

Variation in plasticity of personality traits implies that the ranking of personality measures changes between environmental contexts: calculating the cross-environmental correlation

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Abstract Studies increasingly explore whether there is variation between individuals in how they adjust their behavior to different environmental contexts using random regression analysis (RR). RR estimates the between-individual variance in elevation (expected behavior in the mean environment) and variance in plasticity (individual-specific adjustment of behavior to the environment) and the covariance between these properties. These (co)variances allow deriving both environment-specific repeatability estimates and the individual-level correlation in behavior between environmental conditions, both of which are of key interest for understanding consistency in behavior over space and time, a core issue in animal personality research. However, very few studies use the RR estimates to produce this information. In this paper, I outline how to extract this information (including example code in R) and apply the approach to 16 estimates based on nine published RR studies. Despite the fact that the behaviors have a decent repeatability under different environmental conditions, I find that in half the cases, the cross-environmental correlation is low (<0.4). This implies that individuals differ in their behavioral trait values but that the ranking of these individual values tends to change between environmental conditions. This level of inconsistency in animal

personality traits appears not to have been fully appreciated, and future studies on plasticity using RR should explicitly include it.

Keywords Behavioral traits · Cross-environmental correlation · Random regression analysis

Introduction

Part of the variance in most behavioral traits is repeatable or even heritable (van Oers et al. 2005; Bell et al. 2009; van Oers and Sinn 2011). Repeatable behavioral metrics are considered as traits showing individual consistency and quantify aspects of animal personality (Réale et al. 2007). To explain individual consistency in behavior is typically viewed as a challenge, because classic behavioral ecological theory is based on the assumption of individuals making facultative adjustments in their behaviors to the prevailing environmental conditions (Sih et al. 2004). Despite a certain level of consistent differences between individuals, the population mean behavior often varies across an environmental gradient, indicating plasticity. In the last decade, the concept of individual-level plasticity has entered the realm of evolutionary and behavioral ecologists working in wild populations (Nussey et al. 2007; Dingemanse et al. 2010). A critical question asked by this framework is whether plasticity is also present at the individual level and whether there is between-individual variance in plasticity. The main statistical tool to analyze these questions has been random regression (Henderson 1982; Kirkpatrick and Heckman 1989; Schaeffer 2004), a statistical technique which is sometimes also referred to as “random slopes model.” In evolutionary ecology, random regression models are regularly used to quantify variation across individuals in how they adjust phenological traits to climatic variables (reviewed by Nussey et al. 2007; van de Pol

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2012; Brommer 2013b) or how performance traits vary between individuals across age (Wilson et al. 2008). Behavioral ecologists have used the random regression approach mainly for analyses that consider variation in plasticity between individuals, thereby recognizing that individuals may not all follow the same trait–environment relationship (variance in plasticity or $I \times E$; Nussey et al. 2007). The main consequence of acknowledging this level of variation has been framed in terms of changes in between-individual variance in a behavioral trait across an environmental context (Dingemanse et al. 2010; Dingemanse and Dochtermann 2013). Hence, the focus has been on the fact that $I \times E$ implies that repeatability (the proportion of phenotypic variance which is due to between-individual differences) becomes context specific. In this paper, I highlight a particular aspect of the study of variation in plasticity using random regression which has not received much attention in the behavioral literature, but which has a clear scope to widen our understanding for why behavioral consistency can be maintained in wild populations subjected to environmental heterogeneity.

Random regression is one of several so-called function-valued trait approaches (e.g., Stinchcombe et al. 2012). Instead of considering trait expression as specific for each so-called “character state” (e.g., environmental value or age), function-valued trait models use a mathematical simplification to describe the trait variances and covariances over the various character states (Lynch and Walsh 1998). This is usually a massive simplification, because recognizing n character states requires estimation of $0.5 n(n+1)$ (co)variances, which rapidly becomes overwhelming for most datasets based on a linear environmental covariate. Random regression simplifies this estimation by allowing the trait value to vary as a polynomial function on the level of the “subject” of interest, e.g., the individual. Random regression estimates the variances in elevation and linear slope and their covariance, with the possibility to include higher-level polynomials (quadratic, cubed, etc.) and their covariances to the other terms (Schaeffer 2004; Nussey et al. 2007). While random regression is rapidly becoming an accepted tool in evolutionary ecology, it seems its relationship to the character-state approach is, at present, not fully exploited in behavioral studies. In particular, it is informative to consider, given the random regression estimates, what the individual-level cross-environmental correlation is. The pattern of the reaction norms contains information on how the ranking of the individual-specific trait values changes over the environmental gradient (Fig. 1). Clearly, in the absence of variation in plasticity (all individuals follow the population-level plastic response), the ranking of individual-specific trait values is maintained between environmental contexts A and B (Fig. 1a, b). This ranking is also maintained in the case of a high-magnitude (positive or negative) correlation between elevation and slope (Fig. 1c, d), although this pattern

of reaction norms is associated to a change in between-individual variance (Fig. 1c) and thus repeatability. In contrast, when the correlation between elevation and slope is low, the ranking of individual-specific values changes between environmental contexts (Fig. 1e, f), and this occurs despite the fact that the between-individual variance (repeatability) is high under both contexts (Fig. 1e). Clearly, therefore, understanding how repeatability changes over the environmental gradient is only one aspect of a reaction norm perspective of behavior; the other aspect is provided by the cross-environmental correlation.

