Estimating Nonlinear Selection on Behavioral Reaction Norms

A Preprint

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March 18, 2021

Abstract

Individuals' behavioral strategies are often well described by reaction norms, which are functions predicting repeatable patterns of personality, plasticity, and predictability across an environmental gradient. Reaction norms can be readily estimated using mixed-effects models and play a key role in current theories of adaptive individual variation. Unfortunately, however, it remains challenging to assess the effects of reaction norms on fitness-relevant outcomes, due to the high degree of uncertainty in random effect estimates of reaction norm parameters, also known as best linear unbiased predictors (BLUPs). Current approaches to this problem do not provide a generalized solution for modelling reaction norm effects with nonlinear structure, such as stabilizing, disruptive, balancing, and/or correlational selection, which are necessary for testing adaptive theory of individual variation. To address this issue, I present a novel solution for straightforward and unbiased estimation of linear and nonlinear reaction norm effects on fitness, applicable to both Gaussian and non-Gaussian measurements. This solution involves specifying BLUPs as random effects on behavior and fixed effects on fitness within a Bayesian multi-response model. By simultaneously accounting for uncertainty in reaction norm parameters and their causal effects on other measures, the risks accompanying classical approaches to BLUPs can be effectively avoided. I also introduce a new method for visualizing the consequences of multivariate selection on reaction norms. Simulations are then used to validate that the proposed models provide unbiased estimates across realistic parameter values, and an extensive coding tutorial is provided to aid researchers in applying this method to their own datasets in R.

Keywords mixed-effects · multivariate · Bayesian · reaction norm · adaptation · individuality

1 Introduction

A population will evolve by natural selection whenever heritable variation occurs in fitness-relevant phenotypes (Darwin 1859). Individual differences in behavior are, therefore, a fundamental ingredient for adaptive behavioral evolution. Across taxa, repeatable individual variation is observed not only in animals' average behavior (Bell, Hankison, and Laskowski 2009), but also in the degree of behavioral responsiveness they exhibit toward the environment (Dingemanse et al. 2010; Stamps 2016), as well as in the intra-individual variability of their behavior across time (Biro and Adriaenssens 2013; Westneat, Wright, and Dingemanse 2015). These respective patterns of personality, plasticity, and predictability represent distinct but often integrated components of the behavioral reaction norms (RNs) within a population (see **Figure 1**), which are functions expressing individual-specific behavioral strategies across an environmental gradient (Dingemanse et al. 2010; McNamara and Leimar 2020). The evolution of such function-valued traits is currently a central area of research within evolutionary ecology (Gomulkiewicz et al. 2018), which has led to a host of methodological innovations for estimating the RNs of complex traits subject to measurement error (Dingemanse and Dochtermann 2013; Martin and Jaeggi 2021), as well as the development of a rich theoretical framework for explaining the adaptive processes maintaining individual variation in RNs within populations (Dall and Griffith 2014; Sih et al. 2015; Wolf and Weissing 2010). Attention to RNs has also increased in related fields of inquiry such as personality psychology (Nettle and Penke 2010) and evolutionary anthropology (Jaeggi et al. 2016), suggesting that an integrative framework for studying the evolution of RNs will benefit research on individuality more generally.

For labile phenotypes such as behavior, hormones, and cognition, the magnitude of repeatable between-individual variation in measurements is generally modest in comparison to the total phenotypic variation observed across space and time (Bell, Hankison, and Laskowski 2009; Cauchoix et al. 2018; Fanson and Biro 2015). This is unsurprising, given that these traits are often the primary mechanisms by which organisms can flexibly respond to ephemeral and stochastic variation in their local environments, such as by up-regulating circulating testosterone in response to social challenges (Eisenegger, Haushofer, and Fehr 2011), or by temporarily inducing a fear state in response to odor cues of predation (Mathuru et al. 2012). As such, single measurements of these phenotypes are poor indicators of the underlying between-individual differences that are targeted by selection, and tend to instead reflect various sources of within-individual environmental heterogeneity (Brommer 2013; Dingemanse and Dochtermann 2013). Despite the unfortunate fact that many empirical studies still confound these distinct sources of trait (co)variation (Niemelä and Dingemase 2018; Royauté et al. 2018), the necessity of longitudinal data for studying RNs is increasingly appreciated and enforced within behavioral ecology (Dingemanse and Wright 2020). With the appropriate application of generalized mixed-effect models (GLMMs), such repeated measures data can then be used to estimate the unobserved but statistically identifiable RNs underlying raw trait measurements, thus effectively partitioning stochastic effects and measurement error from repeatable sources of between-individual variation (Dingemanse and Dochtermann 2013; Martin and Jaeggi 2021; Nakagawa and Schielzeth 2010; Nussey, Wilson, and Brommer 2007).

GLMMs are a powerful tool not only for estimating RNs from empirical data using random effects, but also for subsequently modeling the fixed effects of personality, plasticity, and predictability on fitness and other biological outcomes of interest. Nevertheless, although GLMMs provide a quite robust modeling framework (Schielzeth et al. 2020), they can only give as much information about RNs and their effects as the model assumptions and empirical data provided to them. For labile phenotypes like behavior, this means that the predicted random effect values of RN parameters, also known as best linear unbiased predictors (BLUPs), are often inferred with non-trivial degrees of statistical uncertainty. The use of BLUP point estimates to predict outcomes in another response model will, therefore, artificially reduce uncertainty in the estimated effects of RNs and increase the risk of false positives (see Hadfield et al. 2010 for a detailed treatment). Previous solutions to this problem have provided effective antidotes to the anti-conservative inference encouraged by ignoring uncertainty in BLUPs (Houslay and Wilson 2017). However, these solutions also reduce empiricists' capacity to effectively model the nonlinear effects of RNs on fitness-relevant outcomes, which is necessary for understanding the degree to which natural selection is actively maintaining or diminishing individual variation in behavior. The present study therefore introduces a new method to facilitate unbiased estimation of nonlinear RN effects within a Bayesian GLMM framework. The proposed solution is first motivated through a brief discussion of current approaches to the misuse of BLUPs and their benefits and limitations. I then formally introduce the proposed method along with a novel approach to visualizing the effects of multivariate selection on reaction norms. I also provide R code (R Core Team 2020) and tutorials on the accompanying Github repository for this manuscript (https://github.com/Jordan-Scott-Martin/Selection-on-RNs), demonstrating how to estimate these models with the Stan statistical programming language (Carpenter et al. 2017). These tutorials will aid researchers in investigating nonlinear RN effects with their own datasets.

2 Current approaches

The basic challenge of modelling RN effects is to effectively account for the uncertainty in RN parameters (i.e. BLUPs) across all stages of analysis. Variation in phenotypes with low to moderate repeatability is, by definition, largely explained by factors other than between-individual differences. As a consequence, sampling designs with modest repeated measurements and uncontrolled environmental variation typically result in highly uncertain estimation of RNs. Failure to account for the uncertainty of RNs across subsequent stages of analysis artificially reduces uncertainty in the inferred effects of RNs, as uncertainty in individuals' trait values necessarily translates into uncertainty about the effects of these trait values, and can thus undesirably increase the risk of false positives. For this reason, Hadfield et al. (2010) discouraged all future use of

