpha_2(X)} \\ r_{\alpha(X)}\,\sigma_{\alpha_2(X)}\sigma_{\alpha_1(X)} & \sigma^2_{\alpha_2(X)} \end{bmatrix} \tag{1.2}$$
$$\operatorname{atanh}\left(r_{\alpha(X)}\right) = \boldsymbol{X}\,\boldsymbol{\beta_r}$$

where the inverse hyperbolic tangent function atanh(r)=logit($[r+1]/2$)/2 is used as a link function to model additive environmental effects β_r on the logit scale while retaining the [-1,1] scaling of the correlation coefficient *r*. The same approach can be taken to describe changes in within-individual variation across environmental contexts.

$$\boldsymbol{\Sigma}_{(\boldsymbol{X})} = \begin{bmatrix} \sigma^2_{\epsilon_1(X)} & r_{\epsilon(X)}\, \sigma_{\epsilon_1(X)}\sigma_{\alpha_2(X)} \\ r_{\epsilon(X)}\, \sigma_{\epsilon_2(X)}\sigma_{\epsilon_1(X)} & \sigma^2_{\epsilon_2(X)} \end{bmatrix} \qquad (1.3)$$

$$\operatorname{atanh}\left(r_{\epsilon(X)}\right) = \boldsymbol{X}\, \boldsymbol{\beta}_{r_\epsilon}$$

Direct prediction of the transformed correlation coefficient is useful because we are principally interested in $r_{(X)}$ as an indicator of putative within- or among-individual tradeoffs, rather than the covariance $P_{1,2(X)} = r_{(X)}\sigma_1\sigma_2$ per se. Changes in the scale $\sigma_1\sigma_2$ of life history trait variation may occur independently of changes in positive or negative trait association among individuals, but these effects will be confounded together in the covariance $P_{1,2(X)}$. In contrast, the correlation coefficient $r_{(X)}$ is standardized relative to the scale of each phenotype, providing a more robust quantity for directly predicting and comparing estimates of life history tradeoffs across phenotypes and species. Our model also assumes that phenotypic variances can vary across environmental contexts, but no predictions are made on this variation. Greater plasticity is instead expected in the strength of tradeoff expression caused by fluctuating environmental factors (e.g., environmental harshness, resource availability, local predator density). See Martin (2023) for further details on relaxing these assumptions to model environmental effects on among- and within-individual variances.

Non-repeated measures

Estimating **Eq 1** with empirical data requires multiple measurements of the same subjects across time to effectively partition trait correlations due to sources of among- $\mathbf{P}_{(X)}$ and within-individual $\boldsymbol{\Sigma}$ phenotypic variation, relative to a given window of sampling. Repeated individual measurements are often inconsistent or unavailable in a given environmental context (e.g., a single fecundity measurement for individuals in a given year) in long-term field studies, which otherwise provide invaluable datasets for investigating context-specific tradeoffs in the wild. Fortunately, we can still take advantage of long-term environmental variation in such studies to detect variation in tradeoff expression without repeated measurements in a given environmental context. This requires simplifying the CRN model to predict observation-level phenotypic associations across environmental contexts.

$$\boldsymbol{z_1} = \boldsymbol{X}\,\boldsymbol{\beta_{\mu 1}} + \boldsymbol{o_{1(X)}} \tag{2}$$

$$\boldsymbol{z_2} = \boldsymbol{X}\,\boldsymbol{\beta_{\mu 2}} + \boldsymbol{o_{2(X)}}$$

$$\left[\boldsymbol{o_{1(X)}}, \boldsymbol{o_{2(X)}}\right] \sim \boldsymbol{N}\left(\boldsymbol{0}, \mathbf{P}_{\boldsymbol{o(X)}}\right)$$

$$\boldsymbol{P_{o(X)}} = \begin{bmatrix} \sigma^2_{o_1(X)} & r_{o(X)}\,\sigma_{o_1(X)}\sigma_{o_2(X)} \\ r_{o(X)}\,\sigma_{o_2(X)}\sigma_{o_1(X)} & \sigma^2_{o_2(X)} \end{bmatrix}$$

$$\operatorname{atanh}\left(r_{o(X)}\right) = \boldsymbol{X}\,\boldsymbol{\beta_r}$$

Here $o_{1(X)} = a_{1(X)} + \epsilon_{1(X)}$ and $o_{2(X)} = a_{2(X)} + \epsilon_{2(X)}$ are observation-level random effects aggregating variation due to among- and within-individual differences across measurements, within a given environmental context defined by **X** (e.g., a given year, position in space, level of resource abundance). Note that the **Y** matrix from **Eq 1** is no longer necessary in the absence of repeated measurements. As a consequence, we expect that the observation-level correlation $r_{o(X)}$ between these random effects to reflect the combined effect of the among- and within-individual correlations between life history traits, weighted by their geometric mean repeatability *R* (Dingemanse & Dochtermann, 2013; Searle, 1961).

$$r_{o(X)} = r_{\alpha(X)}\sqrt{\frac{\sigma^2_{\alpha 1}}{\sigma^2_{z1}}\frac{\sigma^2_{\alpha 2}}{\sigma^2_{z2}}} + r_{\epsilon(X)}\sqrt{\frac{\sigma^2_{\epsilon 1}}{\sigma^2_{z1}}\frac{\sigma^2_{\epsilon 2}}{\sigma^2_{z2}}} = r_{\alpha(X)}\sqrt{R_1 R_2} + r_{\epsilon(X)}\sqrt{(1-R_1)(1-R_2)} \tag{3}$$