Here, I outline how one can, from random regression estimates, derive the cross-environmental individual-level correlation between behavioral trait values. I compile random regression estimates from the literature on various behavioral traits to demonstrate that published studies indicate that the cross-environmental correlation may be low. I discuss the potential evolutionary implications of such a low cross-environmental correlation and argue that future studies should include information of the cross-environmental correlation and its confidence. I append code to facilitate estimating these quantities.

Methods

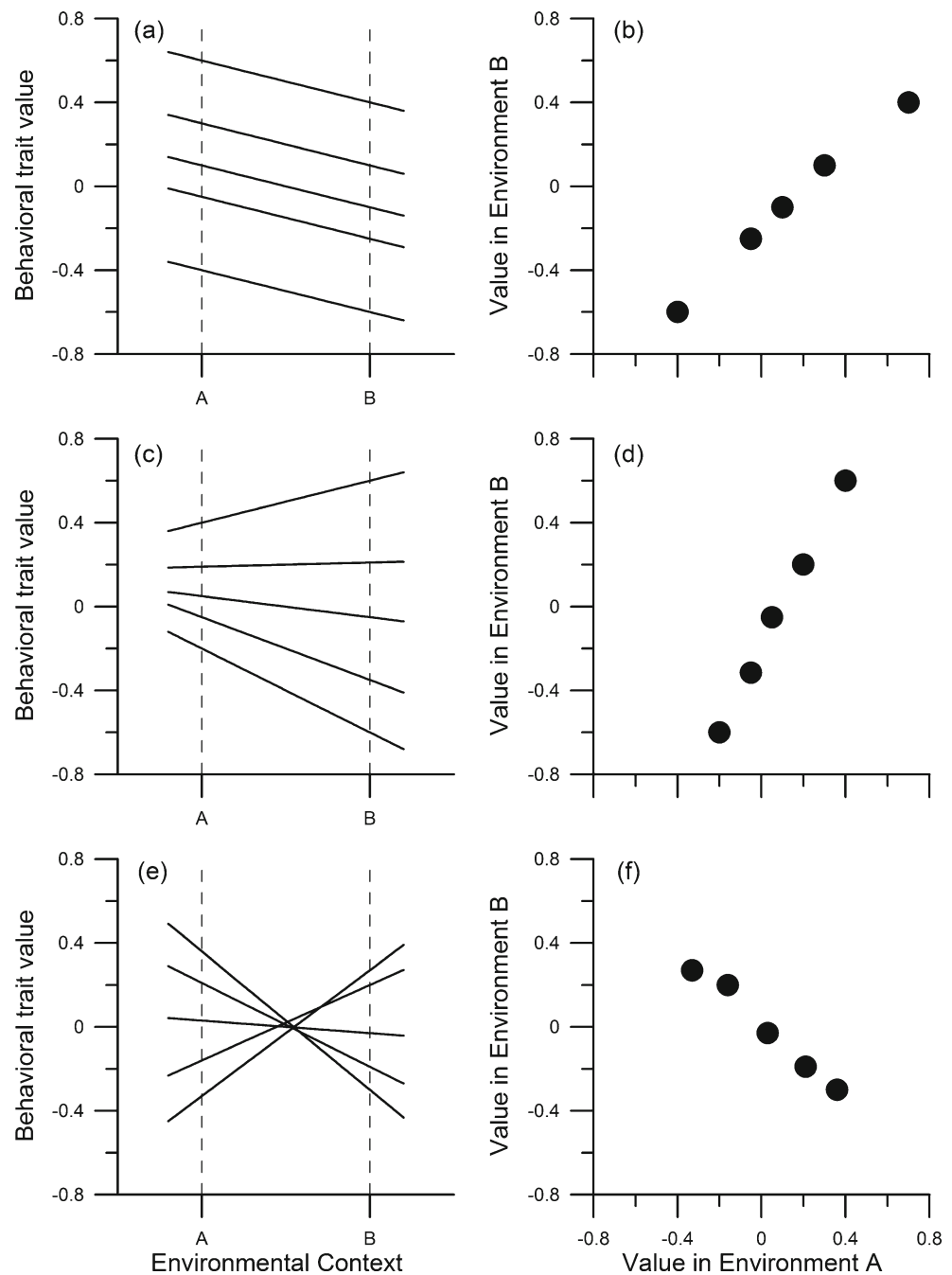
From random regression estimates to character states

Random regression estimates variances in elevation, linear, and higher-order slopes and all the covariances between these (Schaeffer 2004; Nussey et al. 2007; Dingemanse and Dochtermann 2013). A general formulation of random regression on the individual level is that the expression of trait z by individual i at instance t under environmental condition E is modeled as follows:

$$z_{i,t,E} = \mu_F + b_F E_t + f_{\text{ind}}(i, x, E_t) + \varepsilon_{i,t,E}. \quad (1)$$