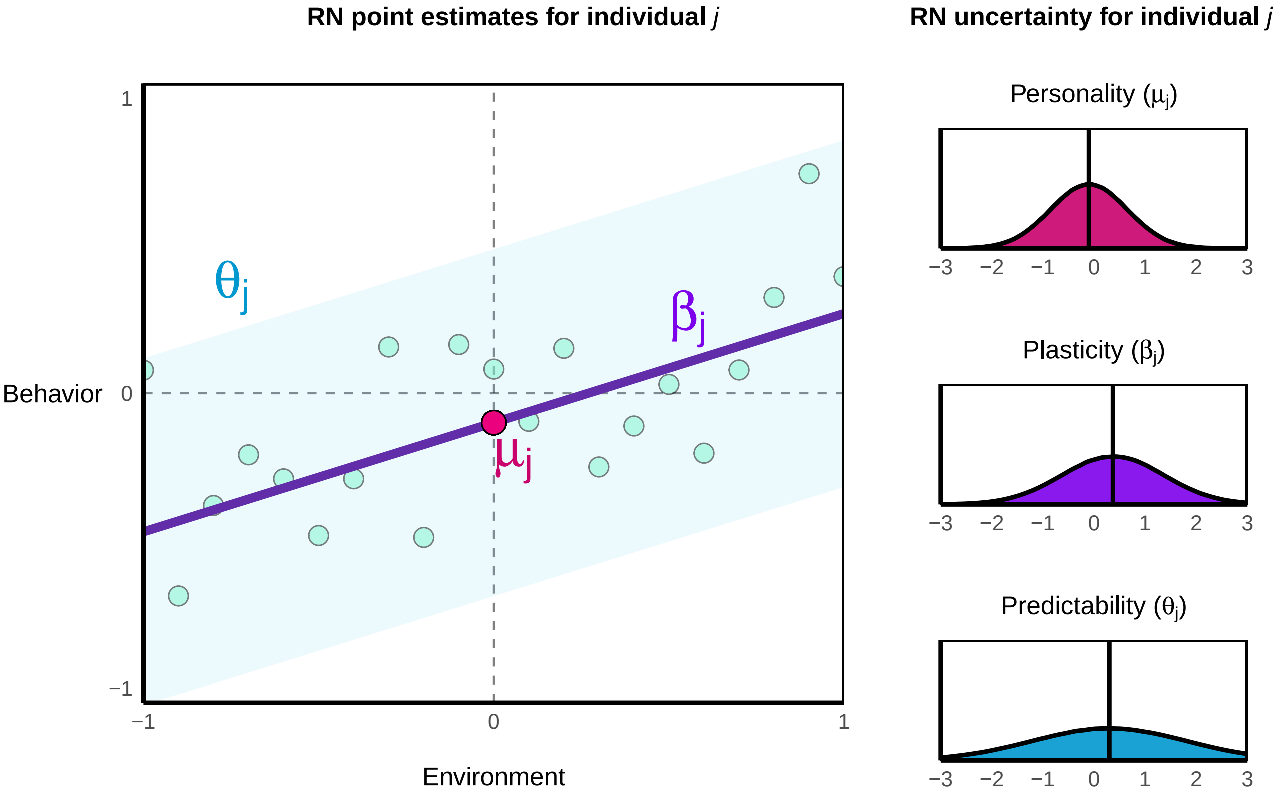


Figure 1: A behavioral reaction norm (RN) for individual j defined across an environmental gradient. The individual's reaction norm is defined by three parameters indicated in the left plot: (i) the RN intercept trait value μ_j describing behavioral consistency (i.e. personality) across environments; (ii) the RN slope trait value β_j capturing behavioral plasticity across environments; and (iii) the RN dispersion trait value θ_j reflecting behavioral predictability across environments, as indicated by the 95% shaded credible interval (i.e. $\pm 1.96 * \theta_j$). Individuals' true RN parameters will be unknown in empirical research and must be inferred from raw longitudinal measurements (teal circles) across the environmental gradient. These inferences will generally be subject to high degrees of statistical uncertainty, as captured by the posterior distributions of each RN parameter shown on the right. RN point estimates (BLUPs) taken from these posterior distributions, such as the mean values indicated by the black vertical lines, ignore this uncertainty and provide misleading confidence in the shape of an individuals' behavioral strategy. For example, it can be seen that there is a wide range of possible values for individual j's parameters with similar degrees of posterior support, particularly for the highly uncertain predictability trait value. As has been previously emphasized in the literature, failure to account for this uncertainty around point estimates can lead to anti-conservative inference and an increased risk of false positives. See the main text for further discussion.

BLUP point estimates in evolutionary ecology, so as to prevent the proliferation of misleading findings in the literature. Nevertheless, because the theoretical significance of RNs is not diminished by the difficulty of appropriately modeling their effects, many behavioral ecologists without clear alternative solutions continued to misuse point estimates of BLUPs in their research. In response, Houslay and Wilson (2017) provided a detailed overview of appropriate strategies for tackling this challenge, emphasizing that multivariate GLMMs with covarying random effects can be used to effectively account for uncertainty in RNs across multiple response models. Despite these repeated cautionary notes, some researchers still continue to utilize BLUP point estimates (e.g. Dingemanse et al. 2020) or raw data (e.g. Brehm et al. 2019) for testing RN effects, even while acknowledging the work of Hadfield et al. (2010) and Houslay and Wilson (2017). This likely reflects the fact that the random effects models proposed by Houslay and Wilson (2017) do not readily extend to a variety of more complex RN effects that cannot be straightforwardly derived from random effect covariances and correlations. This section briefly reviews current solutions for the misuse of BLUPs and discusses their benefits and limitations.

2.1 Multivariate GLMMs with covarying random effects

Popular GLMM software such as the “lme4” R package (Bates et al. 2014) do not readily address multivariate, integrated phenotypes. As a consequence, researchers are often motivated to (i) estimate RNs from a univariate response model of a relevant behavior, and (ii) subsequently enter BLUP point estimates of these RNs as covariates in another response model. Fortunately, the risk engendered by this approach can be readily overcome by specifying a multivariate GLMM that simultaneously accounts for uncertainty in behavioral BLUPs and their associations with other responses. Houslay and Wilson (2017) demonstrate how this can be accomplished with random effect correlations or covariances for phenotypic and quantitative genetic studies, using both frequentist and Bayesian software.

The multivariate GLMMs proposed by Houslay and Wilson (2017) are an extremely valuable tool for behavioral ecologists interested in RNs and integrated phenotypes. These models provide desirable flexibility for addressing a variety of questions beyond simply quantifying random effect variances and covariances, although this is on its own quite an important task. As any student of multivariate statistics is well aware, trait covariance matrices can be readily transformed to provide a veritable treasure chest of biological insights (Blows 2007), such as identifying trajectories of phenotypic conservation and divergence among closely related populations (Royauté, Hedrick, and Dochtermann 2020), discovering latent behavioral characters and networks causing covariance among multiple traits (Araya-Ajoy and Dingemanse 2014; Martin et al. 2019), and calculating linear selection differentials and genetic responses to selection (Stinchcombe, Simonsen, and Blows 2014). Thus, this method can be used to accomplish many empirical goals with relative ease.

Nevertheless, there are important cases where further information is desired that cannot be derived from random effect covariation alone, limiting the utility of these models for explaining the effects of RNs on evolutionarily relevant outcomes. This is why fixed effects remain important for testing evolutionary ecological theory, because we often want to directly parameterize specific functional relationships between traits, as well as to specify the direction of these effects. In other words, we often want to know whether a behavior affects another measure in a specific, potentially nonlinear manner, and perhaps in interaction with other traits or states, rather than merely asking whether the trait and the outcome are linearly associated through any number of possible causal pathways in either direction. This issue is not specific to the models proposed by Houslay and Wilson (2017), but is rather a limitation of variance-partitioning models more generally, which tend to trade off explanatory power and causal insight for accurate description and *in situ* prediction (Briley et al. 2019; Hadfield and Thomson 2017; Okasha and Otsuka 2020).

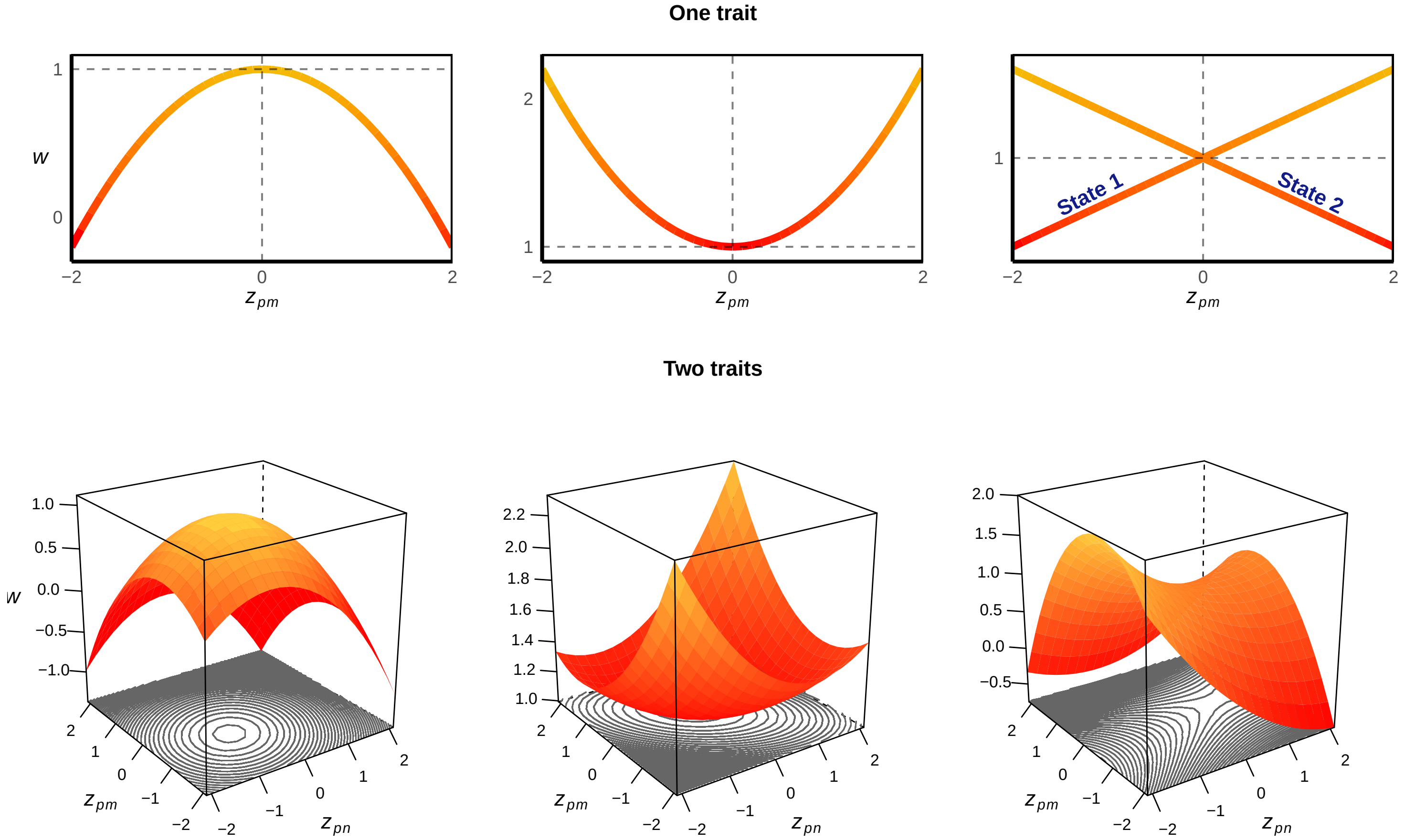
A particular concern is that testing adaptive theory of individual variation often requires evaluating nonlinear selection on behavioral RNs (**Figure 2**). In general, these nonlinear effects cannot be accurately estimated by random effect covariances, as covariance is by definition a measure of linear dependency and thus does not capture nonlinear dependencies among measures. However, it is straightforward to capture these patterns using fixed quadratic and interaction effects in a parametric fitness model (Lande and Arnold 1983). For example, if the population RN is at an evolutionary equilibrium, so that RN variation is non-adaptive within the population and results from processes such as mutation-selection balance or developmental noise (e.g. Bierbach, Laskowski, and Wolf 2017; Tooby and Cosmides 1990), then we should expect to find evidence of stabilizing selection around the population average RN parameters. In the absence of correlational selection, this would be observed in a Lande-Arnold selection analysis as null or weak linear effects and negative quadratic effects (Stinchcombe et al. 2008), assuming the population had not been recently displaced from a fitness peak by non-adaptive processes. Alternatively, strong disruptive selection, potentially indicative of ongoing behaviorally-mediated speciation (Wolf and Weissing 2012), would be expected to surface as the opposite pattern–null or weak linear effects with positive quadratic effects.

