

# Estimating Nonlinear Selection on Behavioral Reaction Norms

Tutorials in Stan

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## Contents

|   |           |
|---|-----------|
| <b>Introduction</b>                         | <b>1</b>  |
| <b>Full Gaussian model</b>                  | <b>2</b>  |
| Formal model . . . . .                      | 2         |
| Simulate dataset . . . . .                  | 3         |
| Code model . . . . .                        | 5         |
| Data . . . . .                              | 5         |
| Parameters . . . . .                        | 6         |
| Transformed parameters . . . . .            | 7         |
| Model . . . . .                             | 8         |
| Generated quantities . . . . .              | 9         |
| Final model code . . . . .                  | 10        |
| Estimate model . . . . .                    | 12        |
| Investigate results . . . . .               | 13        |
| Hypothesis testing . . . . .                | 15        |
| Calculate selection differentials . . . . . | 18        |
| Plot results . . . . .                      | 22        |
| <b>Forthcoming tutorials</b>                | <b>27</b> |
| <b>References</b>                           | <b>28</b> |

## Introduction

This series of tutorials demonstrates how to effectively code and interpret models of nonlinear selection on behavioral reaction norms (RNs), using the Stan statistical programming language (Carpenter et al. 2017) in R (R Core Team 2020). Stan is an open-source programming language for estimating probabilistic models of arbitrary complexity using fully Bayesian inference with state-of-the-art Markov Chain Monte Carlo (MCMC) sampling techniques (Hoffman and Gelman 2014). Stan interfaces with R through the RStan package (Carpenter et al. 2017), but you will first need to install Stan on your computer and ensure that it is appropriately configured with your C++ toolchain. This can be accomplished by following the instructions for your operating system on the **RStan Getting Started** page. Once you are able to effectively use RStan, you can begin creating the `.stan` files necessary for estimating models. These files can be composed using RStudio or any text editor. A file can also be composed directly in R with `write()`

```

write("// for Stan comments
      functions{...} // Stan models are composed of
      data {...} // multiple programming blocks
      transformed data {...} //only data, parameters, and model
      parameters {...} //blocks are necessary
      transformed parameters {...}
      model {...}
      generated quantities {...} ",
      "mod1.stan")

```

Once an appropriate `.stan` file is prepared, it can be compiled in R for the C++ toolchain using the `stan_model()` function and subsequently estimated with an appropriate list of empirical data using the `sampling()` function. The resulting posteriors of a model can then be accessed with the `extract()` function and manipulated for any further quantities or analyses of interest.

```

#load package
library(rstan)

#compiles the model in C++ for MCMC estimation
mod1 = stan_model("mod1.stan")

#samples posterior distribution of the model with default MCMC settings
results = sampling(object = mod1, data = data)

#extracts posterior estimates
samples = extract(results)

```

This series is currently under development and will continue to be extended in the coming months to cover a variety of additional modeling scenarios. For now, a full Gaussian model is presented to provide a general introduction to the proposed approach.

## Full Gaussian model

### Formal model

It's always helpful to write out the formal model we'd like to estimate in Stan before attempting to code it. There are a few reasons for this. Firstly, Stan is a probabilistic programming language and, as such, facilitates coding of formal probabilistic models through direct specification of model parameters and likelihood functions. Therefore, some understanding of the formal structure of any model is necessary to code in Stan. Gaining a deeper understanding of formal statistical models can also be extremely valuable for building researchers' autonomy and ingenuity in data analysis, which opens up the door to developing novel models capturing the most salient features of one's specific empirical system and dataset, rather than pigeonholing things into prepackaged toolkits that may require some undesirable assumptions or simplifications. Researchers unfamiliar with formal statistical models are encouraged to see McElreath (2020) for detailed explanation and examples.

A Gaussian model of selection on a full behavioral reaction norm, i.e. with parameters for personality, plasticity, and predictability, can be given by

$$\begin{aligned}
z_{ij} &\sim \text{Normal}(\mu_{ij}^{(z)}, \sigma_{ij}^{(z)}) \\
\mu_{ij}^{(z)} &= \mu_0^{(z)} + \mu_j^{(z)} + (\beta_1^{(z)} + \beta_j^{(z)}) x_{ij} \\
\log(\sigma_{ij}^{(z)}) &= \theta_0^{(z)} + \theta_j^{(z)} \\
\mathbf{z}_P &= [\boldsymbol{\mu}^{(z)} \quad \boldsymbol{\beta}^{(z)} \quad \boldsymbol{\theta}^{(z)}]' \sim \text{MVNormal}(\mathbf{0}, \mathbf{SRS})
\end{aligned}$$

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

$$\begin{aligned}
\mu_0^{(z)}, \beta_1^{(z)}, \theta_0^{(z)}, \mu_0, \beta_1, \dots, \beta_9 &\sim \text{Normal}(0, 1) \\
\mathbf{S}, \sigma &\sim \text{Exponential}(1) \\
\mathbf{R} &\sim \text{LKJ}(2)
\end{aligned}$$

57 Notation follows Martin (2021), where this model is explained and justified in greater detail. The individual-  
58 specific RN parameter values of behavior  $\mathbf{z}$  for all individuals are contained in the BLUP vector  $\mathbf{z}_P$  and the  
59 selection effects are described by the regression coefficients  $\beta_1, \dots, \beta_9$  on fitness measure  $\mathbf{w}$ . For this tutorial,  
60 we use general-purpose, weakly regularizing priors on model parameters to promote more robust inference  
61 and enhance model identification (Lemoine 2019).

## 62 Simulate dataset

63 With the formal model in place, we can now simulate appropriate data to use for its estimation.  
64 We assume a sample of 500 individuals with 6 repeated behavioral measures across the lifespan and  
65 a single fitness measure. Parameter values are arbitrarily fixed so that the population-level inter-  
66 cepts and slopes are 0, with 0.3 for all regression coefficients in the fitness model and correlations  
67 among random effects, as well as residual variances of 0.5 for the behavior and fitness response models.  
68

```

#simulation parameters
I = 500 #number of individuals
repm = 6 #repeated behavioral measures

#fixed effects
beta = 0.3 #regression coefficients
popint = 0 #population behavior intercept
popslope = 0 #population behavior slope

#random effects
sd = sqrt(0.3) #RN parameter standard deviations
cor = 0.3 #correlations between RN parameters
popdisp = sqrt(0.5) #residual SD of behavior
res = sqrt(0.5) #residual SD of fitness

```

69 As discussed in Martin (2021), we simulate the variance-covariance matrix  $\mathbf{P}$  of RN parameters through  
70 matrix multiplication  $\mathbf{SRS}$  of a matrix  $\mathbf{S}$  with standard deviations on the diagonal and a correlation matrix  $\mathbf{R}$ .  
71

```

#generate RN covariance matrix P
R = matrix(cor, nrow=3, ncol=3 )
diag(R) = 1 #make correlation matrix
S = matrix( c(sd,0,0,0,sd,0,0,0,sd), nrow=3, ncol=3 ) #SD matrix
P = S %*% R %*% S #covariance matrix

#simulate RN parameters for individuals
library(mvtnorm)
z_p = rmvnorm(I, mean = rep(0,3), sigma = P)

#separate each parameter
personality = z_p[,1]
plasticity = z_p[,2]
predictability = z_p[,3]

72 We then simulate a random environmental gradient across individuals, which we assume for simplicity is
73 identically and independently distributed across all observations

#environmental covariate (z-score)
x = rnorm(I*repm, 0, 1)

74 along with an index used to link each observation to the corresponding individual being observed.

#index of repeated individual measures
ind = rep(1:I, each = repm)

75 The mean and standard deviations of behavior can then be used to simulate individuals' raw data.

#behavioral response model
z_mu = popint + personality[ind] + (popslope + plasticity[ind])*x #mean of normal dist
z_sigma = log(popdisp) + predictability[ind] #log link SD of normal dist
z = rnorm(I*repm, mean = z_mu, sd = exp(z_sigma) ) #observations

76 The fitness model is simulated so that each individual has a single measure.

#regression coefficients
betas = rep(beta, 9) #naive assumption of equivalent coefficients

#fitness response model
w_mu = 1 + betas[1]*personality + betas[2]*plasticity + betas[3]*predictability +
        betas[4]*(personality^2) + betas[5]*(plasticity^2) + betas[6]*(predictability^2) +
        betas[7]*(personality*plasticity) + betas[8]*(personality*predictability) +
        betas[9]*(plasticity*predictability)
w = rnorm(I, mean = w_mu, sd = res) #observations

77 Stan expects a list rather than a dataframe of observed values for model estimation. This provides desirable
78 flexibility because it allows for the specification of complex multi-response models with vectors of differing
79 size, as the dimensionality of each variable in this list is declared separately in Stan.

data = list(x = x, z = z, w = w, ind = ind, I = I, N = I*repm)
lapply(data,head) #see initial entries of each list item

80 ## $x
81 ## [1] -0.3825168 -1.3186124 -0.2692418 -1.3648240 0.3046992 0.4927625
82 ##
83 ## $z
84 ## [1] -0.03246759 -3.12880556 1.71340115 -0.10599462 2.03597401 2.02655664
85 ##

```

```

86 ## $w
87 ## [1] 2.629040 2.587576 3.078207 1.367658 1.605288 1.835071
88 ##
89 ## $ind
90 ## [1] 1 1 1 1 1 1
91 ##
92 ## $I
93 ## [1] 500
94 ##
95 ## $N
96 ## [1] 3000

```

## Code model

Stan uses its own language for writing probabilistic models, including a variety of built-in functions designed to aid in efficient computation. The biggest conceptual hurdle for new users of Stan is likely to be the absence of an intuitive R-like syntax for specifying model formulas, such as formulas like  $y \sim x + (1|z)$  that can be used to quickly specify complex generalized linear mixed-effects models. These formulas facilitate highly efficient statistical modeling, but do so at the cost of limiting users' ability to specify atypical model structures. Instead, Stan provides the benefit of nearly unlimited flexibility in model specification, with the added cost of a steeper learning curve. In particular, as noted above, models must be formally specified with mathematically appropriate likelihood functions, rather than this process being handled on the back-end through textual inputs from the user such as `family= poisson(link = "log")`. This may at first seem like a cumbersome task, but it affords a degree of flexibility and autonomy necessary for easily estimating the proposed models in Stan, which to the best of my knowledge cannot be accomplished with other mainstream statistical software. Nonetheless, it is important to recognize that some practice and trial-and-error will also be required to gain competency and comfortability with Stan. I therefore encourage researchers to review the **Stan Reference Manual**, as well the extensive collection of **Stan Case Studies**, which will provide a more robust foundation for estimating any model of interest in Stan.