The environmental values E can be continuous (e.g., millimeter of rainfall in a 2-week period) which then should be standardized to zero mean. The environmental value can also, for example, be a binary (0, 1) variable. The coefficient μ_F is the overall fixed effect mean trait expression (intercept) when the environmental condition E has value “0,” and b_F is the fixed effect slope which gives the population-level plasticity of trait z to environmental condition E . The random regression function $f_{\text{ind}}(i, x, E_t)$ indicates an orthogonal polynomial of order x describing the individual-specific relationship between trait z and the environment E which the individual experienced as instance t . A zero-order ($x=0$) random regression models differences between individuals

Fig. 1 Schematic illustration of how the pattern of reaction norms provides information on the cross-environmental correlation. *Left side panels (a, c, e)* plot reaction norms where the behavioral trait value of individuals is a function of the environment. For two environmental contexts *A* and *B*, the correlation between the values for these individuals is plotted in the *right-hand side panels (b, d, f)* which correspond to the reaction norms plotted on the same “row”



in the extent to which they deviate from μ_F , $f_{\text{ind}}(i, 0, E) = \text{ind}_{0,i}$, which is here termed elevation (cf. Nussey et al. 2007). A first-order polynomial function will, in addition to elevation, also model variation between individuals in the linear slope of their z - E relationships. That is $f_{\text{ind}}(i, 1, E) = \text{ind}_{0,i} + \text{ind}_{1,i} E$. Likewise, higher-order polynomials will also consider curvilinear slopes, for example, $f_{\text{ind}}(i, 2, E) = \text{ind}_{0,i} + \text{ind}_{1,i} E + \text{ind}_{2,i} E^2$. Lastly, the residual $\varepsilon_{i,t,E}$ captures the difference between observed trait value of individual i in

environment E at instance t to what is expected on the basis of the fitted fixed and random effects included in the model.

Equation (1) describes a linear mixed model, where the random regression term constitutes a random effect. On the basis of restricted maximum likelihood or using the Bayesian implementation, the variance in ind_0 and ind_1 and higher order terms, as well as the covariance(s) between these terms, are estimated. These random regression estimates can be summarized in matrix form. For example, for a first-

order random regression, the variance V and covariance C of elevation ind_0 and linear slope ind_1 estimated using random regression can be denoted as the following matrix:

$$\mathbf{K} = \begin{bmatrix} V(\text{ind}_0) & C(\text{ind}_1, \text{ind}_0) \\ C(\text{ind}_0, \text{ind}_1) & V(\text{ind}_1) \end{bmatrix}. \quad (2)$$

Given \mathbf{K} , the variances specific to each environmental value and the covariances between these can be derived (e.g., Meyer 1998), denoted as variance–covariance matrix \mathbf{P} for any series of points along the environmental gradient. This is done by using the estimates provided by the random regression (i.e., variance in elevation, slope, and their covariance) to evaluate what the between-individual variances are at environmental conditions E_1 and E_2 as well as the individual covariance between E_1 and E_2 . The two environmental conditions can be denoted in the following double-column vector:

$$\Phi = \begin{bmatrix} 1 & E_1 \\ 1 & E_2 \end{bmatrix}. \quad (3)$$

The matrix \mathbf{P} is then obtained by taking the product of these matrices

$$\mathbf{P} = \Phi \mathbf{K} \Phi', \quad (4)$$

where Φ' denotes the transposed vector Φ . This product results in the matrix

$$\mathbf{P} = \begin{bmatrix} V_I(E_1) & C_I(E_2, E_1) \\ C_I(E_1, E_2) & V_I(E_2) \end{bmatrix}, \quad (5)$$

where $V_I(E_1)$ and $V_I(E_2)$ are the between-individual variances in trait z in environmental conditions 1 and 2, respectively, and $C_I(E_1, E_2)$ [$C_I(E_2, E_1)$] denotes the individual covariance between these environmental conditions. Note that the residual variance $\varepsilon_{i,t,E}$ [Eq. (1)] is often assumed to be constant for all E and t . A constant residual variance is here called a univariate or homogeneous residual variance. Alternatively, a heterogeneous residual variance can be fitted (e.g., separate residual variances for E_1 and E_2 or separate residuals variances for different instances). The residual covariance between environmental contexts is assumed to be zero, following standard statistical assumptions on residuals. The individual covariance can be scaled following the definition of a correlation to obtain the individual-level cross-environmental correlation:

$$r_I(E_1, E_2) = \frac{C_I(E_1, E_2)}{\sqrt{V_I(E_1)V_I(E_2)}}. \quad (6)$$

Equation (4) is general and applies also when higher-order random regression terms are fitted and when more than two points are evaluated. These can be included by expanding matrix \mathbf{K} and vector Φ . For simplicity, this is not presented here. R example code for Eqs. (2–6) is

provided in the electronic supplement. In constructing Φ , it should be noted that software may internally rescale the environmental covariate provided by the user. The values for E_1 and E_2 must be on the scale used to estimate the random regression (co)variances. Programs R and SAS will not rescale. ASReml will scale the covariate such that the minimal observed value is -1 , and the mean of the covariate values is 0. Other programs may scale the covariate differently.