Where phenotypic variances are adjusted for the mean effects of $X\beta_{\mu 1}$ and $X\beta_{\mu 2}$. We can see that inferences about among-individual tradeoffs from the non-repeated measures model (**Eq. 2**) will be at greatest risk of bias when sign(r_α)≠sign(r_ϵ) and $\sqrt{R_1 R_2} << \sqrt{(1-R_1)(1-R_2)}$. Figure 1 shows these general relationships across correlation and repeatability ranges, identifying regions of sign bias. Fortunately, researchers will generally be able to judge their risk of inferential bias based on *a priori* knowledge about the repeatability of life history traits, which tends to be medium to high (Dingemanse et al., 2021). For example, observation-level correlations of behavioral traits will tend to be dominated by within-individual associations (Bell et al., 2009; Cauchoix et al., 2018; Holtmann et al., 2017), while morphological associations will tend to be dominated by among-individual variation (Dingemanse et al., 2021). Note that our model considers no measurement errors, as we are not able to disentangle it from true within-individual variation using non-repeated measures. Such considerations regarding trait repeatability and measurement error should be explicit when interpreting results without repeated measures.

Hybrid scenarios

Variation in repeated sampling is also likely to occur across phenotypes due to factors such as difficulty of measurement and the rate of trait expression. While a single measure of age at first reproduction or fecundity in a given environmental context may be available per individual, multiple individual measures may be available for traits such as offspring quality. Such scenarios require a hybrid modeling approach. For example, consider a model for an intergenerational tradeoff between fecundity (e.g., clutch size) and offspring quality, but other traits could equally be studied. The model structure for offspring quality (depicted as offspring body mass), a gaussian trait, is given by

$$\boldsymbol{mass} = \boldsymbol{X\beta_{\mu 1}} + \boldsymbol{Y\alpha_{1(X)}} + \boldsymbol{\epsilon_{1(X)}} \tag{4.1}$$

The linear predictor for the mass of an offspring of a given mother in year X includes a year-specific mother random effect $a_{1(X)}$ and $\epsilon_{1(X)}$ being the within-brood/litter variance.

The model for fecundity follows the same basic structure, but using a Poisson distribution where we model the expected rate of offspring production using a log link function.

$$\log(\boldsymbol{fecundity}) = \boldsymbol{X\beta_{\mu 2}} + \boldsymbol{o_{2(X)}} \tag{4.2}$$

Without repeated measures, the random effect $o_{2(X)}$ is specified at the observation-level, accounting for any overdispersion in the Poisson process across measurements of each female.

The context-dependent tradeoff will be estimated between the among-mother random effect in offspring quality and the observation-level random effect in fecundity.

$$\left[\boldsymbol{\alpha_{1(X)}}, \boldsymbol{o_{2(X)}}\right] \sim \boldsymbol{N}\left(\mathbf{0}, \mathbf{P}_{(\boldsymbol{X})}\right) \tag{4.3}$$

$$\boldsymbol{P}_{(\boldsymbol{X})} = \begin{bmatrix} \sigma^2_{\alpha_{1(X)}} & r_{(X)}\, \sigma_{\alpha_1(X)}\sigma_{o_2(X)} \\ r_{(X)}\, \sigma_{\alpha_1(X)}\sigma_{o_2(X)} & \sigma^2_{o_2(X)} \end{bmatrix}$$

$$\operatorname{atanh}\left(r_{(X)}\right) = \boldsymbol{X\beta_r}$$

Reducing **Eq. 3**, the correlation r_X between the individual- $a_{1(X)}$ and observation-level $o_{2(X)}$ effects will necessarily be proportional to the among-individual correlation across life history traits.

$$r_{o(X)} = r_{\alpha(X)}\sqrt{\frac{\sigma^2_{\alpha 2}}{\sigma^2_{z2}}} = r_{\alpha(X)}\sqrt{R_2} \tag{5}$$

Note that this method does not allow the inclusion of non-continuous traits (e.g., Bernoulli traits) in the absence of repeated measurements within a given environmental context (e.g., a given year). In addition, another limitation is that this model does not partition context-invariant differences between individuals (fixed among-individual heterogeneity across environmental contexts) from context-dependent among-individual variation.

Validation on simulated datasets

We validated the CRN model on two different types of tradeoffs, an intergenerational tradeoff between offspring quantity and quality (hybrid CRN model), and an intraindividual tradeoff between fecundity and parental growth (non-repeated measures CRN model). See Martin (2023) for a more extensive simulation-based calibration of CRN models over a broad range of parameter values.

Intergenerational tradeoff (offspring quantity-quality)

We first focused on an intergenerational tradeoff between offspring quantity and quality (hybrid CRN model). This quantity-quality tradeoff has been the focus of numerous studies since Lack’s pioneering work on bird clutch sizes (Lack, 1947). We simulate 30 years of individual-based data in which 25 new individuals enter the population each year, reproduce with an average clutch/litter size of 2.5, and then have a probability to survive to next year of 0.6. This yielded a final simulated dataset of 750 individuals, totaling 1578 reproductive events and 4783 offspring. An observation-level correlation was included between offspring mass and clutch size, and this correlation was made dependent on a single climatic predictor. The same climatic predictor was also included to influence both mean clutch size and offspring mass.