When individual variation is adaptive and maintained through balancing selection caused by spatially and/or temporally varying fitness effects (e.g. Gurven et al. 2014; Le Cœur et al. 2015), interaction effects will be expected between local ecological conditions (e.g. season, population density, resource abundance) and individuals' RN parameters (Wright et al. 2019). Similar considerations apply to social contexts addressed by evolutionary game theory, in which frequency-dependent fitness functions, such as cooperative strategies with diminishing returns or threshold effects as a function of partners' strategies (McNamara and Leimar 2020), will be observed through interactive selection effects (Araya-Ajoy, Westneat, and Wright 2020; Martin and Jaeggi 2021; Queller 2011). When adaptive individual variation is maintained through state-dependent calibration or feedback processes (e.g. von Rueden, Lukaszewski, and Gurven 2015; Sih et al. 2015), then phenotypes should also interact with state variables to determine fitness outcomes. Adaptive behavioral syndromes may further evolve through correlational selection for specific RN parameter combinations. Cichlid *Pelvicachromis pulcher* females' mating preferences, for example, select for males with high levels of both personality and predictability in aggressiveness (Scherer, Kuhnhardt, and Schuett 2018). When RNs are under such correlational selection, interaction effects are expected between RN parameters on fitness (Blows 2003). Of course, these considerations also apply to a host of RN effects on outcomes other than fitness, such as the exponential effects of personality in activity level and anxiety on seed removal and dispersal among small mammals (Brehm et al. 2019). In all such cases, one would not detect these theoretically pertinent relationships using linear covariances among random effects, but must instead directly specify fixed quadratic and interactive effects caused by behavioral RNs. A variety of more complex fitness surfaces can also be captured through the combination of these quadratic and interaction effects (Phillips and Arnold 1989), or higher term polynomials, as shown in **Figure 2** for a bivariate analysis.

A potential solution to this challenge is to model the squared and product values of raw measurements as additional responses with covarying random effects, which can subsequently be used to calculate nonlinear selection gradients (Dingemanse, Araya-Ajoy, and Westneat 2021). However, this approach does not differentiate between the fitness effects of personality, plasticity, and predictability, and it does not appropriately partition between- and within-individual (co)variation in non-Gaussian measurements. To calculate nonlinear selection gradients for non-Gaussian responses, expected trait values should be first estimated on a latent linear scale, through the use of an appropriate GLMM link function, before being squared or multiplied together. This ensures that nonlinear mean and variance effects are correctly predicted on the original data scale (Nelder and Wedderburn 1972).

2.2 Two-stage analyses

Another solution to the challenges posed by the random effects method is to instead (i) estimate BLUP posteriors in a Bayesian random effects model, and then (ii) estimate a separate model with fixed RN effects, running the analysis repeatedly over the posterior distribution of BLUPs estimated in the first model. While this approach technically carries the uncertainty in RNs forward, thus avoiding the undesirable consequences of point estimates, it can nevertheless result in downwardly biased estimates of the RN fixed effects, as Dingemanse et al. (2020) observed in supplementary simulations. Although these authors did not provide an explanation for the observed bias, it can be attributed to a more general statistical phenomenon known as attenuation bias, in which independent measurement error in a predictor variable causes downward bias in its association with an outcome measure (Adolph and Hardin 2007; Spearman 1904). This is caused by the BLUPs in the initial model being estimated independently of the RN effects on the outcome of interest, so that the estimated uncertainty in BLUPs is by design statistically independent of uncertainty in the RN effects estimated in the second stage of the analysis. This does not, however, make the use of BLUP point estimates any less risky or more desirable, but is simply an artifact of not simultaneously accounting for both sources of uncertainty in the same model. It is important to remember that BLUPs and RNs are latent, statistical inferences, not directly measured trait values or mere averages of raw trait values, and as such are particularly sensitive to correct model specification (Hadfield et al. 2010; Postma 2006). A related alternative solution is to handle attenuation bias by adjusting selection coefficients on raw trait values with repeatability estimates, rather than directly using BLUPs in the fitness model (Dingemanse, Araya-Ajoy, and Westneat 2021). However, this approach does not provide a means of differentiating nonlinear selection on personality, plasticity and predictability, nor does it generalize to non-Gaussian measurements where repeatability is best expressed on a transformed linear scale due to non-linear mean and variance effects on the original scale.



One trait

Two traits

Figure 2: Nonlinear selection surfaces for behavioral RNs. Adaptiveness is indicated by the color of the line or surface, with red indicating lower relative fitness (w) and gold indicating higher relative fitness.

Top row. Patterns of nonlinear selection on a single behavioral RN parameter z_{pm}, which also apply to selection on multiple traits in the absence of correlational selection between traits. Dashed lines intercept the expected population-level trait value and relative fitness at ($z_{\text{pm}} = 0, w = 1$). *Left panel*: stabilizing selection on trait values, which maintains the population average trait value at an evolutionary equilibrium and reduces individual variation. *Middle panel*: disruptive selection, which increases the frequency of extreme trait values and increases individual variation as a consequence. *Right panel*: balancing selection, in which the fitness consequences of a trait value vary across different states, causing the maintenance of individual variation across multiple selection events. States refer to any factors that modulate the fitness consequences of a behavior, such as differing spatial and/or temporal contexts, population densities, or frequencies of social partner strategies. States may also be endogenous factors that determine whether it is adaptive to express a particular RN trait value, such as the effects of body size and condition on the fitness consequences of boldness and aggression.

Bottom row. Patterns of nonlinear selection on two behavioral RN parameters z_{pm} and z_{pn}. Due to the presence of correlational selection, the adaptiveness of any trait value for parameter m is contingent on the trait value for parameter n (and vice versa). *Left panel*: a dome-shaped selection surface, where a combination of slightly negative parameters has the highest fitness. *Middle panel*: a bowl-shaped selection surface, with the most adaptive phenotypes combining extremely high or low trait values in both parameters. *Right panel*: a saddle-shaped selection surface, where phenotypes combining moderate trait values for m and extremely low trait values for n achieve the highest relative fitness.

3 A novel solution

Given the limitations of relying solely on covarying random effects, behavioral ecologists stand to benefit from adding an additional modeling approach to their toolkit, one capable of directly estimating nonlinear RN effects of arbitrary complexity. Here I propose a novel solution that is a straightforward extension of Houslay and Wilson (2017) 's previous work: Bayesian multi-response GLMMs in which individuals' RNs are simultaneously treated as random effects on their observed behaviors as well as fixed effects on outcome measures of interest (e.g. survival and reproduction, habitat choice, performance in an experimental task, etc.). In this section, this basic modelling approach is formally introduced, along with various extensions of interest for specific empirical scenarios. I also end by proposing a novel and straightforward method for visualizing the within-generation effects of multivariate selection on reaction norms.