The difference between the covariance in elevation and slope and the cross-environmental covariance

Above specifies in general terms how the estimates which one readily obtains from a random regression (e.g., variation in elevation, slope, and their covariance), matrix \mathbf{K} , can be “translated” to variances specific to each environment and the cross-environmental covariance, matrix \mathbf{P} . In this section, I use a simple scenario to exemplify the relationship of \mathbf{K} to \mathbf{P} and explain verbally how and why these are not equivalent. Assumed that there are two environmental values, E_1 and E_2 , which are coded as values 0 and 1, respectively. It then follows from the above that $V_I(E_1) = V(\text{ind}_0)$. That is, the variance between individuals when the environment has value 0 is given by the variance between individuals in elevation, because an individual's elevation is its deviation from the overall mean when the environmental covariate E equals 0 (E_1). Furthermore, when $E_1=0$ and $E_2=1$, an individual's slope quantifies the change in its expected behavior between E_1 and E_2 . Equation (4), when written out for this example scenario, states that $V_I(E_2) = V(\text{ind}_0) + V(\text{ind}_1) + 2C(\text{ind}_0, \text{ind}_1)$. That is, the variance when $E=1$ is the sum of the variance between individuals when $E=0$ and the variance between individuals in the difference between their expected behavior z in E_1 and E_2 (i.e., their slope) plus twice the covariance between elevation and slope. The latter can be loosely interpreted as taking into account whether elevation and slope are completely independent ($C(\text{ind}_0, \text{ind}_1)=0$) or whether they are compounding and thus increase the total individual variance in E_2 ($C(\text{ind}_0, \text{ind}_1)>0$) or have opposite effect sizes and hence reduce the total individual variance in E_2 ($C(\text{ind}_0, \text{ind}_1)<0$).

Although the covariance between elevation and slope (which is provided by the software) is related to the cross-environmental correlation (which needs to be calculated a posteriori following the above-outlined equations), these two quantities do not necessarily reflect one another in effect size or even in sign. Consider, for example, the above-outlined simple scenario with $E_1=0$ and $E_2=1$ and assume that the correlation between elevation and slope is zero ($C(\text{ind}_0, \text{ind}_1)=0$). Under these conditions, the cross-environmental covariance is positive [$C_I(E_1, E_2) = V(\text{ind}_0)$], since a variance cannot be negative. Likewise, when the cross-environmental

covariance is zero [$C_I(E_1, E_2) = 0$], the covariance between elevation and slope is negative [$C_I(E_1, E_2) = V(\text{ind}_0) + (C(\text{ind}_0, \text{ind}_1) = 0 \leftrightarrow (C(\text{ind}_0, \text{ind}_1) = V(\text{ind}_0))$].

The above-outlined considerations illustrate that calculation of the variances specific to relevant environmental conditions as well as the cross-environmental covariance (correlation) between these environmental conditions is a worthwhile exercise. This is because it adds information on (1) between-individual variances and, hence, repeatability specific to multiple environmental conditions and (2) whether the ranking of individual-specific values under one environmental condition correlates to the ranking of individual-specific values under another environmental condition.

Confidence intervals of the cross-environmental correlation

The above equations concern the point estimates of the cross-environmental correlation. Obtaining its confidence interval is more challenging. This further depends on the software used to implement the random regression. The cross-environmental correlation is a function of the random regression (co)variances. When these (co)variances are estimated in a likelihood framework as random effects, the only option to obtain their confidence interval is the use of the delta method (algorithm provided by Fischer et al. 2004). However, application of these algorithms requires information on the variances of the random regression (co)variances and the covariance between these variances on the data scale. For the commonly used R routines “lme” and “lmer,” this information is not available on the data scale, but on an internally transformed scale (Pinheiro and Bates 2000). This transformation is done to assure that the random regression (co)variance matrix is positive definite, but it does not lend itself for applying the delta method. A parametric bootstrap (Faraway 2006) for the cross-environmental correlation could then be an option (R code for this is provided by Klueen and Brommer 2013). For software that does provide the variances of the random regression (co)variances and the covariances between these variances (such as ASReml), applying it is cumbersome and assumption laden. The assumption made by the delta method is that the elevation and slope variances stem from a bivariate normal distribution, but variances rarely are symmetrical. A good alternative, therefore, is to use the Bayesian statistics to obtain the posterior distribution of the random regression (co)variances and applying Eqs. (1–5) directly on these. A possible implementation of this approach in the R package MCMCglmm is provided in the supplement.

Literature estimates of cross-environmental correlations

To obtain random regression estimates, I scanned the literature based on a search in the web of science for “plasticity”

and “behavior.” I further investigated studies included in the reviews presented by van de Pol (2012) and Mathot et al. (2012). I considered only studies which have quantified the variance between individuals in how trait value changes in response to an environmental covariate and separated this aspect from the residual variance. To arrive at estimates of between-individual variance requires both replication and explicit analysis of the between-individual variance. It is not uncommon to find studies on plasticity which confuse variance in plasticity (between-individual variation in slope) with residual variance. For example, Ouyang et al. (2011) calculated, as a measure of plasticity, the difference in corticosterone titer between two time periods for each individual based on one measure per individual per time period. This design does not allow separation of variation in plasticity between the time periods from any residual (within-individual noise) variance. Hence, interpreting the difference between the two measures taken in each time period as plasticity necessarily assumes a complete absence of residual variance, which is biologically unlikely. Other studies quantify plasticity but do so for each individual separately. For example, Rodriguez-Prieto et al. (2011) used linear regression to estimate the plasticity (slope) of each tested individual, but this approach does not provide information on the variances and covariance across individuals in a fashion comparable to random regression (Pinheiro and Bates 2000).