As mentioned above, a basic Stan model consists of multiple programming blocks that together specify the data, parameters, likelihood, and quantities of interest for a model. Rather than tackling the model in a single step, we consider the blocks in turn before putting them together in a single file.

## Data

The first component of a Stan model is the data block, where we'll tell the model what to expect from our data list, as well as how to treat that data inside the model.

```

119 data {
120   int<lower=1> I; //total individuals
121   int<lower=1> N; //total number of observations
122   int<lower=1> ind[N]; //index of individual observations
123   vector[N] x; //environmental covariate
124   vector[N] z; //behavioral measurements
125   vector[I] w; //fitness measurements
126 }

```

We first tell the model to expect integers with values greater than 1 for the total number of individuals observed `I` and the total number of observations for the repeatedly measured behavioral measure `N`. We know we only have a single fitness measure per individual, so `I` also tells us the total number of fitness observations. The next step is to specify an index for connecting repeated observations of the behavior `z` to the identity of the individual being observed. This index should be represented with integers specified according to the order of the data vectors `z` and `w`. The argument `ind[N]` tells Stan that these integer values should in total be of length `N`. If one has indexed observations in their data using character strings, they will need to first be converted to integers. For the simulated dataset, this index looks like

```
head(cbind(z,ind),15)
```

```
135 ##           z ind
136 ## [1,] -0.03246759 1
137 ## [2,] -3.12880556 1
138 ## [3,] 1.71340115 1
139 ## [4,] -0.10599462 1
140 ## [5,] 2.03597401 1
141 ## [6,] 2.02655664 1
142 ## [7,] -1.58081492 2
143 ## [8,] 3.14586707 2
144 ## [9,] -2.83441498 2
145 ## [10,] -0.55485803 2
146 ## [11,] 3.43832081 2
147 ## [12,] -0.24288337 2
148 ## [13,] -1.20127234 3
149 ## [14,] -0.99404926 3
150 ## [15,] -0.79708052 3
```

151 The remaining arguments tell Stan to expect vectors of appropriate length for the environmental covariate **x**  
 152 used to estimate plasticity, the behavioral measure **z**, and the fitness measure **w**.

## 153 Parameters

154 The parameters block will take all of the basic parameters that are specified in the model. We begin by  
 155 considering the fixed effects in the formal model, although the order of specification in the parameters block  
 156 is entirely arbitrary.

```
157 parameters {
158   //fixed population effects
159   real mu_0z; //z population intercept
160   real beta_1z; //z population slope
161   real theta_0z; //z population dispersion
162   real mu_0; //w population intercept
163   real<lower=0> sigma_0; //w dispersion
164   vector[9] betas; //fitness regression coefficients
165   //...
```

166 **mu\_0z** is the population intercept  $\mu_0^{(z)}$  of the linear predictor of behavior **z**, **beta\_1z** is the population slope  
 167  $\beta_1^{(z)}$ , and **theta\_0z** is the population intercept of the dispersion parameter  $\theta_0^{(z)}$ . For the fitness model, we  
 168 specify **mu\_0** for the global intercept  $\mu_0$ , **sigma\_0** for  $\sigma$ , as well as a vector **betas** containing 9 regression  
 169 coefficients for each of the selection effects  $\beta_1, \dots, \beta_9$ . Note that this could be equivalently specified by giving  
 170 each element of this vector separately, e.g.

```
171   real beta_1;
172   real beta_2;
173   real beta_3;
174   real beta_4;
175   //...
```

176 For the random effects, a slightly more complicated setup is used.

```
177   //...
178   //random effects
179   vector<lower=0>[3] sd_zp; //RN parameter SDs
180   matrix[I,3] std_dev; //individual-level RN deviations
181   cholesky_factor_corr[3] R_chol; //RN parameter correlations
```

182 }

183 We specify a vector `sd_zp` of length 3 for each of the SDs of the RN parameters (personality, plasticity, and  
 184 predictability). The matrix **S** in the formal model has `sd_zp` on its diagonal. Importantly, because SDs by  
 185 definition cannot take on values below zero, we need to specify `<lower=0>` so that these parameters also do  
 186 not take on values lower than 0 during model estimation. A matrix of dimension (I x 3) is also specified  
 187 for the standardized deviations of each individual's RN parameter values from the population values. As  
 188 explained below, these standard normal deviates are scaled by the SDs and correlations among RN parameters  
 189 to derive BLUPs of appropriate magnitude.

190 Finally, a matrix parameter `R_chol` is specified for the RN parameter correlation matrix **R**. However,  
 191 rather than using the function `corr_matrix` for a full correlation matrix, we instead use a special function  
 192 `Cholesky_factor_corr` to estimate a so-called *Cholesky decomposition* of **R**. To understand why we do this,  
 193 note that for any positive definite matrix **R**, a Cholesky decomposition can be defined such that

$$\mathbf{R} = \mathbf{R}_L \mathbf{R}_L^T$$

194 where **R<sub>L</sub>** is a lower-triangular matrix and <sup>T</sup> indicates matrix transposition. This property means that we  
 195 can always estimate the model using a smaller lower-triangular matrix **R<sub>L</sub>** and subsequently recover the full  
 196 positive-definitive matrix **R** by post-multiplying **R<sub>L</sub>** with its transpose. This trick is useful for making any  
 197 Stan model sample more efficiently, as computations can be done more quickly with the reduced matrix of  
 198 lower dimensionality that lacks the redundant features of the full symmetric correlation matrix.

## 199 Transformed parameters

200 With these basic parameters in place, we can also further specify parameters in the transformed parameters  
 201 block that are simply combinations of the basic parameters. In this model, we specifically need to derive RN  
 202 parameters (BLUPs) that are appropriately scaled by the RN covariance matrix **P** in the formal model. This  
 203 is accomplished as follows

```
204 transformed parameters {
205   matrix[I,3] zp; //individual phenotypic RN parameter values
206   zp = std_dev * diag_pre_multiply(sd_zp, R_chol)' ;
207 }
```

208 This specification gives the appropriate BLUPs for each individual, as described in the formal model by

$$\mathbf{z}_P = \begin{bmatrix} \boldsymbol{\mu}^{(z)} & \boldsymbol{\beta}^{(z)} & \boldsymbol{\theta}^{(z)} \end{bmatrix}' \sim \text{MVNormal}(\mathbf{0}, \mathbf{SRS})$$

209 To see how this works, note that any normally distributed random variable **z**

$$\mathbf{z} \sim \text{Normal}(0, \sigma_z)$$

210 can also be expressed as a standard normal variable **z<sub>std</sub>** scaled by the original SD

$$\mathbf{z} \equiv \mathbf{z}_{\text{std}} \sigma_z$$

211

$$\mathbf{z}_{\text{std}} \sim \text{Normal}(0, 1)$$

212 Similarly, for an (I x p) matrix **Z** of p phenotypes where

$$\mathbf{Z} \sim \text{MVNormal}(\mathbf{0}, \mathbf{P})$$

213 we can derive the appropriately scaled values with a matrix of standard normals **Z<sub>std</sub>** and a Cholesky  
 214 decomposition of **P**, so that

$$\mathbf{Z} \equiv \mathbf{Z}_{\text{std}} \mathbf{P}_L^T$$

215

$$\mathbf{P}_L^T = \text{Chol}(\mathbf{P})^T = \text{Chol}(\mathbf{SRS})^T = (\mathbf{S}\mathbf{R}_L)^T$$

216 In this case,  $\mathbf{Z}_{\text{std}}$  corresponds to `std_dev` and the function `diag_pre_multiply()` first creates a matrix with  
 217 `sd_zp` on the diagonal, i.e.  $\mathbf{S}$ , and then multiplies it with the lower Cholesky matrix `R_chol` representing  $\mathbf{R}_L$ .  
 218 The `'` symbol applies the transpose operator  $^T$  in Stan. Although this so-called *non-centered parameterization*  
 219 may seem like a lot of unnecessary work, separating out the scale and associations of the random effects in  
 220 this way will often lead to better model convergence and thus more efficient model estimation. Therefore,  
 221 these mathematically equivalent reparameterizations of the formal model are generally worth implementing  
 222 although not always strictly necessary.