Intraindividual tradeoff (fecundity-growth)

We then simulated data for an intraindividual tradeoff between fecundity and growth (non-repeated measures CRN model). This simulated dataset is also made of 30 years and 750 individuals, for a total of 1974 reproductive events, with a variable observation-level correlation between individual growth and fecundity, which is itself dependent on a single climatic predictor.

Study systems and application on empirical datasets

Marmots

We applied the hybrid CRN model (one trait with repeated individual measurements within a given year and one trait without) on data from a yellow-bellied marmot population monitored at the Rocky Mountain Biological Laboratory in Gothic, Colorado (38°57’N, 106°59’W) during the summer season each year, whereby extensive individual-based data is collected (Armitage, 2014; Blumstein, 2013). In Alpine marmots *Marmota marmota*, an offspring quality-quantity tradeoff has been found (Berger et al., 2015), while it remained mostly elusive in yellow-bellied marmots, being only found for older mothers (Kroeger et al., 2020), whereby within-cohort selection has likely reduced the amount of among-individual variance in resource acquisition, thus making the tradeoff visible (Kendall et al., 2011; van Noordwijk & de Jong, 1986). Therefore, we searched for an intergenerational tradeoff between mothers’ fecundity and offspring estimated mass (offspring quality-quantity tradeoff). We used repeated measurements of offspring mass for each mother (one mass estimate for each offspring in a given litter). The offspring weaning mass was imputed based on the date of emergence for each litter and mass measurements from captures later in the season, following the method of Ozgul et al. (2010). For the observation-level correlation sub-model, we included measures quantifying environmental conditions for the year.

First, the total amount of snow during the preceding winter, with years of little overwinter snow considered harsher for marmots as it offers limited thermal insulation during the hibernation (Barash, 1973; Cordes et al., 2020; Wells et al., 2022). Second, the average daily maximum temperature during the month of June, with warmer summer temperatures considered unfavorable conditions for marmots as they are prone to overheating, hence limiting the time that can be allocated to foraging (Cordes et al., 2020; Krajick, 2004; Melcher et al., 1990). Note that we used temperature in June and not July as commonly used in this system (Cordes et al., 2020), because this is more likely to represent the conditions experienced for most offspring before emergence and weaning. For the mass sub-model, we included as covariates the total amount of snow during the winter, June average maximum temperature, age of the mother, and mother's estimated mass in early June. We also included these parameters as covariates for the fecundity sub-model, except June average maximum temperature, since it cannot affect fecundity as pregnancies mostly occur before this period. We expected tradeoffs to be more strongly expressed among individuals in years with little overwinter snow or high summer temperature. In total, we used 2540 offspring mass from 597 reproductive events, from 279 females across 42 years.

Soay sheep

We applied the non-repeated measures CRN model on Soay sheep data, as we have no repeated individual measurement within a given year available for neither of the traits studied. We used data from an unmanaged population of feral sheep in the Village Bay area of the island of Hirta (57°48'N, 8°37'W), which has been monitored since 1985 (Clutton-Brock & Pemberton, 2004). In Soay sheep, survival costs of reproduction were found for breeding ewes, particularly in populations at high densities or following stormy winters (Tavecchia et al., 2005). Therefore, we searched for an intraindividual tradeoff between ewes' fecundity defined as the number of lambs born in Spring (ranging from 0 to 2) and their log mass in the following summer, with both traits conditional on ewes surviving the winter. Regarding the observation-level correlation sub-model, we included two covariates characterizing the ecological harshness faced by the sheep: population density and winter NAO (North Atlantic Oscillation), with high NAO values corresponding to wet and stormy winters (Coulson et al., 2001; Regan et al., 2022). For the ewe's fecundity sub-model, we included as covariates the individual's log mass preceding the reproductive event, age (linear term), and population density. For the sub-model on the log mass in the following summer, we included the same covariates, as well as winter NAO. We expected tradeoffs to be more strongly expressed in years of high population density or high NAO. In total, we used data from 2497 reproductive events across 37 years, for 861 ewes with known mass in the summer preceding the reproductive event, as well as known mass in the following summer.

Model implementation

We implemented all multivariate models described above in a Bayesian framework using the Stan statistical language (Carpenter et al., 2017), through the software R (R Core Team, 2021) using the R package *CmdStanR* (Gabry & Češnovar, 2020). Stan was preferred for model implementation because of its flexibility. Common regularizing priors were used for all model parameters: normal distributions of mean 0 and standard deviation of 1 for intercepts and slopes coefficients, and exponential distributions of rate 2 for variance parameters. Each model ran on 3 chains, with a burn-in period of 1000 iterations, sampling for 1000 iterations when analyzing simulated data, and 3000 iterations when analyzing empirical data, keeping all the sampled iterations (Link & Eaton, 2012). Convergence of parameter estimates was assessed visually and using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992). We report the full posterior distributions, alongside their mean, 50%, and 89% credible intervals (McElreath, 2020). The Stan code to implement all the CRN models presented in this study is archived on GitHub (https://github.com/lbiard/detecting_tradeoffs_crn_models) and Zenodo (will be added upon acceptance of the manuscript).