In most published studies, the cross-environmental correlation was not reported. To estimate it from the published information, I extracted the (co)variance components needed to apply Eq. (4). Studies where information on all random regression (co)variance components were not reported were not included. When one piece of information was missing in the original publication, I contacted the corresponding author. Because most studies were based on two environmental contexts, I constructed the vector Φ for two environments and also for studies where the environment was a gradient. The values for E_1 and E_2 [Eq. (3)] along such a gradient were chosen to lie at opposite ends, as based on information presented in the publication.

Results

I found 16 estimates based on nine studies (Table 1). The studies and estimates included in this table all showed statistically significant $I \times E$. Studies which quantified variation in plasticity but did not report variance estimates (and thus were excluded) were those by Martin and Réale (2008; no $I \times E$), Adriaenssens and Johnsson (2011; $I \times E$ in one of two traits), Biro et al. (2010; $I \times E$ in three of five traits), Rieucan et al. (2010; no $I \times E$), Ord et al. (2010; $I \times E$ in three out of five traits), and Morand-Ferron et al. (2011; $I \times E$ in two out of two traits). Clearly, statistics of $I \times E$ effect sizes suffer

from poor reporting in the literature. In addition, Bonte et al. (2007) and Quinn et al. (2012) did not include the covariance between elevation and slope, despite the fact that their data allowed to fit this (repeated measures of individuals were collected in different environments). It is this covariance term which specifies how the reaction norm pattern looks like (Fig. 1) and thus what the cross-environmental correlation is. Hence, not estimating, it is problematic for the interpretation

of the cross-environmental correlation, and these studies, therefore, could not be included. Another noteworthy aspect of the literature studies is that almost all assumed univariate residuals (Table 1).

Because the variance in slope across individuals is dependent on how the environmental covariate is scaled, it is not trivial to express the proportion of phenotypic variance in behavior which is due to variation in plasticity. However,

Table 1 Overview of nine published studies which have used a random regression mixed model to evaluate how between-individual variances depend on an environmental covariate. Full reference (“Ref”) is provided below the table. Each estimate is numbered (“Nr”). For each species investigated, the behavioral trait and the environmental covariate are

provided. The software used to implement the approach is given as well as whether the residual variance was assumed to be univariate (“Uni”) or allowed to be heterogeneous (“Het”). From the publication, information on variance in random regression elevation (“ $V(\text{ind}_0)$ ”) and slope (“ $V(\text{ind}_1)$ ”) was extracted as well as the correlation between these (“ $r(\text{ind}_0, \text{ind}_1)$ ”)

Ref	Nr	Species	Trait	Environment	Software	Res	$V(\text{ind}_0)$	$V(\text{ind}_1)$	$r(\text{ind}_0, \text{ind}_1)$
1 ^a	1	Great tit, Boshoeck (<i>Parus major</i>)	Exploration	Experience	WinBUGS	Uni	26.70	11.10	0.86
1 ^a	2	Great tit, Lauwersmeer (<i>Parus major</i>)	Exploration	Experience	WinBUGS	Uni	14.70	15.30	0.91
1 ^a	3	Great tit, Westerheide (<i>Parus major</i>)	Exploration	Experience	WinBUGS	Uni	16.20	12.10	0.85
1 ^a	4	Great tit, Wytham woods (<i>Parus major</i>)	Exploration	Experience	WinBUGS	Uni	11.50	26.00	1.04
2 ^b	5	Ural owl (<i>Strix uralensis</i>)	Aggression	Food availability	R/lme	Uni	1.30	0.17	0.45
3 ^c	6	House sparrow (<i>Passer domesticus</i>)	Provisioning rate	Precipitation	SAS	Uni	2.10	0.09	−1.31
4 ^d	7	Red knot (<i>Calidris canutus</i>)	Vigilance, low–intermediate predation risk	Predation risk	R/lme4	Uni	0.25	0.65	0.06
4 ^d	8	Red knot (<i>Calidris canutus</i>)	Vigilance–intermediate–high predation risk	Predation risk	R/lme4	Uni	0.94	1.95	−0.45
5 ^e	9	Blue tit (<i>Cyanistes caeruleus</i>)	Escape time	Season	R/nlme	Uni	0.06	0.19	−0.74
5 ^e	10	Blue tit (<i>Cyanistes caeruleus</i>)	Neophobia	Season	R/nlme	Uni	0.06	0.60	−0.59
6 ^f	11	Tree swallow (<i>Tachycineta bicolor</i>)	Nest defense	Temperature	R/lmer	Uni	2.90	0.01	0.64
7 ^g	12	Great tit (<i>Parus major</i>)	Dispersal distance from feeder	Time	SAS	Uni	0.20	0.02	−0.14
8 ^h	13	Eastern Chipmunk (<i>Tamias striatus</i>)	Activity in open field test	Time	R/nlme	Uni	0.81	0.01	−0.52
8 ^h	14	House mouse (<i>Mus mus</i>)	Activity, distance (cm/min) in open-field trial	Time	R/nlme	Uni	184.87	25.90	−0.60
9 ⁱ	15	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	Exploration, Cae Mawr population	Time	AsReml	Het	0.44	0.33	0.21
9 ⁱ	16	Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	Exploration, Llyn Alaw population	Time	AsReml	Het	0.45	0.25	0.42