## 223 Model

224 The model block contains the likelihood functions of the model, the priors for the basic parameters, as well  
 225 as any data structures that one may want to create for pragmatic convenience in specifying the model but  
 226 not save in the output (e.g. to reduce memory usage). We can again work through each component of this  
 227 block in turn.

```
228 model{
229   //separate RN parameters
230   vector[I] zp_mu = col(zp,1); //personality
231   vector[I] zp_beta = col(zp,2); //plasticity
232   vector[I] zp_theta = col(zp,3); //predictability
233
234   //initialize vectors for response models
235   vector[N] z_mu; //linear predictor of behavior expectation
236   vector[N] z_sigma; //linear predictor of behavior dispersion
237   vector[I] w_eta; //linear predictor of fitness expectation
238   //...
```

239 In this first step, we specify a few new vectors to separate out each RN parameter from the matrix `zp`  
 240 created in the transformed parameters block. This helps to avoid clutter in the model likelihood caused by  
 241 repeatedly subsetting the matrix for the respective columns `col(zp,1)`, `col(zp,2)`, and `col(zp,3)`, but we  
 242 specify it here because it would be redundant and thus a waste of memory to save these vectors in addition  
 243 to `zp`. Similarly, to tidy up the model likelihood, we create new vectors to hold the linear predictors of each  
 244 behavioral and fitness observation. Note that there is no need to create a linear predictor for the dispersion  
 245 of fitness, as nothing is predicting the residual SD of the fitness model, which is already taken care of by the  
 246 `sigma_0` parameter.

247 The next step is then to fill in these vectors. For the response model of behavior `z`

```
248 //...
249 //behavioral RN response model
250 z_mu = mu_0z + zp_mu[ind] + (beta_1z + zp_beta[ind]).*x ;
251 z_sigma = exp(theta_0z + zp_theta[ind]) ;
252 z ~ normal(z_mu, z_sigma);
```

253 The final line tells Stan that the observed values `z` were generated by a Normal distribution with a likelihood  
 254 function described by the expected means `z_mu` and standard deviations `z_sigma` of each observation. Note  
 255 that `z_sigma` is calculated with the exponential function `exp()` because the formal model is specified with  
 256 a log link function, so that the inverse exponential link function is applied to the linear predictor in order  
 257 return estimates on the appropriate scale, i.e. if  $\log(\sigma) = \theta$  then  $\exp(\theta) = \sigma$ . The operator `.*` indicates  
 258 element-wise multiplication of vectors, which in this case multiplies the slopes `beta_1z + zp_beta[ind]` by  
 259 the observed environmental gradient `x`. These three lines of code are therefore equivalent to

$$\begin{aligned}
 z_{ij} &\sim \text{Normal}\left(\mu_{ij}^{(z)}, \sigma_{ij}^{(z)}\right) \\
 \mu_{ij}^{(z)} &= \mu_0^{(z)} + \mu_j^{(z)} + \left(\beta_1^{(z)} + \beta_j^{(z)}\right) x_{ij} \\
 \log\left(\sigma_{ij}^{(z)}\right) &= \theta_0^{(z)} + \theta_j^{(z)}
 \end{aligned}$$



The index `ind` is here used to appropriately repeat the random effect values of each RN parameter across repeated observations of the behavior. For example, if the first four observations are for individual 1, so that `ind={1,1,1,1,2,...}`, then `zp_mu[ind]` will repeat the first value of `zp_mu` for the first four observations. This is why it is essential to correctly match the order of the index and the response vectors.

The fitness model can also be specified accordingly

```
//...
//fitness response model
w_eta = mu_0 + betas[1]*zp_mu + betas[2]*zp_beta + betas[3]*zp_theta +
          betas[4]*(zp_mu .*zp_mu) + betas[5]*(zp_beta .*zp_beta) +
          betas[6]*(zp_theta .*zp_theta) +
          betas[7]*(zp_mu .*zp_beta) + betas[8]*(zp_mu .*zp_theta) +
          betas[9]*(zp_beta .*zp_theta) ;
w ~ normal(w_eta, sigma_0);
```

There is no need for the `ind` index here because each individual's fitness is only observed once and the order of individual observations is maintained between the `z` and `w`. The final necessary step is to introduce priors for all basic parameters listed in the parameters block.

```
//...
//model priors

//fixed effects
mu_0z ~ normal(0,1);
beta_1z ~ normal(0,1);
theta_0z ~ normal(0,1);
mu_0 ~ normal(0,1);
betas ~ normal(0,1);

//random effects
sd_zp ~ exponential(1);
R_chol ~ lkj_corr_cholesky(2);
to_vector(std_dev) ~ std_normal();
sigma_0 ~ exponential(1);
}
```

For the matrix of standard normal RN parameter deviations `std_dev`, we should always specify that the vector of all elements in this matrix are described by a `std_normal()` distribution, which is necessary for the non-centered parameterization introduced in the transformed parameters block. The other parameters can be given whatever priors are intended for the analysis, which in this case are the weakly regularizing priors used in the formal model, i.e.

$$\mu_0^{(z)}, \beta_1^{(z)}, \theta_0^{(z)}, \mu_0, \beta_1, \dots, \beta_9 \sim \text{Normal}(0, 1)$$

$$\mathbf{S}, \sigma \sim \text{Exponential}(1)$$

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

## Generated quantities

The final programming block in our Stan model concerns the calculation of any quantities of interest which weren't directly estimated in earlier blocks.

```
generated quantities{
matrix[3,3] R = R_chol * R_chol'; //RN correlation matrix
matrix[3,3] S = diag_matrix(sd_zp); //RN SD matrix
matrix[3,3] P = S*R*S; //RN covariance matrix
vector<lower=0>[3] V_P = sd_zp .* sd_zp; //RN variances
}
```

308 We derive the full correlation matrix  $\mathbf{R}$  by multiplying the Cholesky matrix  $\mathbf{R}_L$  used for model estimation with  
 309 its transpose, accomplished with the transpose operator `'`. The covariance matrix  $\mathbf{P}$  is derived by multiplying  
 310 the full correlation and standard deviation matrices  $\mathbf{SRS}$ , and the variances of the RN parameters are  
 311 derived by squaring the SDs in `sd_zp`.

## 312 Final model code

313 With each programming block coded, we can put them all together and write to a single `.stan` file in R

```
write("
data {
  int<lower=1> I; //total individuals
  int<lower=1> N; //total number of observations
  int<lower=1> ind[N]; //index of individual observations
  vector[N] x; //environmental covariate
  vector[N] z; //behavioral measurements
  vector[I] w; //fitness measurements
}
parameters {
  //fixed population effects
  real mu_0z; //z population intercept
  real beta_1z; //z population slope
  real theta_0z; //z population dispersion
  real mu_0; //w population intercept
  real<lower=0> sigma_0; //w dispersion (sigma for Gaussian)
  vector[9] betas; //fitness regression coefficients

  //random effects
  vector<lower=0>[3] sd_zp; //RN parameter sds
  matrix[I,3] std_dev; //individual-level RN deviations
  cholesky_factor_corr[3] R_chol; //RN parameter correlations
}
transformed parameters {
  matrix[I,3] zp; //individual phenotypic RN parameter values
  zp = std_dev * diag_pre_multiply(sd_zp, R_chol)' ;
}
model{
  //separate RN parameters
  vector[I] zp_mu = col(zp,1); //personality
  vector[I] zp_beta = col(zp,2); //plasticity
  vector[I] zp_theta = col(zp,3); //predictability

  //initialize vectors for response models
  vector[N] z_mu; //linear predictor of behavior expectation
  vector[N] z_sigma; //linear predictor of behavior dispersion
  vector[I] w_eta; //linear predictor of fitness expectation

  //behavioral RN response model
  z_mu = mu_0z + zp_mu[ind] + (beta_1z + zp_beta[ind]).*x ;
  z_sigma = exp(theta_0z + zp_theta[ind]) ;
  z ~ normal(z_mu, z_sigma);

  //fitness response model
  w_eta = mu_0 + betas[1]*zp_mu + betas[2]*zp_beta + betas[3]*zp_theta +
    betas[4]*(zp_mu .*zp_mu) + betas[5]*(zp_beta .*zp_beta) +
```

```

        betas[6]*(zp_theta .*zp_theta) +
        betas[7]*(zp_mu .*zp_beta) + betas[8]*(zp_mu .*zp_theta) +
        betas[9]*(zp_beta .*zp_theta) ;
w ~ normal(w_eta, sigma_0);

//model priors

//fixed effects
mu_0z ~ normal(0,1);
beta_1z ~ normal(0,1);
theta_0z ~ normal(0,1);
mu_0 ~ normal(0,1);
betas ~ normal(0,10);

//random effects
sd_zp ~ exponential(1);
R_chol ~ lkj_corr_cholesky(2);
to_vector(std_dev) ~ std_normal();
sigma_0 ~ exponential(1);
}

generated quantities{
matrix[3,3] R = R_chol * R_chol'; //RN correlation matrix
matrix[3,3] S = diag_matrix(sd_zp); //RN SD matrix
matrix[3,3] P = S*R*S; //RN covariance matrix
vector<lower=0>[3] V_P = sd_zp .* sd_zp; //RN variances
}",
"mod1.stan")

```

## Estimate model

To estimate this model, we first pass it to Stan for C++ compilation.

```
#load package
library(rstan)

#compiles the model in C++ for MCMC estimation
mod1 = stan_model("mod1.stan")

#basic settings for rstan
options(mc.cores = parallel::detectCores())
rstan_options(auto_write = TRUE)
```

The compiled model in `mod1` is now ready to be sampled immediately using Markov Chain Monte Carlo (MCMC), which is accomplished by passing it to the `sampling()` function. For default MCMC settings in Stan, we could run

```
#sampling posterior dist of the model with default MCMC settings
results = sampling(object = mod1, data = data)
```

However, given that our model is somewhat complex, it is helpful to use custom settings for the sampler that will reduce the risk of poor performance. In particular, we can manually specify that the MCMC sampler should use 1500 iterations per chain to converge on the target joint posterior distribution `warmup=1500`, with the subsequent 1500 iterations/chain used as posterior samples `iter = 3000` (i.e. `iter - warmup` = number of MCMC samples per chain). `init = 0` initializes the samplers near null values, which is not necessary but can aid sampling of complex models. Four MCMC chains are used to assess model convergence across independent random samplers `chains=4`, with one core assigned to each chain for parallel processing `cores=4`. The appropriate number of cores to use will be contingent on one's hardware. The `adapt_delta=0.95` argument reduces the risk of divergent transitions during sampling.

```
#progress of MCMC chains can be tracked in the viewer pane of RStudio
results = sampling(object = mod1, data = data, warmup=1500, iter = 3000, init = 0,
                  chains=4, cores=4, control=list(adapt_delta=0.95) )

#save model
saveRDS(results, "results_mod1.RDS")
```

Some readers may note that there is no argument specified for thinning the chain, which implicitly specifies the default argument `thin=1`. Although there are specific contexts where thinning is useful for MCMC sampling, it is generally unnecessary and computationally inefficient (Link and Eaton 2012).

