

Demystifying animal “personality” (or not): why individual variation matters to experimental biologists

Dominique G. Roche¹, Vincent Careau², Sandra A. Binning¹

¹ *Éco-Éthologie, Institut de Biologie, Université de Neuchâtel, Neuchâtel, CH 2000, Switzerland*

² *Canada Research Chair in Functional Ecology, Department of Biology, University of Ottawa, Ottawa, Ontario K1N 6N5, Canada*

Measuring among- and within-individual correlations using multivariate LMMs

Whenever two or more traits are repeatedly assayed simultaneously in a set of individuals, bivariate linear mixed-effects models (LMMs) can be used to partition the total phenotypic correlation (r_P) into an among-individual correlation (r_{ind}) and a within-individual, or residual, correlation (r_e) (Dingemanse and Dochtermann 2013). A bivariate LMM allows a straightforward estimation of r_{ind} and r_e between two repeatedly measured traits by including a term for the correlation between the random intercepts of each individual fitted to both dependent variables (i.e., r_{ind}) and a term for the correlation between the residual variances for each trait (i.e., r_e). r_{ind} indicates whether individual mean values of trait one correlate with individual mean values of trait two, and r_e indicates whether an individual's change in trait one between time period t and $t + 1$ is correlated with the change in trait two over the same period (Dingemanse and Dochtermann, 2013). In summary, r_e represents combined, reversible changes in two traits within-individuals (i.e. phenotypic plasticity), as well as correlated measurement error; in contrast, r_{ind} represents the genetic and permanent environmental effects resulting in the association between the two traits (Brommer, 2013; Careau et al., 2014). We provide a script (<https://figshare.com/s/8acf1c73ee3a1bab8d00>) to run an example bivariate LMM using the R package MCMCglmm and compute r_P , r_{ind} , and r_e between standard and maximum metabolic rate in 60 juvenile barramundi (*Lates calcarifer*), each sequentially exposed to five different environmental treatments consisting of different temperature, salinity and oxygen levels (900 measurements in total; data from Norin et al., 2016).

Running multivariate LMMs on pairs of repeatedly measured traits is particularly informative when two different processes occur at the among- and within-individual levels. For example, a fundamental energy allocation trade-off occurring at the within-individual level (e.g., between growth and reproduction) can be masked by heterogeneity in energy acquisition at the among-individual level (e.g., because of variation in the amount of resources available to individuals, faster growing individuals might also produce bigger clutches if they live in a habitat where food is not limiting) (see van Noordwijk and de Jong, 1986). In this case, a researcher that focuses only on the phenotypic correlations (i.e., correlations without partitioning among- and within-individual variation) would miss potentially contrasting patterns occurring at the among- and within-individual levels because they would cancel each other out at the phenotypic level. As another example, one may expect a positive among-individual correlation between daily energy expenditure (DEE; total metabolic rate of an animal summed over 24 h) and resting metabolic rate (RMR), such that animals with a high RMR will also have a high DEE. In contrast, one might find a nil within-individual correlation between these two traits because animals with a restricted energy budget might reduce their RMR to allow increasing other non-resting sources of energy expenditure such as reproduction and activity. For visual representations of these patterns, refer to Figs 1 and 2 in van de Pol and Wright (2009) and Fig. 1 in Careau et al. (2014).

References

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