Missing information was complemented by contacting the corresponding author. The variance in slope was always significant for the traits listed here (there was $I \times E$), and none of these studies tried to fit higher order random regression

^a Dingemanse et al. (2012b)

^b Kontiainen et al. (2009)

^c Westneat et al. (2011)

^d Mathot et al. (2011)

^e Kluen and Brommer (2013)

^f Betini and Norris (2012)

^g van Overveld and Matthysen (2010)

^h Montiglio et al. (2010)

ⁱ Dingemanse et al. (2012a)

there are eight estimates in Table 1 which are based on the same scale, contrasting two environments (0 vs. 1). For these studies, the variances between individuals' elevation $V(\text{ind}_0)$ denote the variance across individuals in behavior when measured in environment value 0, and the variance in slope $V(\text{ind}_1)$ denotes the variance in the change of these individuals' behavior when moving from environmental value 0 to "1". Inspection of the effect sizes in Table 1 thereby show that in six of these eight studies, more than 50 % of the between-individual variance (sum of variance in elevation $V(\text{ind}_0)$ and variance in slope $V(\text{ind}_1)$) was attributable to how they change their behavior (i.e., plasticity). This indicates that variation in plasticity, when present, can be a strong factor in driving between-individual differences.

Based on the literature estimates (Table 1), I calculated the change in repeatability over the environmental gradient and the individual-level correlation between these contextual environments (Table 1), based on Eqs. (1–6). This can only be done for point estimates, so confidence intervals are lacking. The choice of the environmental values was usually clear from the publication. However, in two cases (estimate Nr 6 and 11 in Tables 1 and 2), I extracted climatic information following the link to the climatic weather station presented in the original publication. With the exception of the study by Westneat et al. (2011) (estimate Nr 6 in Table 2), the trait repeatability (R) was typically reasonably high (>20 %) under both environmental conditions (Table 2). Thus, between-individual variation was typically present. However, the cross-environmental correlation in individual-specific behavioral trait values was often low, lying below 0.4 in half of the cases (Table 2). Four of the cross-environmental correlations close to 1 found by Dingemanse et al. (2012b) (estimates Nr 1–4 in Table 2) concern plasticity of exploration between testing an individual for the first vs. any consecutive time, which is a special case of "environment," for which a high correlation is expected.

The correlation between elevation and slope, which describes the level of crossing (Fig. 1), only partly reflects the cross-environmental correlation (Fig. 2). This is because the latter is also determined by how much variation there is in plasticity relative to the variation in elevation. When there is little variation in slope across individuals, most of the ranking of the individual trait values in each environmental context is determined by the variation in elevation rather than how they change their behavior. Thus, even negative correlations between elevation and slope need not imply a negative cross-environmental correlation (Tables 1 and 2, Fig. 2). Hence, the literature estimates underline the theoretical expectations of differences in the sign and magnitude between the elevation–slope correlation provided by the software and the derived calculations of the cross-environmental correlation.

Table 2 The environment-specific repeatability and the cross-environmental correlation calculated for the estimates provided in Table 1 following Eqs. (1–5)

Ref	Nr	Environment	V_R	E_1	E_2	R (1)	R (2)	R (12)
1	1	Experience (0, 1)	65.90	0	1	0.29	0.51	0.98
1	2	Experience (0, 1)	49.00	0	1	0.23	0.54	0.98
1	3	Experience (0, 1)	53.40	0	1	0.23	0.49	0.97
1	4	Experience (0, 1)	59.60	0	1	0.16	0.55	1.01
2	5	Food availability (Z)	1.00	−2	2	0.53	0.74	0.35
3	6	Precipitation	31.60	−1.8	1.8	0.12	0.01	1.47
4	7	Predation risk (0, 1)		0	1	0.07	0.22	0.56
4	8	Predation risk (0, 1)		0	1	0.22	0.34	0.26
5	9	Season (0, 1)	0.31	0	1	0.16	0.23	−0.26
5	10	Season (0, 1)	1.34	0	1	0.04	0.25	−0.32
6	11	Temperature	1.55	−2	2	0.61	0.68	0.98
7	12	Time (days)	0.70	0	6	0.22	0.56	0.34
8	13	Time (6 30-s periods)	1.18	0	6	0.41	0.33	0.86
8	14	Time (min)	153.24	0	4	0.55	0.63	0.08
9	15	Time (0, 2, and 4 h)	0.33/ 0.17	−1	0.84	0.65	0.83	0.21
9	16	Time (0, 2, and 4 h)	0.52/ 0.18	−1	0.84	0.45	0.83	0.36