If you estimate a model in Stan and receive a warning or error, it may indicate issues with the MCMC sampler, which should always be taken seriously. Further description of these and other warnings can be found in the **Stan Warning Guide**. Some warnings can be safely ignored in particular contexts, but efforts should always be taken to first remove the issue before interpreting or reporting results from the sampler. If you receive a warning regarding divergent transitions, a straightforward first step is to increase the `adapt_delta` value closer to 1, e.g. from 0.95 to 0.99. The higher this value, the slower the model will sample but the less likely that divergent iterations will occur. Similarly, if warnings of bulk or tail ESS are received, a first step is to simply let the chains sample for longer by increasing the `iter`, e.g. from 3000 to 3500 or 4000.

Assuming that the sampling procedure worked as intended, we can then extract the posterior MCMC samples from the model.

```
#extracts posterior estimates
samples = extract(results)

#MCMC samples for linear selection coefficients
head(samples$betas[,1:3])
```

```

341 ##
342 ## iterations      [,1]      [,2]      [,3]
343 ##      [1,] 0.4286686 0.13072399 0.2313102
344 ##      [2,] 0.4047872 0.12240215 0.1741672
345 ##      [3,] 0.1281531 0.26382081 0.1530637
346 ##      [4,] 0.5762619 0.18941427 0.2699328
347 ##      [5,] 0.3410815 0.05963205 0.2641004
348 ##      [6,] 0.1497065 0.22204168 0.3474415

```

## 349 Investigate results

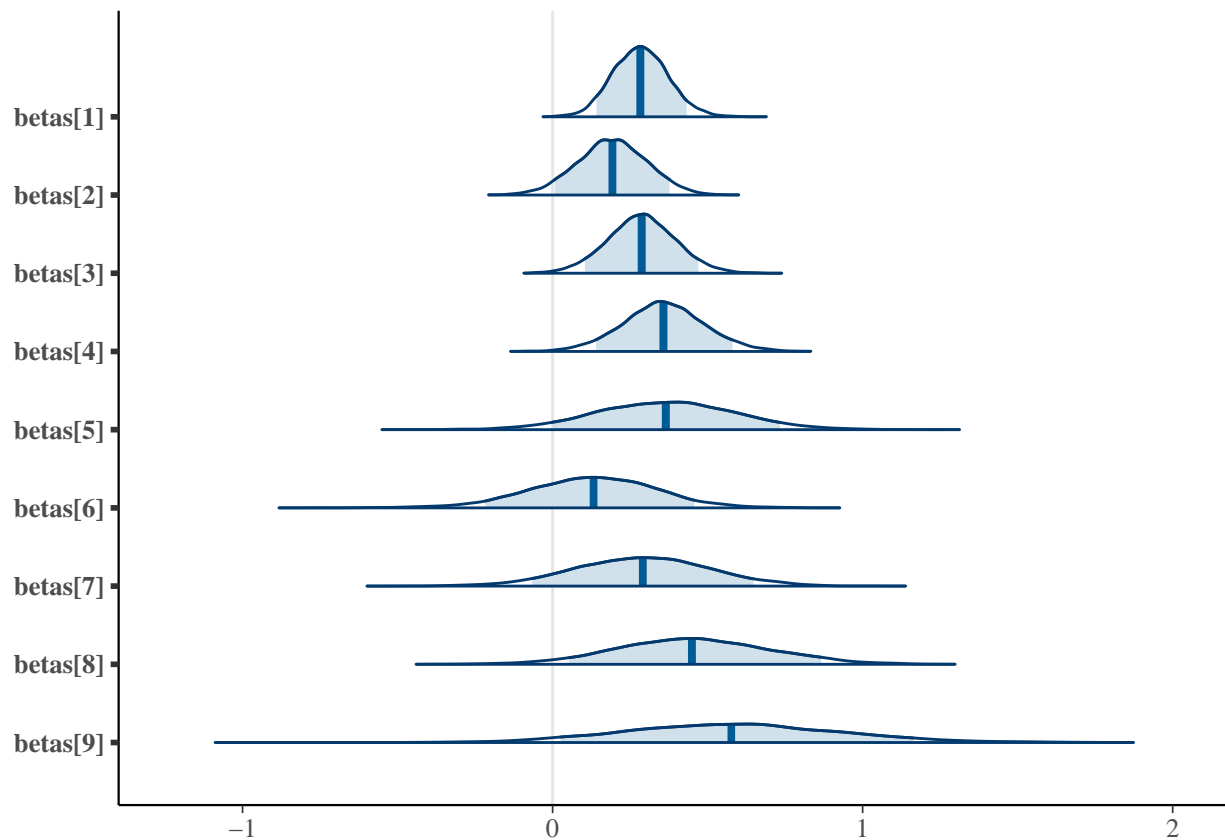
350 Before hypothesis testing, it is useful to visualize the shapes and locations of the posterior distributions of  
 351 model parameters. There are many ways this can be accomplished. For example, the `bayesplot` package can  
 352 be used to generate a variety of useful plots.

```

library(bayesplot)

#selection coefficients, with shaded central tendencies and 90% CIs
mcmc_areas(results, pars = c( paste0("betas[",seq(1:9),"]" ) ), prob = 0.9 )

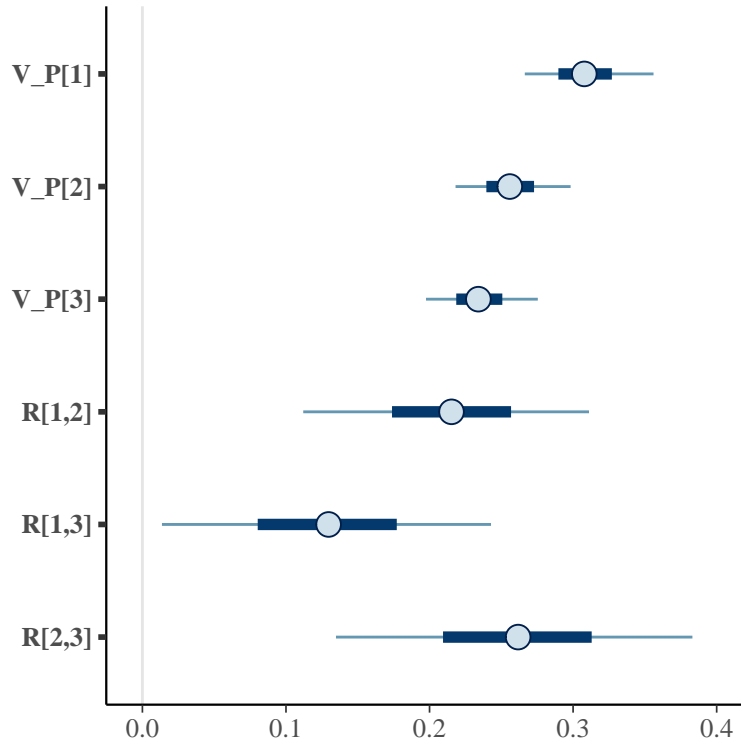
```



353

354

```
#variance & corrs of RN parameters, mean and 50% CIs (dark line) and 90% CIs (light line)
mcmc_intervals(results, pars = c( paste0("V_P[",seq(1:3),"),"), "R[1,2]", "R[1,3]", "R[2,3]" ) )
```