Results

The model validation performed on simulated datasets showed that parameters were correctly recovered for both intergenerational tradeoffs (Figure 2) and intraindividual tradeoffs (Figure 3). While these simulation examples do not quantify bias of estimations (more details from a simulation-based calibration of CRN models are available in Martin (2023)), they still confirm that the model presented in the methods is able to detect context-dependence in the expression of tradeoffs.

The model applied to yellow-bellied marmot data shows trends towards tradeoffs being more strongly expressed in years with harsh environmental conditions, albeit with high uncertainty in the estimates (Figure 4). We found a positive mean effect of the amount of overwinter snow on the correlation (Figure 4), meaning that the tradeoff between fecundity and offspring quality was more strongly expressed after winters with little snow. We also found a negative mean effect of the average maximum June temperature on the correlation (Figure 4), where females with more offspring were more likely to have lighter offspring during warmer summers.

Estimated effects of covariates on the correlation also had high uncertainty in the Soay sheep dataset (Figure 5). Overall, we found that the correlation tended to be negative across all environments, which means that ewe's growth was lower for the ones that weaned offspring (Figure 5). Contrary to our expectations, while we hypothesized that the tradeoffs should be more strongly expressed in wet and stormy winters (high NAO index), we found a positive effect of winter NAO on the correlation between fecundity and growth (Figure 5). We did not find any clear effect of population density on the expression of the tradeoff (Figure 5).

Discussion

Our proof-of-concept study demonstrates that the hierarchical multivariate CRN model (Martin, 2023) can be used successfully to detect and estimate context-dependent changes in tradeoff expression. In agreement with theoretical predictions, we found that reproductive tradeoffs in yellow-bellied marmots tend to be more strongly expressed under unfavorable climatic conditions, even though uncertainty of the estimation was large. In Soay sheep, our proxies of ecological harshness were not clearly linked with the expression of tradeoffs, and effect directions were even opposite to our initial prediction. This hierarchical model has the potential to be used on many long-term individual-based datasets and could help improve our understanding of tradeoff expression and life-history theory.

Although the initial motivation to use this method partly rested on the observed difficulty of finding tradeoffs in empirical datasets, we found that in both sheep and marmots, the tradeoffs tend to be expressed across all environments, with mean phenotypic correlations being negative regardless of the environmental conditions. Thus, ironically, in these two empirical datasets, tradeoffs would have been detected using simpler multivariate methods without the need for context dependence. However, this should not come as a surprise for Soay sheep, as this negative correlation between growth and fecundity was already found on a smaller dataset (Fung et al., 2022). Nonetheless, the results still highlight that context-dependence has the potential to hinder our ability to detect tradeoffs in some cases. For instance, when marmots experience favorable environmental conditions, the average correlation is closer to null with credibility intervals nearing or overlapping zero (Figure 4), while the intergenerational tradeoff is found to be more strongly expressed during harsh years. However, context dependence appears to be limited or absent for the expression of the tradeoff in Soay sheep. Since ewes' mass is measured in the following summer and not directly after parturition, harsh winter conditions are expected to increase overwinter mortality (Milner et al., 1999), lowering spring population density and reducing competition. This could potentially help surviving ewes to recover their body condition between spring and summer, which is the period of greatest grass growth, hence masking context dependence of the tradeoff. While this tradeoff might also just be invariant in regard to the ecological context, we speculate that the result could have arisen from two potential pitfalls due to idiosyncrasies of the Soay sheep data. First, among-individual variation in fecundity is limited in sheep, ranging from no offspring to twins, potentially making it more complicated for the model to estimate variances accurately (Fay, Authier, et al., 2022; Kain et al., 2015). Second, both ewes' growth and fecundity are conditional on survival in the data, hence individuals who suffered most from the cost of reproduction and did not survive are not present in the analysis, potentially biasing the results.

Despite the potential of this modeling approach to study context-dependent tradeoffs, a few methodological limitations are to be considered. A recent study conducted by Fay et al. (2022) highlighted that multivariate models with correlated random effects for Bernoulli traits performed rather poorly, resulting in a potentially large bias and imprecise estimates of variances and covariances. This is in part because Bernoulli traits contain less information than continuous variables, making estimations of variances complicated (Fay, Authier, et al., 2022), but also because the data needed to estimate individual heterogeneity is usually scarce (Browne et al., 2007). The model we present suffers from this limitation, and even more so when there is only a single individual observation per individual per sampling occasion (e.g., parental survival). This issue renders the model, as well as any other multilevel model, unable to meaningfully estimate distinct mean and variance parameters for Bernoulli traits, due to the fact that the mean p of a Bernoulli variable determines its variability $p(1-p)$ without scope for overdispersion. Therefore, environmental effects on the mean of Bernoulli measures will necessarily change their variances (Skrondal & Rabe-Hesketh, 2007). However, when repeated Bernoulli observations or a binomial measure are available within each sampling occasion (e.g., survival of each offspring within a litter), the CRN model can then be used to partition distinct environmental effects on trait means and (co)variances. As we have shown in the present study, despite this limitation, the CRN remains applicable to single measures of continuous traits and count measures (e.g., growth, fecundity, phenology, behavioral traits), as well as proportions and various other kinds of non-Gaussian measures. Another limitation of the proposed method is that sample sizes needed are likely to be large, with enough individuals in each environmental context, and importantly enough sampling occasions across which to estimate the context dependence of tradeoff expression. Nonetheless, many long-term individual-based studies should have enough data to fulfill these requirements (de Villemereuil et al., 2020).