The environmental covariate is specified as being linear (printed in bold) with the units between parentheses on the scale used to calculate the variance in slope (program dependent) or as a factorial level (not in bold) with the coding of the factors between parentheses. The residual variance (V_R) is taken from the published study. In one study that used heterogeneous error variances, the residual variances are reported for the two environments used. Elements of the matrix \mathbf{K} [Eq. (1)] are based on the estimates given in Table 1. The double-vector Φ [Eq. (2)] is constructed using the values for E_1 and E_2 specified in this table. Based on Eq. (4), the environment-specific between-individual variance $V_I(E)$ was then calculated for E_1 and E_2 in order to calculate repeatability R for environment E_1 and E_2 [R (1) and R (2), respectively] as $V_I(E)/(V_I(E)+V_R+V_{\text{other}})$. For study 6, $V_{\text{other}}=0.02$, but other studies did not include another variance component. The cross-environmental correlation R (12) was calculated following Eq. (5). Residual variances were not reported in study 4, but this study did report the environment-specific repeatabilities. For Ref and Nr, see Table 1

An outline of methods for estimating the cross-environmental correlation

The literature overview above suggests that it is worthwhile to calculate the cross-environmental correlation because it provides additional information of interest to behavioral ecologists. In particular, it is not very intuitive to interpret the correlation between the elevation and slope provided by the random regression. The cross-environmental correlation more directly informs of the consistency of individuals in

terms of their behavior over the environmental gradient. Point estimates for this correlation can be calculated using any software which allows carrying out matrix multiplications (R code provided in [Electronic Supplement](#)). Code for carrying out the Bayesian characters state and Bayesian random regression using the package MCMCglmm (Hadfield 2010) is provided in the [Electronic Supplement](#). An example dataset is simulated, and the output of these approaches is compared for this dataset.

Discussion

In this paper, I outline how one can extract the cross-environmental correlation for individual-specific trait values based on random regression estimates and show some possible implementation of how to do so. Whenever we find variation in plasticity between individuals ($I \times E$ variance, Nussey et al. 2007), the cross-environmental correlation is of interest. This is because it informs us whether the ranking of individual behavioral trait values tends to be maintained when moving from one environmental context to the other (Fig. 1c, d) or whether the ranking changes (Fig. 1e, f). This information is important, because individual-level consistency in a behavioral metric is considered the hallmark of animal personality. Hence, we typically, at least implicitly, assume that the finding of repeatability in, say, aggression implies that an aggressive individual is aggressive under all environmental contexts. However, the presence of between-individual variation in plasticity immediately implies that the

same individual, while being still different from other individuals, may alter its behavior relative to others as a function of the environment (Kluen and Brommer 2013). Thus, the individual which is most aggressive under one environmental condition need not be the most aggressive individual under another environmental condition. Because natural environments are heterogeneous, individual variation in plasticity makes it possible that a plastic behavioral trait, although repeatable under various contexts, still harbors considerable individual-level inconsistency when investigated over an environmental gradient. My review of literature estimates indeed suggests considerable environmental inconsistency in the ranking of individual trait values. About half of the estimated cross-environmental correlations were below 0.4, suggesting that the individual-specific behavioral trait values measured in one environmental context explain less than 16 % (0.4^2) of the between-individual variance in another environmental context. Clearly, the level of behavioral consistency across environmental conditions, therefore, seems low in many cases when between-individual variation in plasticity is present. The notion of plasticity and between-individual variance in plasticity is increasingly addressed in behavioral ecology (reviewed by Dingemanse et al. 2010; Mathot et al. 2012; Brommer 2013b). Nevertheless, the review presented in this paper shows that explicit calculation of the cross-environmental correlation and, hence, its potential implications for the study at hand typically remained unidentified by those who conducted the study.

A second aspect is that the review of the literature of estimates of between-individual variation in plasticity of behavioral traits reveals under-reporting of its statistics. Not reporting $I \times E$ variance when not significant is understandable, but many studies also lack information on between-individual variance and $I \times E$ variance and covariance, when these are significant. Future work should improve on reporting if we are to understand the generality of the various potential patterns of reaction norms. The cross-environment correlation was only estimated in one of the studies on plasticity in behavior, which demonstrates that the method of how to extract this information from the random regression coefficients is not widely appreciated within the literature on behavioral traits.

A third point of the literature review is that it shows that homogeneous residuals are typically assumed. This is striking, given that the purpose in using random regression is to allow for heterogeneous between-individual variance across the environmental gradient and that, hence, by extension, it would seem reasonable to also allow for heterogeneous residual variances. It is possible that by assuming a constant residual, the between-individual variance is inflated, although I am not aware of any systematic exploration of this possibility. In addition, it is noteworthy that no study has explored random regression polynomials higher than the first order. Nevertheless, many studies only contrasted two or