3.1 Multivariate GLMMs for nonlinear selection on RNs

Our goal in overcoming the limitations of previous approaches is to specify a GLMM with one response model estimating RN parameters of a relevant behavior, as well as another response model that estimates the effects of these RN parameters on a fitness-relevant measure. To enhance comprehension, the RN response model is first considered in isolation before being integrated into a single multi-response model below.

3.1.1 Reaction norm response model

To model the RN parameters $\boldsymbol{z}_{\mathbf{p}}$ for a repeatedly measured behavior $\boldsymbol{z}$ across an environmental gradient $\boldsymbol{x}$, we specify a GLMM for observation i of individual j such that

$$\begin{aligned} z_{ij} &\sim f\left(\eta_{ij}, \theta_{ij}\right) \\ g_{\eta}\left(\eta_{ij}\right) &= \mu_0 + \mu_j + \left(\beta_1 + \beta_j\right) x_{ij} \\ g_{\theta}\left(\theta_{ij}\right) &= \theta_0 + \theta_j \\ \boldsymbol{z}_{\mathbf{p}} = \left[\boldsymbol{\mu} \quad \boldsymbol{\beta} \quad \boldsymbol{\theta}\right]' &\sim \mathrm{MVNormal}\left(\mathbf{0}, \mathbf{P}\right) \end{aligned} \tag{1.1}$$

Bold values are used to distinguish vectors and matrices from scalars and primes $'$ are used to indicate the transpose operation. Individuals' traits values are specified as being generated by some probability density function f with corresponding location $\boldsymbol{\eta}$ and dispersion $\boldsymbol{\theta}$ parameters, such as the means and standard deviations of normal distributions or the means and shape parameters of gamma, negative binomial, and beta distributions. For GLMMs, these nonlinear parameters are modelled on a latent linear scale using link functions g_η and g_θ (e.g. identity, log, logistic, or reciprocal transformations). We therefore refer to $g_\eta(\eta_{ij})$ and $g_\theta(\theta_{ij})$ as the linear predictors for the respective location and dispersion parameters of observation i on individual j.

Typically, personality and plasticity are modelled through the linear predictor of the location parameters, capturing variation in expected behavior (i.e. predicted behavior averaged over dispersion). This is accomplished through the estimation of random intercept μ_j and random slope β_j for individual j, which are expressed as deviations from the population-average intercept μ_0 and slope β_1. These parameters correspond to the elevation and slope of the individual's behavioral RN. We assume that environmental exposures are randomized across individuals, so that there is no need to within-individual center the covariate used for scaling RN slopes (van de Pol and Wright 2009). Predictability is modelled through a random intercept effect θ_j on the dispersion parameters, deviating from the population-average dispersion θ_0, which captures individual-specific variability independent of the linear predictor. The effect of each parameter in $\boldsymbol{z}_{\mathbf{p}}$ on the shape of an individual's RN can be seen in **Figure 1**. For simplicity, we ignore the possibility that individuals may also exhibit plasticity in their predictability as a function of the environment, although this could be readily estimated, along with other fixed and random effects. For distributions without an explicit dispersion parameter, such as Poisson or binomial distributions, individual differences in predictability cannot be directly modelled in this way. However, this limitation can be easily avoided by using a closely related distribution accounting for overdispersion, such as the negative binomial and beta binomial distributions.

The associations among RN parameters are captured by the trait covariance matrix $\mathbf{P}$. Note that covariance and correlation matrices can always be translated to one another by $\mathbf{P} = \mathbf{SRS}$, where $\mathbf{S}$ is a diagonal matrix with standard deviations and $\mathbf{R}$ is a correlation matrix. This identity is often useful for efficiently estimating Bayesian GLMMs by separating out the scale and association parameters among random effects. We therefore substitute $\mathbf{SRS}$ for $\mathbf{P}$ in subsequent formula.

3.1.2 Multi-response model for selection analysis

Our goal is to now specify a single multi-response model that estimates (Eq 1.1) while also estimating the effects of RN parameters $\boldsymbol{z}_{\mathbf{p}}$ on fitness. Given that researchers will often lack repeated measures of fitness or fitness-proxies (e.g. bodily condition, clutch size, mate choice), the presented models assume that a single fitness measure is available per individual, although this assumption can be relaxed by including additional random effects to account for unobserved heterogeneity in repeated fitness measures. For simplicity, we also begin by assuming that the fitness measure can be effectively described by a Gaussian distribution, which simplifies the estimation of selection gradients and differentials below. As is appropriate for modelling relative fitness (Lande and Arnold 1983), w is mean-scaled so that $w_j = W_j/\bar{W}$ where $\bar{W}$ is the mean absolute fitness across individuals. For notational clarity, we now introduce superscripts (z) to distinguish parameters that are specific to the z behavioral response model from those in the w fitness response model.

$$
\begin{gathered}
z_{ij} \sim f\left(\eta_{ij}^{(z)}, \theta_{ij}^{(z)}\right) \\
g_\eta\left(\eta_{ij}^{(z)}\right) = \mu_0^{(z)} + \mu_j^{(z)} + \left(\beta_1^{(z)} + \beta_j^{(z)}\right) x_{ij} \\
g_\theta\left(\theta_{ij}^{(z)}\right) = \theta_0^{(z)} + \theta_j^{(z)} \\
\boldsymbol{z}_{\mathbf{p}} = \begin{bmatrix}\boldsymbol{\mu}^{(z)} & \boldsymbol{\beta}^{(z)} & \boldsymbol{\theta}^{(z)}\end{bmatrix}' \sim \text{MVNormal}\left(\mathbf{0}, \mathbf{SRS}\right)
\end{gathered}
\tag{1.2}
$$

$$
\begin{gathered}
w_j \sim \text{Normal}\left(\mu_j, \sigma_j\right) \\
\mu_j = \mu_0 + \beta_1\left(\mu_j^{(z)}\right) + \beta_2\left(\beta_j^{(z)}\right) + \beta_3\left(\theta_j^{(z)}\right) \\
+\beta_4\left(\mu_j^{(z)}\mu_j^{(z)}\right) + \beta_5\left(\beta_j^{(z)}\beta_j^{(z)}\right) + \beta_6\left(\theta_j^{(z)}\theta_j^{(z)}\right) \\
+\beta_7\left(\mu_j^{(z)}\beta_j^{(z)}\right) + \beta_8\left(\mu_j^{(z)}\theta_j^{(z)}\right) + \beta_9\left(\beta_j^{(z)}\theta_j^{(z)}\right)
\end{gathered}
$$

Readers familiar with structural equation modelling (Araya-Ajoy and Dingemanse 2014; Martin et al. 2019) may note that each RN parameter in this model can be conceptualized as an exogenous latent variable, with its loading on trait z fixed to 1, thus scaling the zero-centered latent variable, and its loadings on trait w estimated with the regression coefficients. These latent variables separate out the portions of variance in trait $\boldsymbol{z}$ due to each latent RN parameter and, therefore, isolate distinct RN effects on fitness from all other sources of non-repeatable variation in the raw trait values. The proposed model can also be conceptualized as an extension of the so-called 'errors-in-variables' models discussed by Dingemanse, Araya-Ajoy, and Westneat (2021), which do not disentangle repeatable variation in raw measurements due to personality, plasticity, and predictability. This multi-response GLMM thus provides a flexible and intuitive means of integrating the benefits as well as overcoming the limitations of multiple previously suggested statistical approaches. It is also important to note that the proposed model can always be simplified to facilitate studies of selection on individual RN parameters, should researchers lack sufficient repeated samples or environmental data to simultaneously address personality, plasticity, and predictability.