355

356 Point estimates summarizing these posteriors can be quickly generated by summarizing the model.

```
#only first 17 parameters, round to ease interpretation
round(summary(results)$summary[1:17,],2)
```

```
357 ##          mean se_mean   sd  2.5%  25%  50%  75% 97.5%  n_eff Rhat
358 ## mu_0z      0.00    0.00 0.03 -0.06 -0.02  0.00  0.02  0.06 2495.95   1
359 ## beta_1z    -0.05    0.00 0.03 -0.11 -0.07 -0.05 -0.03  0.01 2962.68   1
360 ## theta_0z   -0.36    0.00 0.03 -0.42 -0.38 -0.36 -0.34 -0.31 3038.88   1
361 ## mu_0       0.92    0.00 0.08  0.76  0.87  0.92  0.97  1.08 2577.48   1
362 ## betas[1]   0.28    0.00 0.09  0.12  0.22  0.28  0.34  0.46 3876.57   1
363 ## betas[2]   0.19    0.00 0.11 -0.03  0.12  0.19  0.27  0.41 3035.44   1
364 ## betas[3]   0.29    0.00 0.11  0.07  0.21  0.29  0.36  0.51 4394.43   1
365 ## betas[4]   0.36    0.00 0.13  0.10  0.27  0.36  0.44  0.62 4453.06   1
366 ## betas[5]   0.37    0.01 0.22 -0.07  0.21  0.37  0.52  0.81 1960.91   1
367 ## betas[6]   0.13    0.00 0.21 -0.30 -0.01  0.13  0.27  0.53 2362.55   1
368 ## betas[7]   0.29    0.00 0.22 -0.14  0.14  0.29  0.44  0.71 2653.50   1
369 ## betas[8]   0.45    0.00 0.25 -0.02  0.28  0.45  0.62  0.93 2638.06   1
370 ## betas[9]   0.58    0.01 0.35 -0.07  0.35  0.58  0.81  1.29 1515.57   1
371 ## sigma_0    0.73    0.00 0.03  0.68  0.71  0.73  0.75  0.79 5177.85   1
372 ## sd_zp[1]   0.56    0.00 0.02  0.51  0.54  0.55  0.57  0.60 2375.14   1
373 ## sd_zp[2]   0.51    0.00 0.02  0.46  0.49  0.51  0.52  0.55 2368.15   1
374 ## sd_zp[3]   0.48    0.00 0.02  0.44  0.47  0.48  0.50  0.53 2296.65   1
```

375 The extracted posterior samples can also be manually plotted and summarized using base R functions. For  
376 example, we can look at the population average residual variance of behavior  $\theta_0^{(z)}$  on the original data scale by  
377 manually applying the inverse link function `exp()` to the log-scale SD `theta_0z` and subsequently squaring

```

378 to return the variance.
#discrete approximation of posterior dist
hist(exp(samples$theta_0z)^2)

```



```

379
380 The shinystan package also provides a very helpful graphical user interface for looking at all aspects of
381 model fit and estimation. Running this code will open a new window in your internet browser for looking at
382 the model in greater detail.
library(shinystan)
launch_shinystan(results)

```

## 383 Hypothesis testing

384 MCMC not only facilitates sampling complex Bayesian models but also conducting straightforward and direct  
 385 forms of hypothesis testing. For example, if we want to know how much support there is for positive linear  
 386 and nonlinear selection effects, we simply need to calculate the proportion of the MCMC samples for these  
 387 parameters with positive magnitude, which approximates the area under the posterior distribution providing  
 388 support for positive effects.

```

#for each column, calculate probability of positive effect
apply(samples$betas, 2, FUN = function(x) sum(x>0)/length(x) )

389 ## [1] 0.9996667 0.9553333 0.9948333 0.9963333 0.9493333 0.7398333 0.9096667
390 ## [8] 0.9690000 0.9595000

```

391 Overall, the model provides consistent support for positive linear and nonlinear selection across the RN  
 392 parameters, with most effects showing posterior probabilities  $\geq 0.90$ . However, the evidence for the quadratic  
 393 effect of predictability  $\beta_6$ , or  $\beta_6 \left( \theta_j^{(z)} \theta_j^{(z)} \right)$ , is much weaker, with a posterior probability of only 0.74 in  
 394 support of a positive effect, suggesting that there is a 0.26 probability or  $\sim 1/4$  chance of a negative effect being  
 395 observed. Another way to think about these probabilities is in relation to Bayesian credible intervals (CIs).

396 In particular, we expect that if there is at least 0.95 probability of a directional effect, the 90% Bayesian CI  
 397 will exclude zero.

```

#for each column, calculate quantile based CI
apply(samples$betas, 2, FUN = function(x) quantile(x, c(0.05, 0.95)) ) #90% CI

398 ##
399 ##           [,1]           [,2]           [,3]           [,4]           [,5]           [,6]
400 ##    5%  0.1411164 0.006752543 0.1041608 0.1403970 -0.0006781906 -0.2164636
401 ##    95% 0.4325692 0.377335106 0.4701338 0.5801455 0.7331204912 0.4563855
402 ##
403 ##           [,7]           [,8]           [,9]
404 ##    5% -0.06665065 0.05239159 0.02603818
405 ##    95% 0.64781650 0.86620450 1.16348908

```

406 We can see, for example, that the lower bound of `beta[5]`, corresponding to  $\beta_5 \left( \beta_j^{(z)} \beta_j^{(z)} \right)$ , is just at the  
 407 negative boundary of zero, consistent with the posterior probability of 0.949. It is important to emphasize  
 408 that although 0.95 is a useful heuristic for designating clear evidence of an effect, discretizing this information  
 409 into “significant” or “non-significant” is generally a waste of information. Put another way, these Bayesian  
 410 hypothesis tests provides a continuous measure of evidence that should also be interpreted continuously. Much  
 411 as the difference between a significant and non-significant result is itself often not statistically significant  
 412 (see McShane et al. 2019 for discussion), so too is the difference between e.g. a posterior probability of  
 413 0.93 and 0.97 not necessarily indicative of crossing a biologically or mathematically meaningful threshold.  
 414 Thus, one should eschew the notion that a posterior probability <0.95 indicates “no evidence of an effect,”  
 415 and instead get comfortable describing varying degrees of support (weak, moderate, and strong) for or  
 416 against hypothesized effects. Any probability greater than 0.50 provides some support for an effect, but most  
 417 researchers would be uncomfortable to confidently assert empirical claims without much greater empirical  
 418 support in their favor, e.g. only a 1/20 chance of an effect in the opposite direction (i.e. a posterior probability  
 419 of 0.95). Therefore, the posterior probability of 0.74 for a positive `beta[6]` indicates that our data provides  
 420 *some* evidence for a positive quadratic selection effect on predictability, but this evidence is nonetheless very  
 421 weak/highly uncertain and warrants cautious description and interpretation. Encouraging this Bayesian  
 422 attitude toward evidence within behavioral ecology will be an important tool for promoting the goals of open  
 423 science, as it may help to dampen file-drawer effects and reduce the risk of *P*-hacking. A continuous approach  
 424 to statistical inference also encourages researchers to put greater emphasis on effect sizes, credible intervals,  
 425 and additional metrics which can collectively increase or decrease the overall “significance” of an empirical  
 426 finding (McShane et al. 2019).

427 As discussed in Martin (2021), A variety of other hypotheses can be easily tested for any parameter in the  
 428 model. For instance, we could ask whether there is support for directional selection on personality being  
 429 greater than directional selection on plasticity among individuals.

```

sum(samples$betas[,1] > samples$betas[,3])/length(samples$betas[,1])

430 ## [1] 0.4845

```

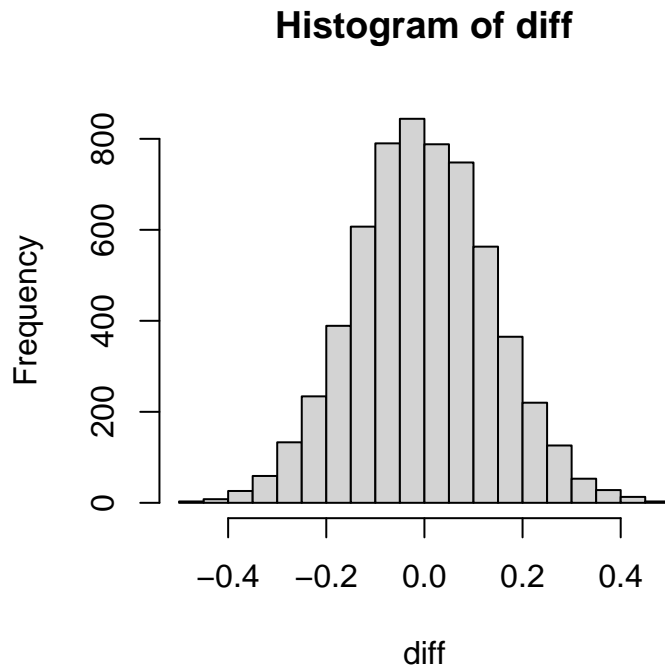
431 This value lower than 0.50 indicates that there is 0.52 probability in favor of the plasticity selection effect  
 432 being greater than the personality effect. As we expect based on simulating equivalent regression coefficients,  
 433 this indicates little to no evidence in support of a difference between these selection effects. We can also use  
 434 further pieces of information about the difference of these effect sizes to inform our inferences

```

diff = samples$betas[,1] - samples$betas[,3] #posterior of the difference in coefs
hist(diff) #visualize the posterior

```





435

```
mean(diff) #expected difference between regression coefs
```

436 ## [1] -0.003190825

```
mad(diff) #median absolute deviation (robust SD) of expected difference
```

437 ## [1] 0.1390162

```
quantile(diff, c(0.05,0.95)) #90% CI of expected difference
```

438 ## 5% 95%

439 ## -0.2320389 0.2300859

440 We can see that the posterior is centered near zero, with an expected difference of -0.003 and a very wide 90% CI.  
 441 One might report this in a manuscript by stating that, “Little to no evidence was found for stronger directional  
 442 selection on personality as compared to plasticity ( $\Delta\beta = -0.00$ ,  $MAD = 0.14$ ,  $90\%CI[-0.23, 0.23]$ ,  $p_+ = 0.48$ ),  
 443 suggesting that these RN parameters had approximately equivalent effects on individual fitness.”