Despite the abovementioned caveats and limitations of the methodology in the absence of repeated measurements, this new model is a development that could be useful for many datasets. Thanks to its implementation in a Bayesian framework using Stan (Carpenter et al., 2017), it offers great flexibility and can be easily repurposed and modified to fit the idiosyncrasies of a given dataset or species life history. It is also straightforward to extend the model by adding a pedigree for quantitative genetic analysis (see Martin, 2023), even though phenotypic correlations should suffice in most cases (Cheverud, 1988; Dochtermann, 2011; Roff, 1995). While we presented a bivariate model, this model is not necessarily limited to two traits, and more continuous traits and their covariances could also be analyzed simultaneously. We also restricted our proof-of-concept study to the reaction norm of the correlation between traits, but researchers interested in the canalization of traits variances as a response to the environmental context could also benefit from this modeling approach (Péron et al., 2016).

Life-history tradeoffs have long been sought after, but difficult to detect in empirical data due to individual heterogeneity (Metcalf, 2016; Reznick et al., 2000; van Noordwijk & de Jong, 1986). Previous studies have also highlighted that life-history tradeoffs could be expressed only under unfavorable ecological conditions (Cohen et al., 2020; Stearns, 1989). Yet, despite our knowledge of the issues hindering tradeoff detection, we still lacked a statistical framework that permits the detection of context-dependence in tradeoff expression. Our proof-of-concept study shows that this context dependence can be detected. This method has the potential to be applied by demographers and evolutionary ecologists having long-term individual-based datasets at hands, with many study systems having the required data (Culina et al., 2021; de Villemereuil et al., 2020). Altogether, this method has the potential to help us improve our understanding of life history theory, and in part resolve van Noordwijk and de Jong's (1986) conundrum of tradeoff detection, by accounting for the context-dependence of their expression.

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Authors contributions

LB, JSM, AO, MP, DZC conceived the study. JSM designed the initial modeling framework and LB analyzed the data. DTB, JGAM, JMP, DHN collected and curated the data. LB and JSM wrote the first draft with input from AO, MP, DZC. All authors contributed to the editing of the manuscript.

Data and code availability

The data, as well as the R and Stan code necessary to reproduce the results are available on GitHub (https://github.com/lbiard/detecting_tradeoffs_crn_models). They will be archived on Zenodo upon acceptance.

Figures

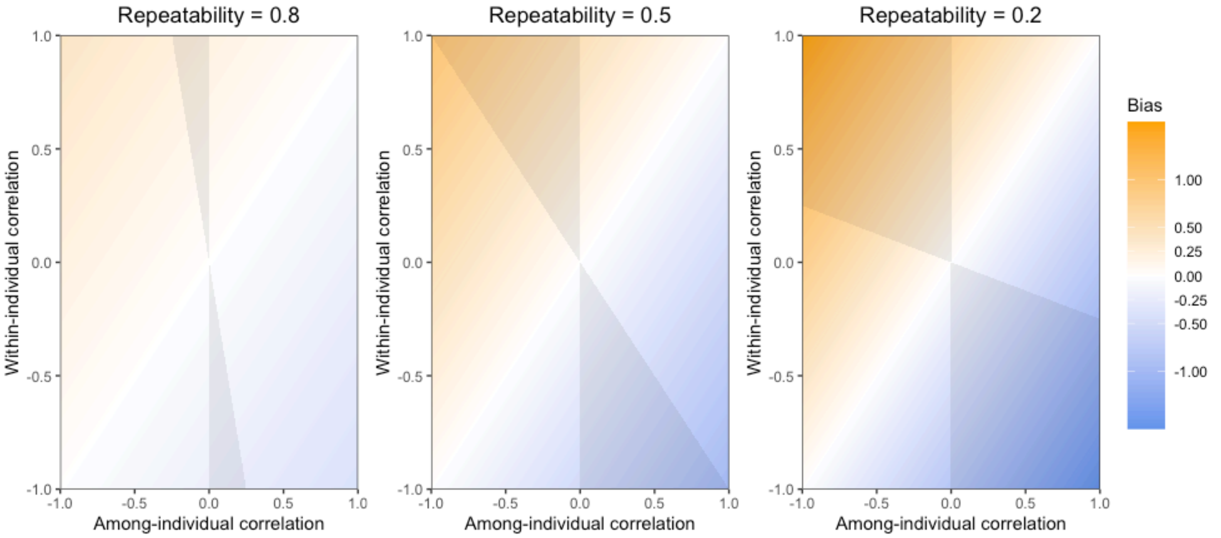

Figure 1: General relationships across correlations and repeatability ranges based on **Eq 3** for a non-repeated measures CRN (model of **Eq 2**), identifying the magnitude of correlation bias and the regions of sign bias. The bias is here defined as the difference between the observation-level correlation and the among-individual correlation, using the latter as a reference. Parameter spaces in gray represent the regions of sign bias, where the observation-level correlation has a sign opposite to the among-individual correlation. This highlights that the observation-level correlation is mostly influenced by the among-individual correlation for traits with high repeatability, while it is mostly influenced by the within-individual correlation for traits with low repeatability.