When this quadratic regression model effectively approximates the individual selection surface (Lande and Arnold 1983; Phillips and Arnold 1989), $\boldsymbol{\beta} = [\beta_1, \beta_2, \beta_3]$ indicates the expected direction and magnitude of unconstrained adaptation in the average population RN values, which are also known as directional selection gradients. Nonlinear effects are instead captured by $\boldsymbol{\gamma}_{\mu,\mu} = \beta_4 * 2$, $\boldsymbol{\gamma}_{\beta,\beta} = \beta_5 * 2$, and $\boldsymbol{\gamma}_{\theta,\theta} = \beta_6 * 2$, which indicate convex or concave curvature in the selection surfaces of RN parameters (Stinchcombe et al. 2008), and $\boldsymbol{\gamma}_{\mu,\beta} = \beta_7$, $\boldsymbol{\gamma}_{\mu,\theta} = \beta_8$, and $\boldsymbol{\gamma}_{\beta,\theta} = \beta_9$, which indicate further curvature due to the presence of correlational selection between trait pairs. The regression coefficients capturing nonlinear curvature in the selection surface can then be grouped into a matrix $\boldsymbol{\gamma}$ of quadratic selection gradients and the fitness model can be simplified to matrix notation for individual j such that

$$
\begin{gathered}
\mu_j = \mu_0 + \boldsymbol{\beta}'\boldsymbol{z}_{\mathbf{p}j} + \boldsymbol{z}_{\mathbf{p}j}'\boldsymbol{\gamma}\boldsymbol{z}_{\mathbf{p}j} \\
\boldsymbol{\gamma} = \begin{pmatrix} \gamma_{\mu,\mu} & \gamma_{\mu,\beta} & \gamma_{\mu,\theta} \\ \gamma_{\beta,\mu} & \gamma_{\beta,\beta} & \gamma_{\beta,\theta} \\ \gamma_{\theta,\mu} & \gamma_{\theta,\beta} & \gamma_{\theta,\theta} \end{pmatrix}
\end{gathered}
\tag{1.3}
$$

If one desires to express gradients in standardized units for effect size comparison, then $\boldsymbol{z}^*_{\mathbf{p}j} = \boldsymbol{z}_{\mathbf{p}j} \oslash \text{diag}(\mathbf{S})$ can instead be specified in the fitness response model, where the Hadamard division $\oslash$ indicates element-wise division of each parameter by its standard deviation, which are contained on the diagonal of the **S** matrix. The selection model can also be extended to account for various kinds of balancing selection (see **Figure 2**) by including additional interaction effects for the relevant state variables. For example, $\beta_I(\mu_j^{(z)} * \text{N})$ could be estimated to assess the presence of density-dependent selection on personality across differing population sizes N.

It is common in selection analyses to estimate linear and nonlinear gradients on observed trait values $\boldsymbol{z}$, rather than directly on RN parameters $\boldsymbol{z}_{\mathbf{p}}$ as proposed here. However, it is ultimately the repeatable individual variation in a phenotype that is available to selection, with all other trait variation effectively representing measurement error from the perspective of evolutionary inference at the population level (Martin and Jaeggi 2021). Thus, it is genetically encoded behavioral strategies (i.e. RNs) that are adapted within a population, rather than the specific actions animals are observed taking in any particular measurement context (McNamara and Leimar 2020). Moreover, when RN parameters are not completely integrated, so that $\mathbf{R} \neq \mathbf{1}$, selection can further act on independent variation in each element of $\boldsymbol{z}_{\mathbf{p}}$, leading to distinct changes in the population RN intercept, slope, and dispersion within and across generations. These adaptive processes will be confounded when solely considering selection on observed trait values $\boldsymbol{z}$. The global effects of RN parameter selection on the shape of the population RN function can also be straightforwardly estimated and visualized using methods developed further below.

3.1.3 Fully Bayesian inference

To the best knowledge of the author, the proposed multi-response model for RN selection analysis cannot be straightforwardly estimated with mainstream statistical software. This does not, however, reflect any fundamental issue with its parameterization or interpretation, but rather pragmatic limitations of the estimators and/or syntax used in these software, which generally do not allow the same latent parameters to be specified across different GLMM response models. Fortunately, the Stan statistical programming language (Carpenter et al. 2017), which relies on cutting-edge and computationally efficient Markov Chain Monte Carlo (MCMC) algorithms, provides exceptional flexibility for specifying and straightforwardly estimating such atypical GLMMs within a Bayesian framework. Researchers unfamiliar with the general benefits of fully Bayesian inference are encouraged to see McElreath (2020) for detailed discussion, as well as Gelman et al. (2020) for helpful tips on developing an effective Bayesian workflow for data analysis. A brief review of some fundamentals will facilitate robust estimation and hypothesis testing with the proposed model.

To estimate Eq 1.2 within a Bayesian framework, we simply need to specify prior distributions for all the population-level parameters, which are transformed within the model to derive the individual-level RN parameters during model estimation.

$$\mu_0^{(z)}, \beta_1^{(z)}, \theta_0^{(z)}, \mathbf{S}, \mathbf{R}, \mu_0, \sigma, \beta_1, ..., \beta_9 \sim \boldsymbol{f}(\boldsymbol{\Phi})$$

As above, $\boldsymbol{f}$ are probability density functions for each parameter and $\boldsymbol{\Phi}$ are the corresponding distributional parameters for all priors. Although it is common for ecology methods papers to use and/or recommend using highly diffuse or flat priors (e.g. Houslay and Wilson 2017; Villemereuil et al. 2016), it is also well established within the statistics literature that weakly informative, regularizing priors–which slightly pull parameters toward null values and provide low prior probability to extreme effect sizes–facilitate more robust inferences and should generally be preferred over flat priors whenever possible (Gelman and Tuerlinckx 2000; McElreath 2020; Lemoine 2019). This does not require that one has access to a relevant meta-analysis or is in a position to make strong a priori assumptions about the true effect size (cf. Ellison 2004). Rather, one can simply use general-purpose, conservative priors as a means of increasing the generalizability and robustness of their findings, even in a state of relative ignorance about the true effect size. For most GLMMs, priors such as $\mu, \beta \sim \text{Normal}(0, 1)$, $\text{diag}(\mathbf{S}), \sigma \sim \text{Exponential}(1)$, and $\mathbf{R} \sim \text{LKJ}(2)$ provide effective weakly regularizing priors. See Lemoine (2019) for more detailed discussion and recommendations in ecological research.

By specifying priors in the model, all parameters can subsequently be estimated as posterior distributions. For example, $\boldsymbol{z}_{\mathbf{p}}$ will no longer be estimated with BLUP point estimates $\hat{\mu}_j^{(z)}$, $\hat{\beta}_j^{(z)}$, and $\hat{\theta}_j^{(z)}$, but will instead be estimated with probability distributions capturing all of the statistical uncertainty in the BLUPs

$$\Pr\left(\mu_j^{(z)} \mid \boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w}, ..., \boldsymbol{\Phi}\right), \quad \Pr\left(\beta_j^{(z)} \mid \boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w}, ..., \boldsymbol{\Phi}\right), \quad \Pr\left(\theta_j^{(z)} \mid \boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w}, ..., \boldsymbol{\Phi}\right)$$

These posterior distributions are conditional on the observed measures $(\boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w})$ and all other model parameters and priors $(...\boldsymbol{\Phi})$. Given that all statistical uncertainty is captured in these and other posterior distributions, the proposed multi-response model (Eq 1.2) provides nearly unlimited flexibility for direct forms of hypothesis testing. For example, to quantify our confidence that positive correlational selection occurs for plasticity and predictability, we simply need to manipulate the relevant posteriors to calculate

$$\Pr\left(\gamma_{\beta,\theta} > 0 \ \mid \ \boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w}, ..., \boldsymbol{\Phi}\right)$$

When posterior distributions are estimated with Markov Chain Monte Carlo (MCMC), this value can be quantified by assessing this inequality across the relevant vectors of posterior samples and calculating the proportion of samples for which it is satisfied. Similarly, if we want to quantify our confidence that there is stronger directional selection on personality than plasticity, we can calculate

$$\Pr\left(\beta_{\mu} > \beta_{\beta} \ \mid \ \boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w}, ..., \boldsymbol{\Phi}\right)$$

One could similarly perform a direct hypothesis test of a more robust null hypothesis than is typically considered, given that true effect sizes are almost never exactly zero in reality (Amrhein, Trafimow, and Greenland 2019; Meehl 1978; Gelman and Carlin 2017). Instead, a direct test of a null hypothesis can provide the probability that an effect is of a biologically trivial magnitude (e.g. $< |0.1|$ for a standardized predictor). For instance, considering the correlation among personality and predictability in the $\mathbf{R}$ correlation matrix

$$\Pr\left(-0.1 < \mathbf{R}_{\mu,\theta} < 0.1 \ \mid \ \boldsymbol{x}, \boldsymbol{z}, \boldsymbol{w}, ..., \boldsymbol{\Phi}\right)$$

Note that these tests are *not* indirect null hypothesis tests, which give the probability of observing the data under the assumption that a null hypothesis is true. Instead, these are direct tests of biologically substantive hypotheses given the observed data, the evaluation of which is generally the primary goal of scientific research. As such, intuitive interpretation can be made of the posterior probabilities, so that values closer to 1 indicate greater support for the tested hypotheses and values closer to 0 indicate stronger support for the opposite hypotheses. These Bayesian hypothesis tests help to avoid many common misinterpretations of classical tests, such as interpreting confidence intervals as reflecting the probable range of the true effect, interpreting P-values as providing the probability of the null hypothesis being true, or interpreting the rejection of a null hypothesis test as being indicative of the substantive ("alternative") hypothesis being correct (Greenland et al. 2016; McElreath 2020; McShane et al. 2019). Furthermore, these Bayesian posteriors can be easily manipulated to address a variety of questions which may not be easily specified directly in a statistical model. This provides theoretically important benefits such as being able to easily quantify uncertainty in and perform direct hypothesis tests on derived quantities such as selection differentials, R^2 values, and repeatabilities.

