Moving away from repeatability: a comment on Stuber et al.

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Niels J. Dingemanse[1], Anne R. Hertel[1] & Raphael Royauté[2]

[1]Behavioural Ecology, Department of Biology, Ludwig Maximilians University of Munich, Planegg-Martinsried, Germany

[2]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

Behavioural ecologists increasingly acknowledge that among- and within-individual processes are important; this notion also reached movement ecology (Hertel et al., 2020). Stuber et al. (2021) show that movement behaviours are individually repeatable but caution that "repeatability itself does not indicate the mechanisms by which consistent differences arise". We here point out that comparing repeatabilities is, in fact, a comparison of apples and oranges. This is because repeatability (R) is a proportion that varies as a function of multiple variance components:

$$R = \frac{V_I}{V_P} = \frac{V_I}{V_I+V_E+V_e} \quad \text{(Eqn. 1)}$$

In its simplest form, the phenotypic variance (V_P) is the sum of among-individual variance (V_I), within-individual variance (V_E), and measurement error (V_e). R is the proportion of V_P explained by V_I. Differences in R therefore do not necessarily imply equivalent differences in V_I (the statistical definition of 'consistent differences'; Dingemanse et al., 2010). We give an example (with exaggerated made-up numbers). Location fixes form the input of most movement metrics. Spatial measurement errors associated with location fixes are smaller when comparing, for example, satellite-based (GPS-tags) with telemetry-based (VHF-transmitters) fixes. Even when V_I (set to 0.3) and V_E (set to 0.6) do not vary with methodology, repeatability will thus be greater for satellite-based (R_A) vs. telemetry-based (R_B) datasets:

$$R_A = \frac{V_I}{V_I+V_E+V_e} = \frac{0.3}{0.3+0.6+0.1} = 0.30,$$

$$R_B = \frac{V_I}{V_I+V_E+V_e} = \frac{0.3}{0.3+0.6+1.1} = 0.15 \quad \text{(Eqn. 2)}$$

In Eqn. 2, we set V_{e_A} to 0.1 and $V_{e_B}$to 1.1. Measurement error can also vary with the environment, e.g. precision is typically higher for GPS-fixes acquired from open versus forested areas. From this, we can learn three lessons.

First, effects of fixed/random effects estimated from repeatability meta-analyses result both from biology (V_I, V_E) and methodology (V_e). Drawing unambiguous conclusions is hard. Second, acquiring unbiased estimates necessitate sampling designed to estimate measurement error. This requires not just repeated measures over time spans so long that the animals might have moved but also repeated measures over time spans so short they cannot have moved. Only then can V_I, V_E and V_e be estimated simultaneously, and R re-defined in biological terms (cf. Falconer and Mackay, 1996):

$$R = \frac{V_I}{V_I+V_E} \quad \text{(Eqn. 3)}$$

In our worked example, R_A would then correctly equate R_B. A third lesson is that there is important biology hidden in repeated measures datasets. While repeatability is often discussed as a proxy for V_I, V_E is also of key interest. V_E results from learning, habituation, and reversible plasticity—all important proximate drivers of movement behaviour.

Building upon Stuber et al., we recommend a re-focus from repeatability toward variances. This will reveal processes underpinning movement behavior. For example, high within-individual variability suggests a major role for reversible plasticity. This mechanism makes populations able to respond to environmental change within generations. High among-individual variability instead presents greater opportunity for adaptive evolution among generations. Evolutionary biologists have made similar calls to move away from proportions. This is because variances—but not proportions—are comparable across samples, at least when traits are measured in units with natural nulls, and their variances expressed as

coefficients of variation (Houle, 1992). Expanded upon this, behavioural ecologists proposed the usage of coefficients of among-individual variation (CV_I) (Holtmann et al., 2017) in meta-analytical studies of individual variation (e.g., Royauté and Dochtermann, 2021):

$$CV_I = \sqrt{\frac{V_I}{\bar{x}}} \quad \text{(Eqn. 4)}$$

This, notably, requires estimates of both among-individual variances (V_I) and trait means ($\bar{x}$). Similarly, one can compare magnitudes of within-individual variation using coefficients of within-individual variation (CV_E):

$$CV_E = \sqrt{\frac{V_E}{\bar{x}}} \quad \text{(Eqn. 5)}$$

Most papers cited by Stuber et al. (2021) do not report either parameter. As a result, the general conclusion that spatial behaviours are more repeatable than other types of behaviour necessitates further investigation. Shifting our focus away from repeatability will require publications reporting *both* trait means and variance components. Only in this way can we firmly integrate plasticity and individuality of movement behaviours in ecology and evolution.

References

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