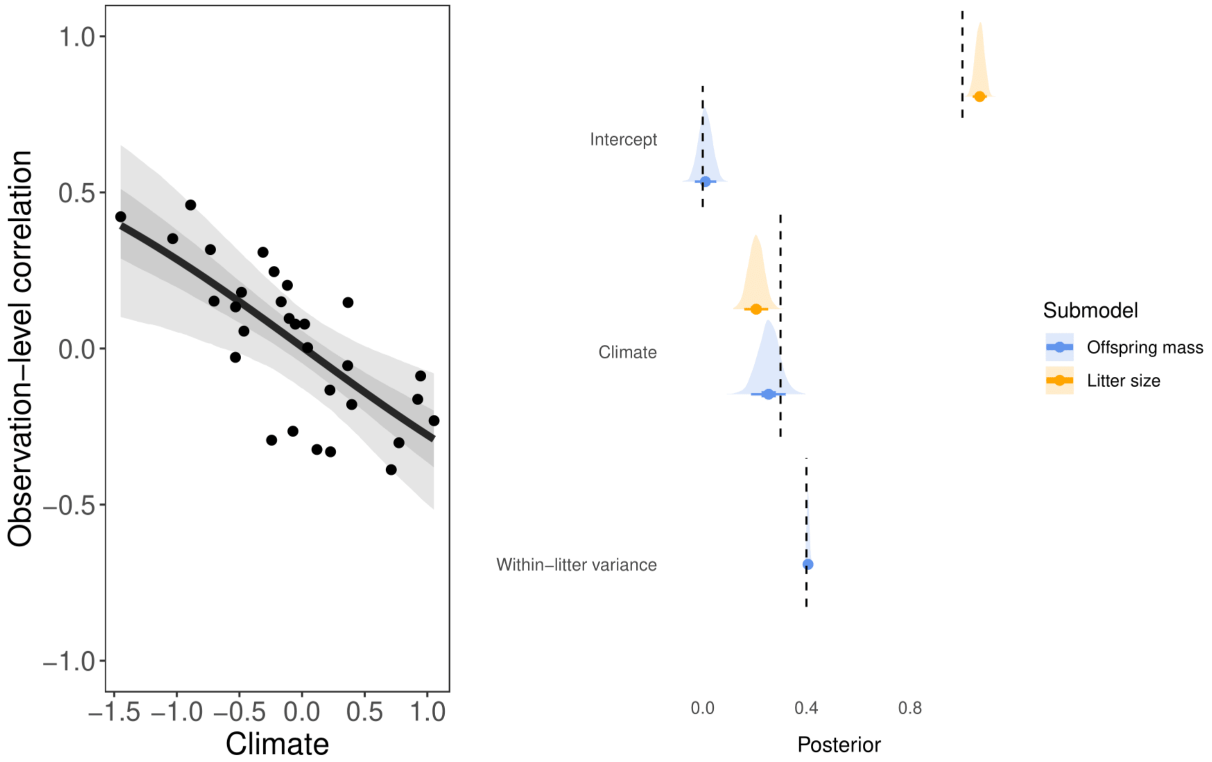

Figure 2: Left panel: estimated vs. simulated observation-level correlation between litter size and offspring mass as a function of climate, after accounting for the effect of climate on both traits. The regression line indicates the mean effect of climate on the correlation, while the shaded areas depict the 50% and 89% credible intervals predicted by the model. Each black dot represents the simulated observation-level correlation between both traits in a given year depending on climate. Right panel: estimated vs. simulated intercepts and slopes for the offspring mass and litter size sub-models. Dashed lines represent the value used to simulate the data, while the distributions and intervals represent the posterior distributions estimated by the model, alongside the mean, 50%, 89% credible intervals. Litter size estimates are presented on the log scale.