3.1.4 Non-Gaussian fitness measures

Despite the expected robustness of LMMs to violations of distributional assumptions, any particular study will be at a non-trivial risk of inferential bias when applying a linear fitness model to outcomes that are clearly better described by a non-Gaussian distribution (Schielzeth et al. 2020). Some common non-Gaussian data types used for fitness-proxies include dichotomous measures of survival or mating success, counts of offspring fledged or surviving to adulthood, and various forms of zero-bounded continuous performance measures such as growth rate or dispersal distance. When considering RN effects on other biologically relevant outcomes, there are of course a variety of non-Gaussian measures which may be similarly employed, such as categorical, mutually exclusive choices or reaction times in cognitive tasks, proportional measures of time spent in an activity, and so on. In all such cases, researchers will benefit from more reliable inferences and model predictions if they try to accurately describe the data generating process with an appropriate non-Gaussian distribution, rather than attempting to pigeonhole their analysis into a linear model. Fortunately, the Stan statistical programming language provides a plethora of possible distributions for GLMM likelihood functions, as well as the capacity to specify any custom likelihood functions of interest. To account for non-Gaussian fitness measure W, we update the fitness model in Eq 1.2 with a generalized distributional function and link transformation.

$$
\begin{gathered}
z_{ij} \sim f\left(\eta_{ij}^{(z)}, \theta_{ij}^{(z)}\right) \\
g_{\eta}^{(z)}\left(\eta_{ij}^{(z)}\right) = \mu_0^{(z)} + \mu_j^{(z)} + \left(\beta_1^{(z)} + \beta_j^{(z)}\right) x_{ij} \\
g_{\theta}^{(z)}\left(\theta_{ij}^{(z)}\right) = \theta_0^{(z)} + \theta_j^{(z)} \\
\boldsymbol{z_{\mathbf{p}}} = \begin{bmatrix}\boldsymbol{\mu}^{(z)} & \boldsymbol{\beta}^{(z)} & \boldsymbol{\theta}^{(z)}\end{bmatrix}' \sim \text{MVNormal}\left(\mathbf{0}, \mathbf{SRS}\right) \\
\\
W_j \sim f\left(\eta_j, \theta\right) \\
g_{\eta}\left(\eta_j\right) = \mu_0 + \beta_1\left(\mu_j^{(z)}\right) + \beta_2\left(\beta_j^{(z)}\right) + \beta_3\left(\theta_j^{(z)}\right) \\
+\beta_4\left(\mu_j^{(z)}\mu_j^{(z)}\right) + \beta_5\left(\beta_j^{(z)}\beta_j^{(z)}\right) + \beta_6\left(\theta_j^{(z)}\theta_j^{(z)}\right) \\
+\beta_7\left(\mu_j^{(z)}\beta_j^{(z)}\right) + \beta_8\left(\mu_j^{(z)}\theta_j^{(z)}\right) + \beta_9\left(\beta_j^{(z)}\theta_j^{(z)}\right) \\
\\
\mu_0^{(z)}, \beta_1^{(z)}, \theta_0^{(z)}, \mathbf{S}, \mathbf{R}, \mu_0, \theta, \beta_1, ..., \beta_9 \sim \boldsymbol{f}(\boldsymbol{\Phi})
\end{gathered}
\tag{2}
$$

Notation follows as above, with priors now specified directly in the model formula. Note that because we do not predict the fitness dispersion parameter θ with individual-level fixed or random effects, there is no need to introduce a linear predictor and corresponding link function. While it was straightforward to translate regression coefficients to selection gradients in the Gaussian fitness model, the link function introduced in the non-Gaussian model complicates matters. However, as discussed by Morrissey and Sakrejda (2013), appropriate gradients can nonetheless be estimated manually using partial derivative functions implemented in base R. In particular,

$$
\begin{aligned}
\beta_m &= \frac{\delta \mathrm{E}\left(\bar{W} \mid \bar{z}_{\mathrm{p}m}\right)}{\delta \bar{z}_{\mathrm{p}m}} \bar{W}^{-1} \\
\gamma_{m,n} &= \frac{\delta^2 \mathrm{E}\left(\bar{W} \mid \bar{z}_{\mathrm{p}k}\right)}{\delta \bar{z}_{\mathrm{p}m} \delta \bar{z}_{\mathrm{p}n}} \bar{W}^{-1}
\end{aligned}
\tag{3}
$$

where m and n index the mth and nth elements of the RN parameter vector $\boldsymbol{z_{\mathbf{p}}}$. Morrissey and Sakrejda (2013) 's method elegantly unifies LMM and GLMM approaches to estimating selection on latent behavioral RNs.

3.1.5 Within-generation effects of selection

With appropriate linear and nonlinear selection gradients, the expected within-generation effect of selection on the population means and covariances of behavioral RNs can be estimated. In particular, selection differentials can be calculated that integrate direct adaptive effects due to $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ with indirect effects caused by trait integration due to $\mathbf{P} = \mathbf{SRS}$. Following Lande and Arnold (1983), linear and quadratic differentials are defined such that

$$
\begin{gathered}
\Delta_{\mathrm{T}} \bar{\boldsymbol{z}}_{\mathbf{p}} = \mathbf{P}\boldsymbol{\beta}, \\
\Delta_{\mathrm{T}} \mathbf{P} = \mathbf{P}\left(\boldsymbol{\gamma} - \boldsymbol{\beta}\boldsymbol{\beta}'\right)\mathbf{P}
\end{gathered}
\tag{4.1}
$$

where Δ_{T} indicates the total (i.e. direct and indirect) within-generation effect of selection. We can also consider the effects of selection in the hypothetical case of complete independence between RN parameters by instead using a diagonal matrix $\mathbf{V} = \mathbf{S}^2$ of trait variances.

$$
\begin{gathered}
\Delta_{\mathrm{D}} \bar{\boldsymbol{z}}_{\mathbf{p}} = \mathbf{V}\boldsymbol{\beta}, \\
\Delta_{\mathrm{D}} \mathbf{V} = \mathbf{V}\left(\boldsymbol{\gamma} - \boldsymbol{\beta}\boldsymbol{\beta}'\right)\mathbf{V}
\end{gathered}
\tag{4.2}
$$

Here, Δ_{D} indicates change expected under trait independence, thus isolating the direct effects of selection on adaptation. Visual and quantitative comparison of the expected patterns of change between the integrated total Δ_T and independent direct Δ_D differentials provides a useful and straightforward means of estimating the degree to which phenotypic integration constrains or facilitates the adaptive process through indirect effects (Conner 2012). Moreover, separation of these differentials allows for straightforward testing of adaptive hypotheses on specific behavioral parameters, even in the presence of high-dimensional data, strong phenotypic constraints, and highly nonlinear selection surfaces. If $\Delta_\mathrm{D}\bar{z}_{\mathbf{p}m} > 0$ for RN parameter m, then selection is acting to increase the mean trait value in the population (and vice versa for negative change). Similarly, $\Delta_\mathrm{D}\mathbf{V}_{m,m} > 0$ indicates that selection is acting to increase individual variation in the population, such that individuality is likely to be adaptive, while $\Delta_\mathrm{D}\mathbf{V}_{m,m} < 0$ indicates that individuality is being selected against. For the off-diagonal elements, $\Delta_\mathrm{D}\mathbf{V}_{m,n} \neq 0$ indicates that selection is actively promoting positive or negative trait integration between RN parameters m and n, suggesting that behavioral syndromes are also adaptive. As shown in **Figure 3**, it will often be helpful to express these covariances as correlations for ease of comparison and visualization.

3.1.6 Visualizing the effects of multivariate selection

When modelling selection on a single RN parameter, it is straightforward to relate concave or convex quadratic gradients in Eq 1.2 or Eq 2 to the shape of the the fitness function, which is standard in presentations of stabilizing and disruptive selection surfaces. With two RN parameters, a response surface methodology can be used to visualize a variety of more complex surfaces characterized by domes, bowls, and saddles, among other 3-dimensional shapes. These scenarios are shown in **Figure 2**. Things become more complicated, however, when three or more parameters experience correlational selection. In such cases, some evolutionary biologists have argued for the use of single value decomposition methods such as canonical analysis to enhance interpretation of the selection process (Blows 2007; Phillips and Arnold 1989). With this approach, the fitness model can be re-expressed on the primary axes of correlational selection, facilitating more intuitive visualization of linear and quadratic selection on conditionally independent dimensions. While undoubtedly useful in particular empirical contexts, this method has many limitations for general application that have inhibited its uptake among empiricists, including sensitivity to sampling error and units of measurement (Morrissey 2014), as well as the general difficulty of interpreting the meaning of traits defined by their statistical rather than biological properties (Brodie and McGlothlin 2007; Conner 2007). While the dimension reduction capacities of this approach are highly desirable when considering selection on multi-trait RNs, more theoretically motivated approaches such as structural equation or generalized network modelling can instead be applied to categorize latent behavioral characters governing multiple RN parameters (Araya-Ajoy and Dingemanse 2014; Martin et al. 2019). In contrast to these causal modelling approaches, which seek to disentangle evolutionarily meaningful patterns of common and unique variance due to latent factors, methods such as canonical analysis are principally data reduction techniques and thus categorize axes irrespective of whether they confound common and unique sources of variation in fitness effects. This is why uncertainty in particular traits is expected to easily bias the axes characterized by canonical analysis (Morrissey 2014), while structural equation models are robust to trait measurement error (Bollen and Noble 2011). When causal modelling techniques are not well-motivated for a multi-trait RN, strong regularization techniques can instead be employed to enhance inferences and reduce the effective parameter space. This can be accomplished with the proposed models by implementing priors such as the regularized horseshoe prior (Piironen and Vehtari 2017), which performs well under conditions where the number of parameters is greater than would otherwise be desirable for the sample size.