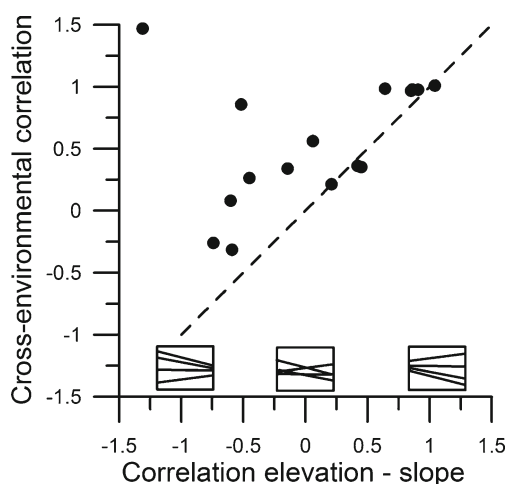


Fig. 2 Plot of the relationship between the elevation–slope correlation estimated by random regression of the studies reported in Table 1 against the estimate of the cross-environmental correlation for the environmental values reported in Table 2. The dashed diagonal line indicates complete correspondence. Boxes along the abscissa graphically illustrate how reaction norms with a correlation between elevation and slope which is negative (furthest most left), zero (middle), or high (furthest right) could look like

three environments, where only first-order polynomials can be fitted.

Fourth, most studies did not critically relate the estimates provided by the random regression to more assumption-free approaches. Because random regression is a mathematical simplification, which a priori assumes that a certain function captures the data, its estimates are possibly misleading. If the assumed function provides a poor fit to the real biological pattern, then the models will be at best non-informative and at worst incorrect and misleading. For example, random regression often predicts large between-individual variance at the extreme values of the environmental covariate, which need not be real, but rather results from the paucity of data at the edges of the environmental range experienced by the population. Hence, relating the variance estimates based on the random regression parameters to the real data is important. This can be done by, for example, plotting the data as well as the environment-specific variances predicted by the random regression with its 95 % confidence interval (e.g., Fig. S1). In addition, the environment-specific repeatability and the cross-environmental correlation can be estimated using a part of the raw data (the data on repeated measures) to assure that the estimates derived from the random regression are sensible. Note, however, that the raw data cross-environmental correlation will be biased towards zero, assuming that the residual cross-environmental correlation is zero (Brommer 2013a). It is further worthwhile to consider fitting the data using a character-state framework (Lynch and Walsh 1998), especially when there are only two or three environments as this directly produces the environment-specific (co)variances. When there are two or three environments, a character-state approach would be a better option, as it requires the same number of parameters but makes fewer assumptions than random regression. For example, Mathot et al. (2011) used two random regressions between environmental values E_1 and E_2 and between E_2 and E_3 , thereby essentially duplicating the data and the results for E_2 . The data structure would have allowed fitting a three-character-state model, which would additionally provide information on the individual correlation between E_1 and E_3 , which was not estimated in the approach used by the authors.

Fifth, the explicit calculation of the cross-environmental correlation underlines that only considering the correlation between reaction norm elevation and slope is not fully informative regarding the pattern of the reaction norms. A low or negative correlation between elevation and slope indicates crossing of the reaction norms at some point along the environmental gradient. However, whether this crossing occurs within the range of environmental values experienced by the population or whether the variation between individuals is mostly determined by variation in elevation (mean trait expression) are additional important aspects which determine the cross-environmental correlation. As a consequence, the

correlation between elevation and slope will correlate with the cross-environmental correlation, but it does not provide the same information. By explicit calculation of the cross-environmental correlation between environmental values which are biologically relevant, one can translate the fairly abstract elevation–slope correlation into a metric with a more intuitive meaning.

A positive cross-environmental correlation lower than unity indicates a change in the ranks of the individual values, and thus some crossing, but the rankings of the individual behaviors are still positively correlated across the environmental context. True reversal of rankings would lead to a cross-environmental correlation significantly below zero, such as found, e.g., by Klueen and Brommer (2013). It is not trivial to decide how much crossing of reaction norms is required for it to have evolutionary implications (Lynch and Walsh 1998). To understand the evolutionary implications of a low cross-environmental individual correlation, one also needs to measure selection. If the direction of selection is consistent over the environmental gradient, such that, e.g., more aggressive individuals are performing better in all environments, a low cross-environmental correlation in behavior implies that different individuals are selectively favored under different environmental conditions. Such a process could therefore help to maintain variation in behavior in a population, which is considered the main question in this field at present (Sih et al. 2004; Réale et al. 2007). Nevertheless, for these evolutionary processes to apply, the $I \times E$ variance must have a heritable basis; thus, there must be a genotype–environment interaction ($G \times E$) producing a low genetic correlation across environmental contexts. Provided information on the relatedness between individuals is available, $G \times E$ can be estimated (Nussey et al. 2007). Statistically, this is a further partitioning of the $I \times E$ variance, which has, thus far, only been done in one study (Dingemanse et al. 2012a). This study not only revealed significant $G \times E$ in the two populations studied but also showed that the reaction norm pattern of the $G \times E$ differed substantially from the pattern suggested by $I \times E$ in one of these populations. Results on $I \times E$ should, therefore, be carefully interpreted as a first-line approximation of $G \times E$.

Conclusion

Random regression is a powerful tool to help us understand how variation in behavior between individuals is modified by environmental conditions. Its application in the behavioral ecological literature to date is increasing. Future studies can benefit from calculating the cross-environmental correlation from the random regression estimates, which is now not commonly done. At the same time, future studies should improve the reporting of the random regression estimates.

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