444 If one is so inclined, robust null hypothesis tests can also be conducted within a Bayesian framework by  
 445 specifying a range of biologically trivial effect sizes. For example, on a standardized scale such as a regression  
 446 coefficient, values  $-0.10 < r < 0.10$  are considered extremely small, explaining less than 1% of variance in a  
 447 measure. We might, therefore, think of these as “trivial hypothesis” tests rather than null hypothesis tests  
 448 per se. Comparing these trivial hypothesis tests with directional hypothesis tests can provide distinct pieces  
 449 of information. Consider the RN parameter correlations

```

R=samples$R[,,] #3d array, 1 dim = samples, 2 dim = rows, 3 dim = columns

#directional hypothesis tests
sum(R[,1,2]>0)/length(R[,1,2]) #cor(personality, plasticity)

450 ## [1] 0.9993333
sum(R[,1,3]>0)/length(R[,1,3]) #cor(personality, predictability)

451 ## [1] 0.9638333
sum(R[,2,3]>0)/length(R[,2,3]) #cor(plasticity, predictability)

452 ## [1] 0.9993333
#trivial hypothesis tests
sum(-0.1< R[,1,2] & R[,1,2] <0.1)/length(R[,1,2]) #cor(personality, plasticity)

453 ## [1] 0.03383333
sum(-0.1< R[,1,3] & R[,1,3] <0.1)/length(R[,1,3]) #cor(personality, predictability)

454 ## [1] 0.3423333
sum(-0.1< R[,2,3] & R[,2,3] <0.1)/length(R[,2,3]) #cor(plasticity, predictability)

455 ## [1] 0.0195

```

The directional and trivial hypothesis tests work together to inform our understanding of the direction and magnitude of the estimated correlations. Firstly, we see clear evidence of positive effect sizes for all RN parameter correlations (probability 0.96-0.99), suggesting that personality, plasticity, and predictability are not developing independently among individuals (and may constrain microevolutionary trajectories as a result). We also see that the correlations between personality and plasticity and between plasticity and predictability are very unlikely to take on trivial effect sizes (probability 0.02-0.03), and thus may be worthy of further attention to explain how and why these correlations arise. However, there is a ~1/3 chance of the correlation between personality and predictability being trivially small, or put the other way, only a 0.66 probability of a non-trivial effect size. Therefore, while there is evidence of a positive correlation between these RN parameters, we cannot be confident that this association is of a biologically meaningful magnitude.

## Calculate selection differentials

We now want to calculate the total  $\Delta_T$  and direct  $\Delta_D$  selection differentials on RN parameters, which respectively quantify the expected change due to direct and indirect selection and the expected change due solely to direct selection. The total differentials are crucial for capturing patterns of evolutionary constrain or facilitation due to phenotypic integration, while the direct differentials are crucial for testing adaptive hypotheses irrespective of integration among traits. As proposed and explained in Martin (2021), these differentials are calculated by

$$\begin{aligned}
 \Delta_T \bar{z}_P &= \mathbf{P} \boldsymbol{\beta}, \\
 \Delta_T \mathbf{P} &= \mathbf{P} \left( \boldsymbol{\gamma} - \boldsymbol{\beta} \boldsymbol{\beta}' \right) \mathbf{P} \\
 \Delta_D \bar{z}_P &= \mathbf{V} \boldsymbol{\beta}, \\
 \Delta_D \mathbf{V} &= \mathbf{V} \left( \boldsymbol{\gamma} - \boldsymbol{\beta} \boldsymbol{\beta}' \right) \mathbf{V}
 \end{aligned}$$

where  $\mathbf{V} = \mathbf{S}^2 = \text{diag}(\mathbf{P})$ . The first step in calculating selection differentials is to multiply the quadratic selection effects by 2 (Stinchcombe et al. 2008) and to create lists containing each posterior sample of the

475 linear vector  $\beta$  and the nonlinear selection matrix  $\gamma$ . This will ensure that posterior uncertainty in the  
 476 selection coefficients is pooled across all stages of analysis (Stinchcombe, Simonsen, and Blows 2014).

```
betas = samples$betas #all coefficients
direct = betas[,1:3] #directional gradients
quad = betas[,4:6]*2 #2x to get appropriate gradients
cor = betas[,7:9] #correlational gradients

#create beta vector
beta_vec = list() #initialize list of vectors
for(i in 1:nrow(direct)) {
  beta_vec[[i]] = matrix(direct[i,],nrow = 3, ncol = 1)
}

#create gamma matrix
gamma_mat = list() #initialize list of matrices
for(i in 1:nrow(quad)) {
  #diagonal with quad gradients
  gamma = diag(quad[i,])
  #add in off-diagonal elements
  gamma[1,2] = cor[i,1] #personality, plasticity
  gamma[1,3] = cor[i,2] #personality, predictability
  gamma[2,3] = cor[i,3] #plasticity, personality
  #make symmetric
  gamma[lower.tri(gamma)] = t(gamma)[lower.tri(gamma)]
  #add to list
  gamma_mat[[i]] = gamma
}
```

477 We then need to create lists of the matrices  $\mathbf{P}$  and  $\mathbf{V}$  for the total and direct selection differentials respectively.

```
P = samples$P

#create list of P matrix
P_mat = list()
for(i in 1:nrow(P)){
  P_mat[[i]] = P[i,,]
}

#create list of V matrix
V_mat = list()
for(i in 1:nrow(P)){
  V_mat[[i]] = diag(diag(P[i,,]))
}
```

478 The posteriors of the  $\Delta_T$  and  $\Delta_D$  differentials can now be calculated.

```
#change in mean
dT_mean = Map('%*%',P_mat,beta_vec)
dD_mean = Map('%*%',V_mat,beta_vec)

#change in (co)variance
dT_vcv = Map('%*%',
  Map('%*%', P_mat,
    Map('-',gamma_mat,
      Map('%*%',beta_vec,lapply(beta_vec,t) ))),
  P_mat )
dD_vcv = Map('%*%',
  Map('%*%', V_mat,
    Map('-',gamma_mat,
      Map('%*%',beta_vec,lapply(beta_vec,t) ))),
  V_mat )
```

479 Let's calculate the expectations and uncertainty of the mean differentials.

```
#expected total mean change (personality, plasticity, predictability)
apply(simplify2array(dT_mean), 1:2, mean)

##           [,1]
## [1,] 0.10865359
## [2,] 0.08432013
## [3,] 0.08924963

#90% CI for mean change
apply(simplify2array(dT_mean), 1:2, function(x) quantile(x,c(0.05,0.95)))

## , , 1
##
##           [,1]           [,2]           [,3]
## 5%  0.06512052 0.03778112 0.04838245
## 95% 0.15569664 0.13134327 0.13111724

#expected direct mean change
apply(simplify2array(dD_mean), 1:2, mean)

##           [,1]
## [1,] 0.08745891
## [2,] 0.04922922
## [3,] 0.06722475

#90% CI for mean change
apply(simplify2array(dD_mean), 1:2, function(x) quantile(x,c(0.05,0.95)))

## , , 1
##
##           [,1]           [,2]           [,3]
## 5%  0.04408368 0.001632592 0.02447695
## 95% 0.13413236 0.097099634 0.10991089
```

498 There is clear evidence that selection is acting to increase the mean levels of the RN parameters for personality,  
 499 plasticity, and predictability in the population, both directly and indirectly through the effects of phenotypic  
 500 integration. It is important to note that the predictability parameters  $\theta^{(z)}$  are defined formally such that  
 501 larger values lead to greater residual variance in individual behavior. Therefore, increasing the mean level of

502 this parameter will lead to *less* predictable behavioral responses (i.e. the residual variance gets larger).

503 For the variances and covariances of these parameters

```
#expected total mean change (personality, plasticity, predictability)
apply(simplify2array(dT_vcv), 1:2, median)

504 ##           [,1]      [,2]      [,3]
505 ## [1,] 0.08050008 0.05643778 0.05098252
506 ## [2,] 0.05643778 0.07430578 0.05651980
507 ## [3,] 0.05098252 0.05651980 0.03480419

#90% CI for mean change
apply(simplify2array(dT_vcv), 1:2, function(x) quantile(x,c(0.05,0.95)))

508 ## , , 1
509 ##
510 ##           [,1]      [,2]      [,3]
511 ## 5%  0.03751402 0.02699874 0.02391278
512 ## 95% 0.13066521 0.08948957 0.08089675
513 ##
514 ## , , 2
515 ##
516 ##           [,1]      [,2]      [,3]
517 ## 5%  0.02699874 0.03377101 0.02855279
518 ## 95% 0.08948957 0.12042274 0.08997154
519 ##
520 ## , , 3
521 ##
522 ##           [,1]      [,2]      [,3]
523 ## 5%  0.02391278 0.02855279 0.001103422
524 ## 95% 0.08089675 0.08997154 0.073057153

#expected direct mean change
apply(simplify2array(dD_vcv), 1:2, median)

525 ##           [,1]      [,2]      [,3]
526 ## [1,] 0.05941041 0.01873089 0.02645083
527 ## [2,] 0.01873089 0.04406009 0.03149115
528 ## [3,] 0.02645083 0.03149115 0.00939549

#90% CI for mean change
apply(simplify2array(dD_vcv), 1:2, function(x) quantile(x,c(0.05,0.95)))

529 ## , , 1
530 ##
531 ##           [,1]      [,2]      [,3]
532 ## 5%  0.01779514 -0.009712015 -0.001034179
533 ## 95% 0.10521728  0.048163066  0.055253205
534 ##
535 ## , , 2
536 ##
537 ##           [,1]      [,2]      [,3]
538 ## 5% -0.009712015 -0.003215799 -0.0006163572
539 ## 95% 0.048163066  0.094942054  0.0658182535
540 ##
541 ## , , 3
```

```

542 ##
543 ##           [,1]           [,2]           [,3]
544 ## 5%  -0.001034179 -0.0006163572 -0.02888327
545 ## 95%  0.055253205  0.0658182535  0.04725932

```

Note that the 90% CIs are calculated across the columns of the  $\Delta_T \mathbf{P}$  and  $\Delta_D \mathbf{P}$  matrices. We find evidence that both direct and indirect selection are increasing the (co)variance of the RN parameters. However, the direct effect of selection on trait (co)variances is less certain and of smaller magnitude. Phenotypic integration among RN parameters is thus leading to greater individual variation and trait correlations than would otherwise be expected by the direct effects of selection alone.