Canonical analysis is, therefore, not considered further as a means of effectively visualizing multivariate selection, though the provided model code can always be modified to carry it out nonetheless. Non-parametric methods are also not considered herein as an alternative. While such methods are useful for hypothesis generation, it is ultimately parametric functions (perhaps of a highly complex nonlinear structure) that will facilitate robust theories of adaptation amenable to formalization and comparative biological research on individual variation. Non-parametric techniques such as projection-pursuit regression (Morrissey 2014; Schluter and Nychka 1994) should thus be considered useful and complimentary tools for the proposed parametric models, which can be always be elaborated upon to capture the essential features of any function generated through exploratory non-parametric analysis. Indeed, one can always extend a parametric GLMM to a generalized additive multilevel model (Pedersen et al. 2019) by including additional non-parametric functions such as splines and Gaussian processes into a selection analysis, facilitating biological comparison and straightforward hypothesis testing while also capturing any unmodelled sources of nonlinear association that may bias parametric inferences. This can be accomplished within a Bayesian framework in Stan using methods implemented in the “brms” R package (Bürkner 2017).

Given these considerations, how can we effectively visualize the effects of multivariate, nonlinear selection on behavioral RNs? I propose a simple method that considers how selection influences behavioral RNs in three dimensions. The motivation for this method begins by considering the unique pieces of information provided by the selection differentials in Eq 4.1 and Eq 4.2. Firstly, $\Delta\bar{\boldsymbol{z}}_{\mathbf{p}}$ inform the expected change in the mean of each RN parameter, while the diagonal elements of $\Delta\mathbf{P}$ informs the change in the variance of each RN parameter. The off-diagonal elements of $\Delta\mathbf{P}$ instead capture changes in the integration among RN parameters, which can be standardized to correlations for ease of interpretation. The effect of direct versus indirect selection effects caused by RN parameter integration can be further informed by the difference between Δ_{D} and Δ_{T} respectively. This allows researchers to assess adaptive hypotheses on specific trait values even when phenotypic integration is expected to diminish or even reverse the direction of evolutionary change caused by direct selection. Finally, because each element of $\boldsymbol{z}_{\mathbf{p}}$ is a parameter in a broader parametric behavioral RN function, we can also consider each of these estimates together to indicate how selection is changing the overall shape of the population behavioral strategy. Each of these pieces of information is to some degree unique and informative for our theoretical understanding of adaptive individual variation. Therefore, the proposed method is simply to plot all of this information together in a single figure of multivariate selection effects on the behavioral RN, along with the posterior uncertainty in the expected effects of selection. This visualization method is demonstrated in **Figure 3** for a hypothetical empirical scenario characterized by directional, quadratic, and correlational selection on personality, plasticity, and predictability. Note that all of these estimates are taken on the latent linear scale defined in the model, but they can always be predicted on the original data scale by applying the appropriate inverse link function on the transformed absolute values (i.e. link-scale population RN value + expected population RN change).

4 Simulation-based calibration of proposed models

I used a simulation-based calibration (SBC) procedure to validate the inferential performance of the proposed Bayesian models and assess whether they provide unbiased estimators of selection. SBC is a procedure for validating the performance of any Bayesian algorithm across a broad range of possible parameter values, as defined by the prior distributions of a generative model. This approach removes the arbitrariness of setting a limited range of fixed parameter values for assessing performance, which can lead to unexpected sources of bias being overlooked in uninvestigated regions of parameter space (e.g. rare but possible combinations of RN correlations, standard deviations, and selection coefficients). Instead, random parameter values are repeatedly imputed during each MCMC iteration of model estimation for a large number of simulations and visual inspection of the correspondence between the generative distributions and subsequent posterior distributions is used to detect any sources of bias, such as overdispersion in the estimator or inconsistent performance for extreme values. While a detailed explanation of SBC implementation and interpretation is beyond the scope of the present study (see Talts et al. 2018 for further details), it suffices to say that a GLMM validated through SBC is an unbiased Bayesian estimator. This method was, therefore, used to ensure that empirical studies using the proposed models would be expected to arrive at unbiased estimates over a plausible range of possible parameter values.

Particular attention was given to the estimation of linear and nonlinear selection coefficients during SBC, using 250 simulated datasets with 400 independent posterior samples each, resulting in the exploration of 100,000 possible random combinations of all model parameters. As recommended by Talts et al. (2018), visual inspection of the SBC diagnostic plots demonstrated that the ranks of posterior selection coefficients were consistent with a random, uniform distribution around the prior simulated values, suggesting desirable performance indicative of unbiased inference. Following the recommendation of Cook, Gelman, and Rubin (2006), I also further tested the uniformity of the rank distribution by sorting ranks into eight evenly distributed bins and applying a simple null-hypothesis test, $\chi^2(7) = 6.06, P = 0.53$, further suggesting that coefficient ranks were randomly and evenly distributed. In other words, posterior inferences were not systematically upwardly or downwardly biased from the true values, indicating that the proposed models are expected to provide unbiased estimators of selection on behavioral RNs across a broad range of parameter space.

5 Conclusion

Understanding the adaptive evolution of individual variation is an exciting and bustling frontier in evolutionary ecology. Repeatable individual differences in behavioral consistency, plasticity, and predictability have now been demonstrated across a broad range of taxa under a variety of ecological conditions. The challenge for