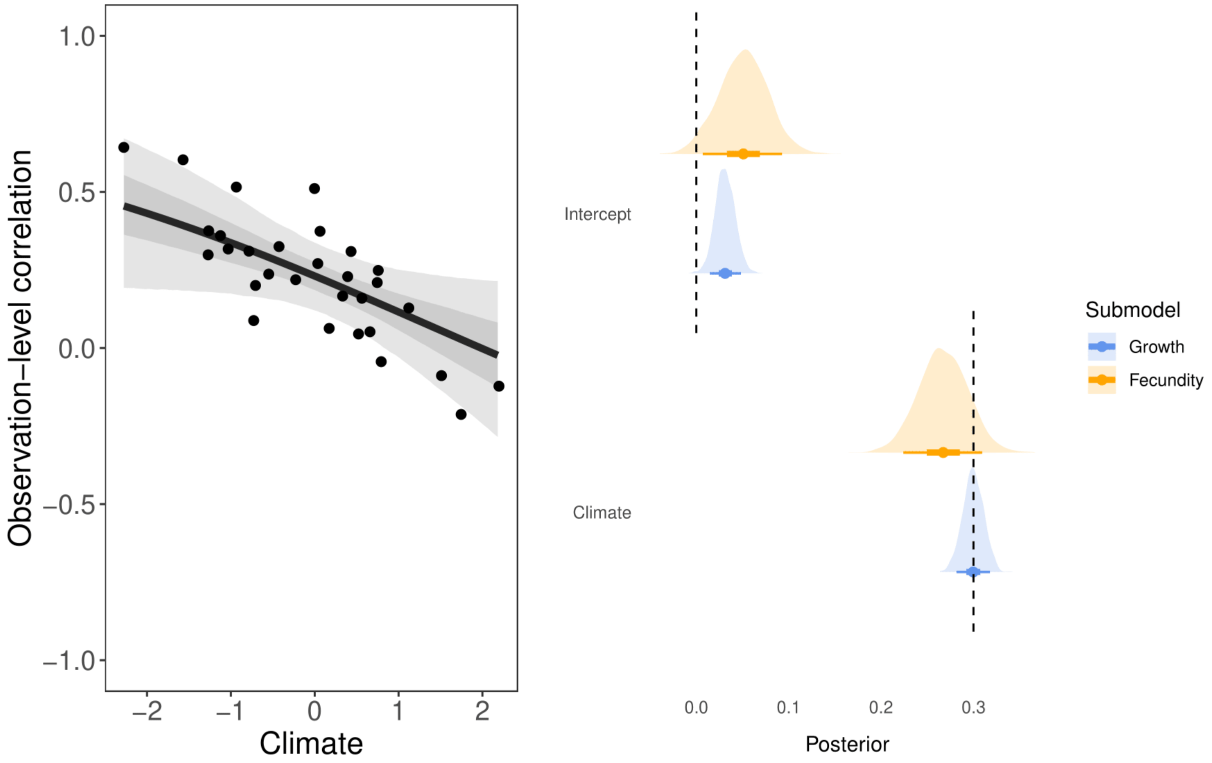

Figure 3: Left panel: estimated vs. simulated observation-level correlation between fecundity and growth as a function of climate, after accounting for the effect of climate on both traits. The regression line indicates the mean effect of climate on the correlation, while the shaded areas depict the 50% and 89% credible intervals predicted by the model. Each black dot represents the simulated observation-level correlation between both traits in a given year depending on climate. Right panel: estimated vs. simulated intercepts and slopes for the growth and fecundity sub-models. Dashed lines represent the value used to simulate the data, while the distributions and intervals represent the posterior distributions estimated by the model, alongside the mean, 50%, 89% credible intervals. Fecundity estimates are presented on the log scale.