## Plot results

While it is helpful to summarize the differentials with point estimates, the models provide posterior distributions that can also be plotted and visually interpreted to gain a fuller sense of the uncertainty in these estimates. We'd also like to know how the expected within-generation changes of each RN parameter will change the overall shape of the population average behavioral RN. First we'll consider plotting the differentials for RN parameters. As argued in Martin (2021), it is helpful to separately visualize the expected change in means, trait variance, and trait correlations, as each provides unique information relevant for testing adaptive hypotheses. First we need to create dataframes in long format for plotting.

```

#change in means (list to matrix)
dT_mean = matrix(unlist(dT_mean), nrow=length(dT_mean), ncol=3, byrow=TRUE,
                  dimnames = list(1:length(dT_mean), c("pers","plst","pred")))
dD_mean = matrix(unlist(dD_mean), nrow=length(dD_mean), ncol=3, byrow=TRUE,
                  dimnames = list(1:length(dD_mean), c("pers","plst","pred")))

#separate change in variance from covariance
dT_V = matrix(unlist(lapply(dT_vcv,diag)), nrow=length(dT_vcv), ncol=3, byrow=TRUE,
              dimnames = list(1:length(dT_vcv), c("pers","plst","pred")))
dD_V = matrix(unlist(lapply(dD_vcv,diag)), nrow=length(dD_vcv), ncol=3, byrow=TRUE,
              dimnames = list(1:length(dD_vcv), c("pers","plst","pred")))

#change in correlations
dT_R = matrix(unlist(lapply(dT_vcv,FUN = function(x) x[lower.tri(x)])),
              nrow=length(dT_vcv), ncol=3, byrow=TRUE,
              dimnames = list(1:length(dT_vcv), c("pers_plst","pers_pred","plst_pred")))
dD_R = matrix(unlist(lapply(dD_vcv,FUN = function(x) x[lower.tri(x)])),
              nrow=length(dD_vcv), ncol=3, byrow=TRUE,
              dimnames = list(1:length(dD_vcv), c("pers_plst","pers_pred","plst_pred")))

#wide to long for plotting
library(reshape)
dT_meanl = melt(dT_mean)
dD_meanl = melt(dD_mean)
d_meanl = rbind(dT_meanl,dD_meanl) #combine
d_meanl$type = rep(c("T","D"), each = nrow(dT_meanl))

dT_Vl = melt(dT_V)
dD_Vl = melt(dD_V)
d_Vl = rbind(dT_Vl,dD_Vl)
d_Vl$type = rep(c("T","D"), each = nrow(dT_Vl))

dT_Rl = melt(dT_R)
dD_Rl = melt(dD_R)

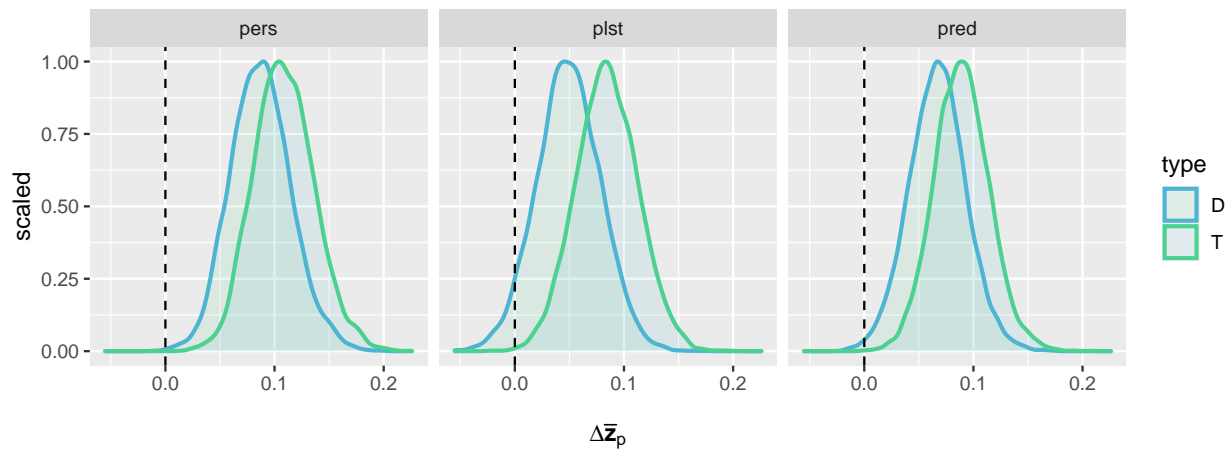
```

```
d_R1 = rbind(dT_R1,dD_R1)
d_R1$type = rep(c("T","D"), each = nrow(dT_R1))
```

559 The data are now ready for plotting.

```
library(ggplot2)

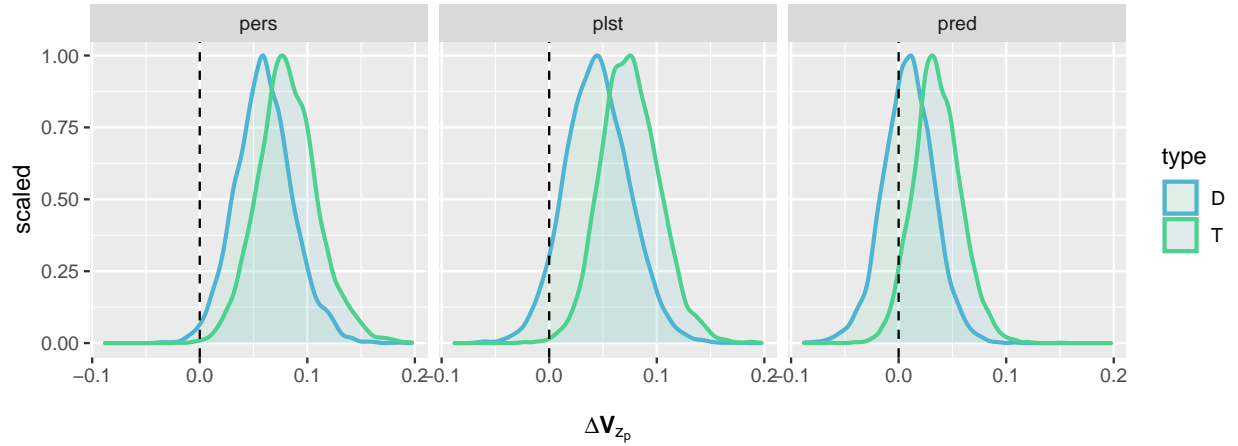
#mean differentials
ggplot(d_mean1, aes( x = value, color = type, fill = type)) +
  geom_density(aes(y=..scaled..), size = 0.9, alpha = 0.10) +
  facet_grid(. ~ X2)+
  scale_color_manual(values=c("#4db4d1","#4dd191"))+
  geom_vline(xintercept = 0, linetype = "dashed", size = 0.5)+
  xlab( bquote(atop("", paste(Delta,bold(bar(z))[p] ))))+
  scale_fill_manual(values=c("#4dd191","#4db4d1"))
```



560

```
library(ggplot2)

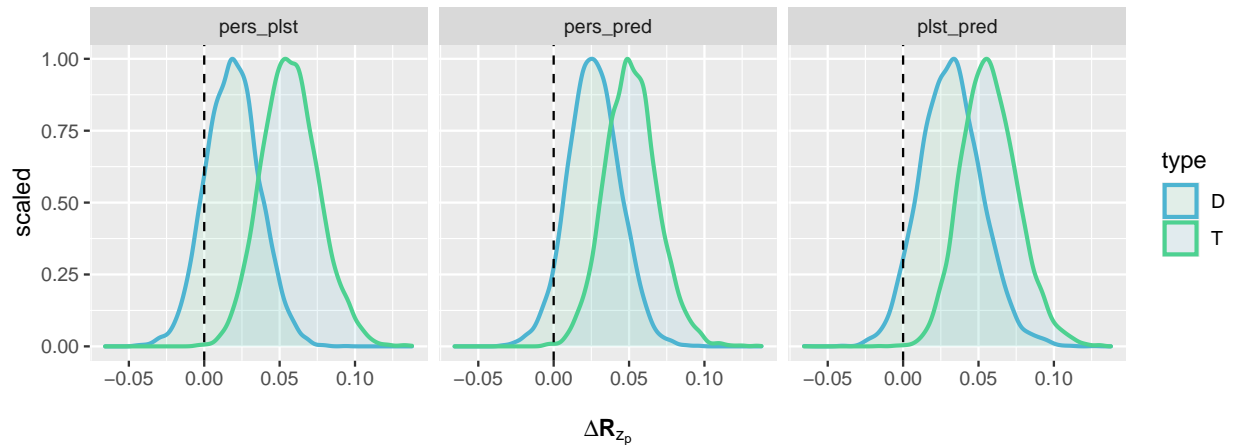
#variance differentials
ggplot(d_V1, aes( x = value, color = type, fill = type)) +
  geom_density(aes(y=..scaled..), size = 0.9, alpha = 0.10) +
  facet_grid(. ~ X2)+
  scale_color_manual(values=c("#4db4d1","#4dd191"))+
  geom_vline(xintercept = 0, linetype = "dashed", size = 0.5)+
  xlab( bquote(atop("",paste(Delta,bold(V)[z[p]] ))))+
  scale_fill_manual(values=c("#4dd191","#4db4d1"))
```