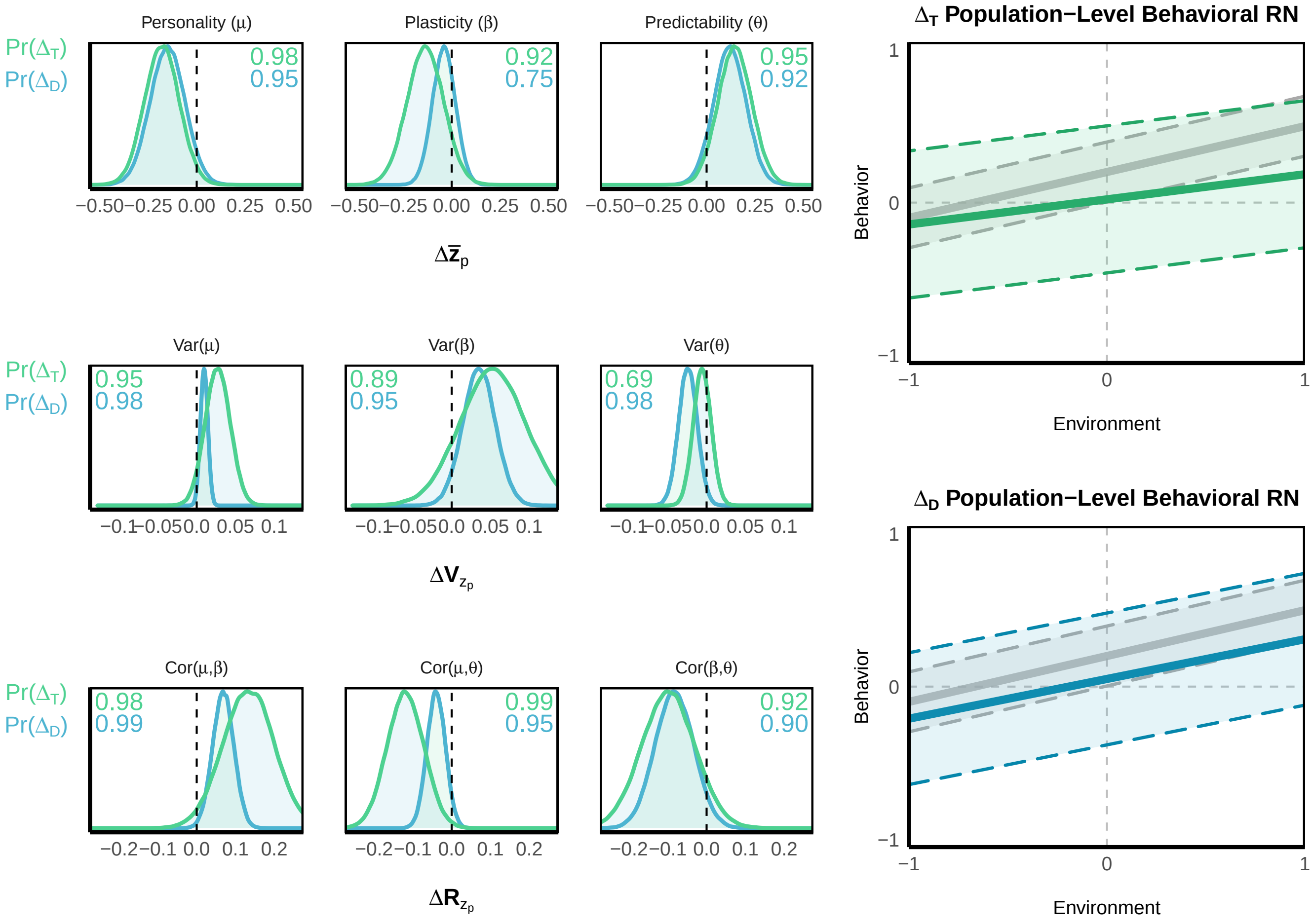


Figure 3: Proposed representation of multivariate selection on a behavioral RN. Plots are shown for the within-generation effects of a hypothetical selection event, where selection was characterized by a combination of directional, quadratic, and correlational fitness effects across RN parameters. Distinct outcomes are shown for the direct effects of selection (Δ_{D}) causing adaptation independent of trait covariation, as well as the total effects of selection (Δ_{T}) accounting for indirect effects due to phenotypic integration among RN parameters.

Left panel: Three rows are shown for the distinct effects of multivariate selection on the average population RN parameter values ($\Delta\bar{\boldsymbol{z}}_{\text{p}}$), individual variation in population RN values (represented by the population variance, $\Delta\mathbf{V}_{\text{z}_{\text{p}}}$), and the integration among RN parameters (represented by the population correlations, $\Delta\mathbf{R}_{\text{z}_{\text{p}}}$). Uncertainty around these predicted changes is captured by posterior distributions of each selection differential, with the posterior probability $\Pr(\Delta)$ supporting the expected direction of change for total and direct effects indicated in the top corner of each plot. If individual differences are adaptive, it is expected that selection will act to directly increase or maintain the population variance of RN parameters ($\Delta_{\text{D}}\mathbf{V}_{\text{z}_{\text{p}}} \geq 0$); similarly, if trait integration is adaptive, selection will directly increase or maintain trait correlations (i.e. $\Delta_{\text{D}}\mathbf{R}_{\text{z}_{\text{p}}} \geq 0$). Adaptation may nevertheless be constrained or accelerated by indirect effects due to phenotypic integration. In this hypothetical scenario, it can be seen that although selection is acting to decrease individual variation in predictability, $\Pr(\Delta_{\text{D}} = 0.98)$, indirect effects lead to no clear expected change in the population variance, $\Pr(\Delta_{\text{T}} = 0.69)$. Similarly, while there is only weak evidence of direct selection to decrease the mean plasticity in the population, $\Pr(\Delta_{\text{D}} = 0.75)$, indirect effects are expected to cause a more pronounced change, $\Pr(\Delta_{\text{D}} = 0.92)$.

Right panel: The expected change in the shape of the population behavioral RN following selection. The population RN prior to selection is indicated by the grey line and band. Point estimates from the posterior distributions of $\Delta\bar{\boldsymbol{z}}_{\text{p}}$ are used to visualize how direct and total selection effects shift the mean population RN across the relevant environmental gradient. The dashed, shaded bands indicate the 95% credible intervals (i.e. $1.96 * \theta$) capturing the expected levels of behavioral predictability in the population.

behavioral ecologists is thus no longer to simply document and describe between-individual differences in behavior, but to instead test theory explaining how and why these patterns are observed (Dingemanse and Wright 2020). It is now well-established that a variety of non-adaptive mechanisms can readily maintain repeatable phenotypic variability and trait correlations within a population, particularly for traits with complex genetic architectures. Therefore, the existence of such variation in itself does not provide strong reason to suspect that natural selection is acting to increase or maintain individuality within a population. Bierbach, Laskowski, and Wolf (2017), for example, found that personality emerged in activity level among clonal fish raised in highly controlled environmental conditions, likely as a result of developmental noise. Similar findings have been obtained for clonal mice, where individuality in behavior can result from subtle differences in neurobiological and epigenetic responses toward standardized early rearing environments (Zocher et al. 2020). Processes such as mutation-selection balance also remain plausible explanations for the maintenance of non-adaptive behavioral variation even in the presence of consistent stabilizing selection (Zhang and Hill 2005), particularly for complex traits with large mutational target sizes caused by highly polygenic and pleiotropic developmental pathways (Houle 1998; Boyle, Li, and Pritchard 2017). Empirical research in humans has, for example, provided support for the role of mutation-selection balance in maintaining repeatable variation in personality (Verweij et al. 2016), psychopathology (Keller 2008; Pardiñas et al. 2018), and general intelligence (Hill et al. 2018). In light of these considerations, the mere existence of differential personality, plasticity, and/or predictability within a population should not be considered biologically surprising, nor should it be considered particularly informative on its own for advancing behavioral ecological theory (Beekman and Jordan 2017). The onus thus remains on empiricists to demonstrate the evolutionary relevance of individual variation within their study system, as well as to identify the common mechanisms and selection pressures that may facilitate or diminish its maintenance across generations. While many such studies are now available (e.g. Dingemanse and Réale 2005; Le Cœur et al. 2015; Le Galliard, Paquet, and Mugabo 2015), there is a clear need for more phenotypic selection analyses on behavioral RNs in the wild. As John Maynard Smith (1978) once noted, "The most direct way of testing a hypothesis about adaptation is to compare individuals with different phenotypes, to see whether their fitnesses vary in the way predicted by the hypothesis" (p. 45).

A fundamental challenge for this research endeavor is to avoid inferential bias caused by using BLUP point estimates of individuals' latent personality, plasticity, and predictability parameters to predict fitness (Hadfield et al. 2010), as these trait values are typically inferred with high degrees of uncertainty from GLMMs. Previous attempts to address this issue (Houslay and Wilson 2017) have proposed using random effects models to account for the uncertainty of BLUPs, but this approach restricts analyses to the estimation of linear correlations and covariances among RNs and fitness. Ignoring non-linear associations fundamentally inhibits researchers' capacity to study adaptive individual differences, as persistent directional/linear selection is expected to diminish rather than promote individuality within a population due to the exhaustion of fitness-relevant additive genetic variance (Walsh and Blows 2009). To overcome this limitation, the present study developed and investigated the properties of novel Bayesian models for studying nonlinear selection on behavioral RNs. These models synthesize the Lande-Arnold selection framework (Lande and Arnold 1983) with the GLMM framework for quantifying individual variation (Dingemanse and Dochtermann 2013) into a single multi-response model, thus integrating uncertainty in BLUPs and their effects into a comprehensive analysis. As a consequence, various complex forms of nonlinear selection–such as stabilizing, disruptive, balancing, and/or correlational selection–can be estimated to test competing hypotheses of why variation in RNs persists within a population. Given the challenge of visualizing high-dimensional selection surfaces (Phillips and Arnold 1989), I further proposed a simple method for visualizing the expected direct and total effects of selection on the evolution of behavioral RNs. This approach facilitates intuitive tests of adaptive hypotheses on specific behavioral parameters, even in the presence of high-dimensional phenotypes and complex selection surfaces.

It is important to note that selection differentials estimated from the proposed models (Eq 1.2 & Eq 2) will be sensitive to missing fitness-relevant phenotypes or functional relationships, which is a deeper issue with any trait-based model of selection and evolutionary change (Morrissey, Kruuk, and Wilson 2010). However, behavioral ecologists are generally interested in developing and testing adaptive theory of selection, rather than most accurately predicting patterns of microevolutionary change within a population. By focusing on trait-based models, rather than pure variance-partitioning analyses, broader comparative patterns of adaptation and selection can be better recognized and evaluated (e.g. Kingsolver et al. 2001). Nevertheless, it is often useful to compare the predicted mean changes in phenotypic values between trait- and variance-partitioning models, which can be used to assess the magnitude of effects that are being overlooked with the fixed effects analysis (Morrissey et al. 2012). The random effect correlation models proposed by Houslay and Wilson (2017) can thus provide complimentary analyses to the models presented here. As discussed above, exploratory, non-parametric analyses can then be employed to detect and better characterize any unspecified nonlinear functions on fitness, which can subsequently be integrated into the parametric model. In this way, the goals of prediction and explanation, while distinct and in many cases best suited to different modelling approaches (Shmueli 2010), can nonetheless be integrated to better inform our understanding of microevolutionary change. The proposed modeling framework should, therefore, readily enhance tests of adaptive theory in the wild.

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