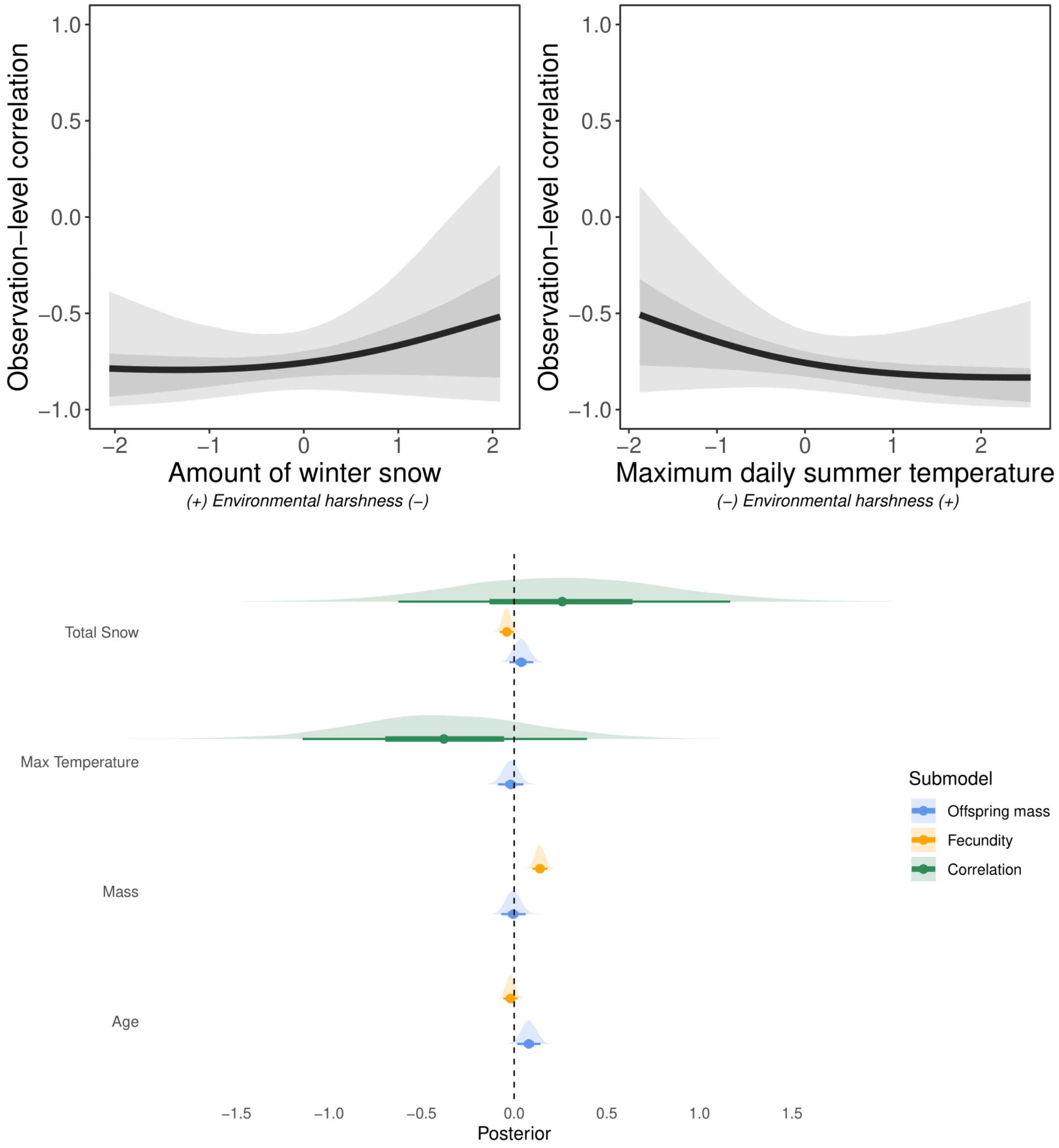

Figure 4: Observation-level correlation between litter size and offspring mass in marmots as a function of the total amount of snow in the preceding winter (top left panel) and the maximum daily June temperature of the year (top right panel). Estimated effects of standardized predictors (bottom panel) on offspring mass, fecundity, and the observation-level correlation between both traits in marmots. The regression line indicates the mean estimated effect, while the shaded areas depict the 50% and 89% credible intervals predicted by the model.

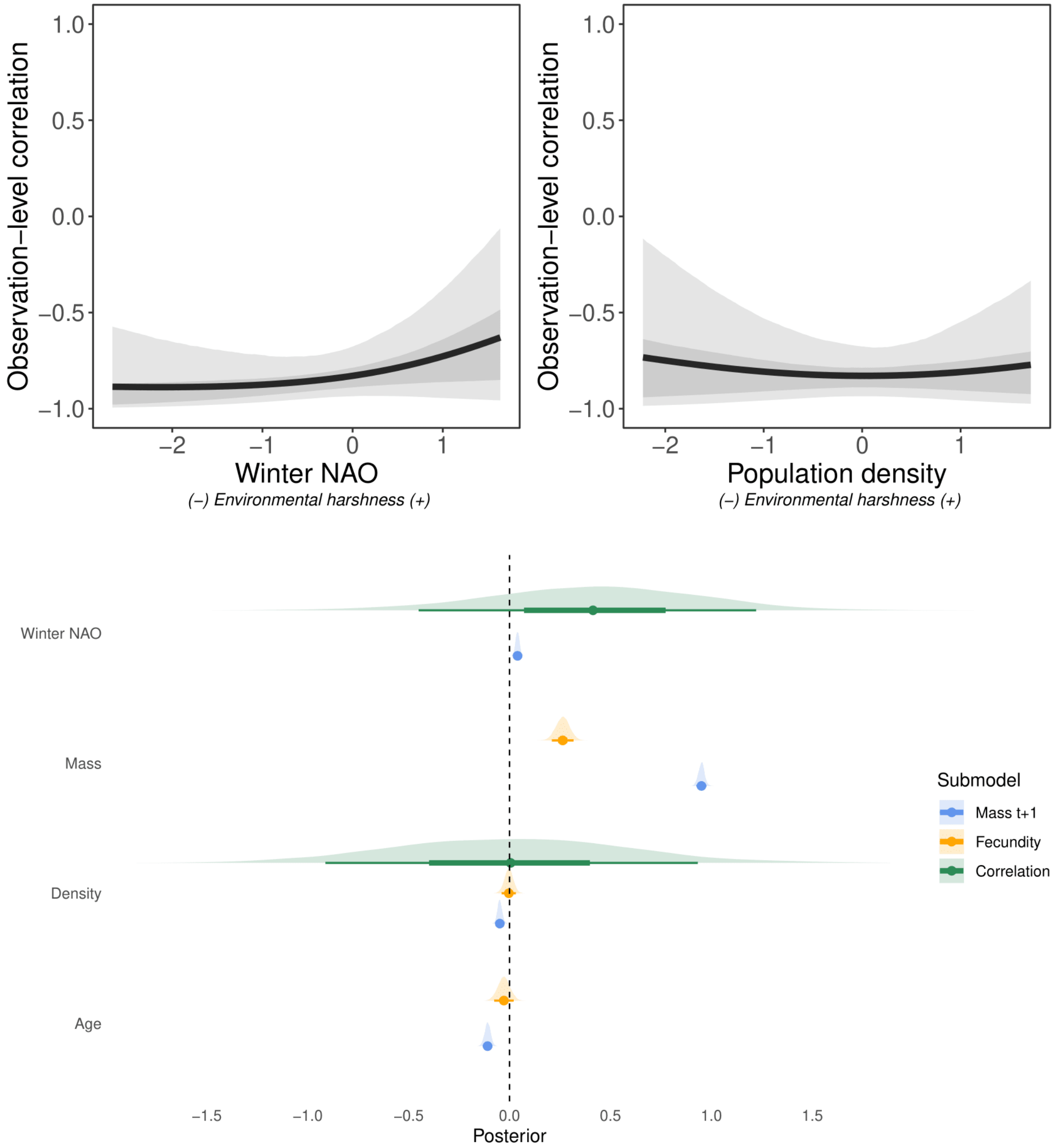

Figure 5: Observation-level correlation between fecundity and mothers' mass in the following year in Soay sheep as a function of the winter NAO (top left panel) and the population density (top right panel). Estimated effects (bottom panel) of standardized predictors on mother's mass in the following year, fecundity, and the observation-level correlation between both traits in Soay sheep. The figure displays the posterior distributions estimated by the model, alongside the mean, 50%, and 89% credible intervals.

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