561

```
library(ggplot2)

#correlation differentials
ggplot(d_Rl, aes( x = value, color = type, fill = type)) +
  geom_density(aes(y=..scaled..), size = 0.9, alpha = 0.10) +
  facet_grid(. ~ X2)+
  scale_color_manual(values=c("#4db4d1","#4dd191"))+
  geom_vline(xintercept = 0, linetype = "dashed", size = 0.5)+
  xlab( bquote(atop("",paste(Delta,bold(R)[z[p]] ))))+
  scale_fill_manual(values=c("#4dd191","#4db4d1"))
```



562

563 To visualize the full shape of the population RN, we need to first add the original population values  $\mu_0^{(z)}$ ,  
 564  $\beta_1^{(z)}$ , and  $\theta_0^{(z)}$  to the  $\Delta_T$  and  $\Delta_D$  to get absolute values following the selection event. We can then use point  
 565 estimates of these posteriors to generate a single plot of the RN function.

```
#personality (pop intercept mu)
mu = median(samples$mu_0z) #linear w/o link function
T_mu = median(samples$mu_0z + dT_mean[,1]) #following selection
D_mu = median(samples$mu_0z + dD_mean[,1])

#plasticity (pop slope beta)
beta = median(samples$beta_1z)
T_beta = median(samples$beta_1z + dT_mean[,2])
D_beta = median(samples$beta_1z + dD_mean[,2])
```



```

#predictability (pop intercept theta)
theta = median(exp(samples$theta_0z))
#exp inverse link of absolute value on the log scale
T_theta = median(exp(samples$theta_0z + dT_mean[,3]))
D_theta = median(exp(samples$theta_0z + dD_mean[,3]))

```

566 We create an arbitrary environmental covariate for visualizing the population RN before and after selection

```
x = seq(-1,1,by = 0.05)
```

567 and calculate the 95% CI (or 90% CI) for the RN.

```

#before selection
z_low = mu + beta*x -1.96*theta #1.96 = 95% CI
z_high = mu + beta*x +1.96*theta

```

```

#after selection
Tz_low = T_mu + T_beta*x -1.96*T_theta
Tz_high = T_mu + T_beta*x +1.96*T_theta

```

```

Dz_low = D_mu + D_beta*x -1.96*D_theta
Dz_high = D_mu + D_beta*x +1.96*D_theta

```

568 We're now ready for plotting.

```

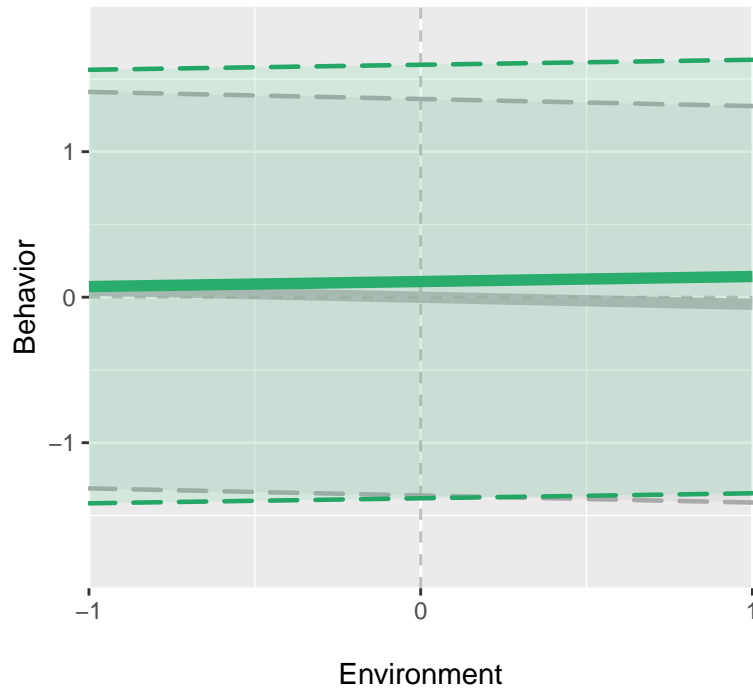
ggplot() +
  coord_cartesian(xlim=c(-1, 1), ylim=c(-2, 2)) +
  scale_x_continuous(expand = c(0, 0), breaks = c(-1,0,1),
    labels = c(-1,0,1) )+
  scale_y_continuous(expand = c(0, 0), breaks = c(-1,0,1),
    labels = c(-1,0,1) ) +
  geom_hline(yintercept=0,linetype="dashed", alpha = 0.25)+
  geom_vline(xintercept=0,linetype="dashed", alpha = 0.25) +

  geom_abline(intercept = mu, slope = beta, size = 2, alpha =0.75, color = "darkgrey") +
  geom_ribbon(aes(x = x, y = mu + beta*x, ymin = z_low, ymax = z_high),
    size = 0.8, linetype = 5, alpha = 0.15, color = "darkgrey", fill = "darkgrey")+

  geom_abline(intercept = T_mu, slope = T_beta, size = 2, color = "#23a666") +
  geom_ribbon(aes(x = x, y = T_mu + T_beta*x, ymin = Tz_low, ymax = Tz_high),
    size = 0.8, linetype = 5, alpha = 0.15, color = "#23a666", fill = "#4dd191")+
  xlab("\nEnvironment")+
  ylab("Behavior")+
  ggtitle(expression(paste(bold(Delta[T]),bold(" Population-Level Behavioral RN"))))+
  guides(fill=FALSE, color=FALSE)

```

## $\Delta_T$ Population-Level Behavioral RN

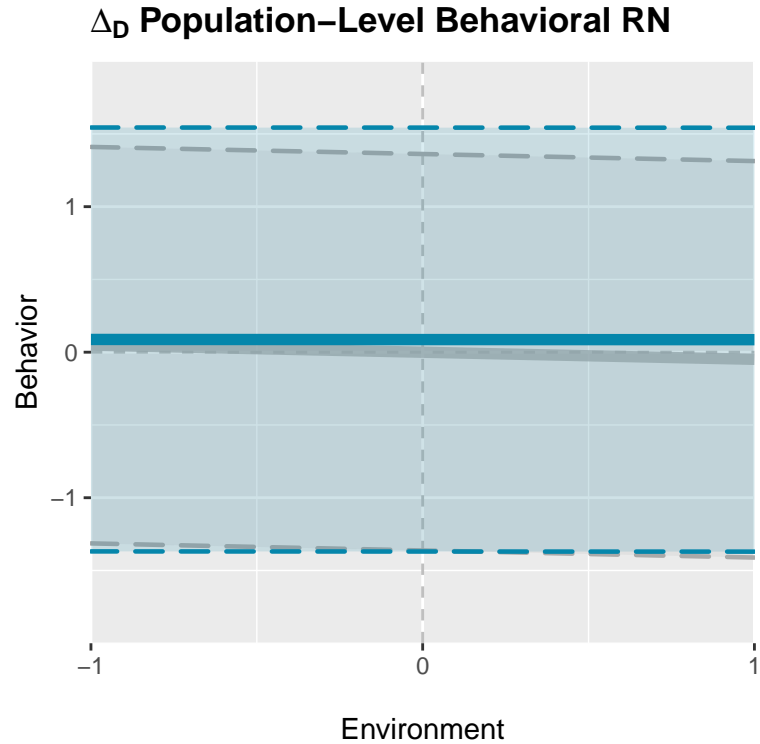


569

```
ggplot() +
  coord_cartesian(xlim=c(-1, 1), ylim=c(-2, 2)) +
  scale_x_continuous(expand = c(0, 0), breaks = c(-1,0,1),
    labels = c(-1,0,1) )+
  scale_y_continuous(expand = c(0, 0), breaks = c(-1,0,1),
    labels = c(-1,0,1) ) +
  geom_hline(yintercept=0,linetype="dashed", alpha = 0.25)+
  geom_vline(xintercept=0,linetype="dashed", alpha = 0.25) +

  geom_abline(intercept = mu, slope = beta, size = 2, alpha =0.75, color = "darkgrey") +
  geom_ribbon(aes(x = x, y = mu + beta*x, ymin = z_low, ymax = z_high),
    size = 0.8, linetype = 5, alpha = 0.15, color = "darkgrey", fill = "darkgrey")+

  geom_abline(intercept = D_mu, slope = D_beta, size = 2, color = "#0586ab") +
  geom_ribbon(aes(x = x, y = D_mu + D_beta*x, ymin = Dz_low, ymax = Dz_high),
    size = 0.8, linetype = 5, alpha = 0.15, color = "#0586ab", fill = "#0586ab")+
  xlab("\nEnvironment")+
  ylab("Behavior")+
  ggtitle(expression(paste(bold(Delta[D]),bold(" Population-Level Behavioral RN"))))+
  guides(fill=FALSE, color=FALSE)
```



As in the main text, grey is used to indicate the current population RN. Overall, we can see that direct and total selection are expected to slightly increase levels of expected personality (RN intercept) and plasticity (RN slope) in the population. There is also an increase in the level of the predictability parameter (RN dispersion, shaded band) due to total selection, which suggests that individuals' behavior will become slightly more random in the population due to an increase in the expected residual variance.

## Forthcoming tutorials

Further examples will be added in the future for simplifying the full model (e.g. only considering selection on personality), estimating non-Gaussian response models and selection gradients, introducing repeated fitness measures, and including structural equation models of RNs.

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