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Commentary

The mean matters: going beyond repeatability to interpret behavioral variation

1 Research regarding among-individual variation, typically under the label of “animal
2 personality”, often makes use of the estimation of repeatability for inference. This usage
3 makes sense: variance standardized ratios like repeatability allow for straightforward
4 interpretations. For example, repeatabilities greater than 0.5 demonstrate that most of the
5 observed variation in behavior is due to differences among individuals. However,
6 behavioral researchers are interested in a variety of questions vis-à-vis “personality” and,
7 for some of these questions, the inferences that can be drawn from repeatability will be
8 limited (Wilson, 2018). Here we discuss these limitations and additional metrics that may
9 be useful to researchers.

10 Repeatability, defined as the among-individual variance (V_I) divided by the total
11 variance (V_P ; (Boake, 1989; Hayes & Jenkins, 1997; Nakagawa & Schielzeth, 2010;
12 Dingemanse & Dochtermann, 2013), is what is known as a variance standardized measure
13 (Houle, 1992). Variance standardized measures have limitations of which potential users
14 should be aware. First, comparing these measures between sexes, among populations, taxa,
15 trait types etc. is problematic. This is because these ratios can differ between groups
16 because of differences in either the numerator or denominator (or both; Fig 1 & 2).
17 Alternatively, this ratio can be the same between groups despite differences in both the
18 numerator and denominator. Whether repeatability is found to be similar or different

19 among groups is therefore ultimately uninformative without considering the specific
20 changes in variance components.

21 Second, repeatability is often discussed as a metric of “individual consistency” (de
22 Villemereuil, Morrissey et al., 2017). Unfortunately consistency on its own is difficult to
23 interpret and it is instead consistency relative to the mean that will often be more
24 biologically important. Put another way, how variable individuals are only makes sense on
25 the scale of the behavior of interest. In this regard, the inferential limitations for the use of
26 repeatability are similar to those associated with heritability. For example, as detailed by
27 Houle (1992) and Hansen, Pélabon et al. (2011), standardizing additive genetic variances
28 (V_A) by total phenotypic variances (V_P)—that is, calculating narrow-sense heritability—is
29 not appropriate for most of the questions researchers ask. This assertion is based on the
30 observation that most of the variation expressed in a trait can be genetically based (i.e. high
31 heritability) even when there is little total variation in that trait. In such a case the
32 observed genetic differences result in only small differences in trait values. Similarly, for
33 repeatability, individuals can exhibit high “consistency”, and thus high repeatability, but
34 actually vary little on the scale of the traits of interest. Therefore, repeatability says nothing
35 about whether individuals exhibit large differences in phenotype: individuals can exhibit
36 substantial repeatability but ultimately differ little from one another (e.g. Figure 1C versus
37 1D). Instead, whether repeatability—which combines additive genetic variation, non-
38 additive genetic variation, and permanent environmental effects (Boake, 1989;
39 Dochtermann, Schwab et al., 2015; Niemelä & Dingemanse, 2017)—represents biologically
40 relevant variation depends on the mean of a trait and how individuals vary around that
41 mean.

42 One alternative is the use of mean standardization rather than variance
43 standardization. Mean standardization places the observed magnitude of variation directly
44 in the context of the mean. One mean-standardization approach is to divide the among-
45 individual variation (V_I) in a trait by the square of its mean (for applications of this
46 approach to understanding heritability see Houle, 1992; Hansen, Pélabon et al., 2011). For
47 V_I (Fig. 2C):

$$48 \quad I_I = 100 \times \frac{V_I}{\bar{x}^2}$$

49 where \bar{x} is the mean of the population.

50 This mean-standardization can also be applied to any other estimate of variance,
51 including residual variances (e.g. I_R for V_R ; following Houle (1992) and Hansen, Pélabon et
52 al. (2011)) and variances due to fixed effects (I_F for V_F , with V_F calculated following
53 (Nakagawa & Schielzeth, 2013; de Villemereuil, Morrissey et al., 2017). Mean-
54 standardization allows direct comparison of *magnitudes* of variation across traits measured
55 on different scales between groups (Figure 2). In contrast, repeatability only indirectly
56 provides an indication of *relative magnitude*. There are other dimensionless mean
57 standardizations that similarly allow the direct comparison of magnitudes, including the
58 coefficient of variation (CV, $\frac{\sqrt{V_I}}{\bar{x}}$) which is likely more familiar than I (see also Holtmann,
59 Lagisz et al., 2017). We prefer the use of I over CV and other measures because the former
60 is more directly linked to understanding evolutionary responses to selection (Houle, 1992;
61 Hansen, Pélabon et al., 2011). For example, when calculated for additive genetic variance, I
62 estimates the percent change in a trait's mean underselection (Hansen, Pélabon et al.,
63 2011). By using I , the study of individual variation in behavior can therefore be more

64 directly linked to the broader evolutionary literature. Regardless of whether *I* or CV is
65 preferred, we encourage authors to report all the unstandardized variance components
66 their statistical models estimate, along with behavioral means, so as to facilitate future
67 meta-analyses.

68 Mean standardization provides several benefits that complement those of
69 repeatability. Most notably, mean standardization allows variation to be compared across
70 scales of measurement and traits (e.g. time allocated to parental care versus propensity to
71 engage in agonistic interactions), without the assumptions necessary for doing so with
72 repeatability. Mean standardization allows for different biological inferences to be made
73 than can be made based on variance standardization alone. For example, in regards again
74 to heritability, it is a general prediction that traits that are closely linked to fitness will
75 exhibit lower variation and this is generally borne out when examining heritabilities
76 (Mousseau & Roff, 1987; Stirling, Reale et al., 2002). However, when this question is asked
77 using mean standardization it becomes clear that there is considerable additive genetic
78 variation in fitness affecting traits and that the observation of low heritabilities is due to
79 there also being considerable environmental variation in these traits (Houle, 1992; Hansen,
80 Pélabon et al., 2011). Similarly, behavioral traits linked to mating, habitat selection and
81 aggression typically show high repeatability while activity, mate preference and migration
82 have lower repeatability (Bell, Hankson et al., 2009). However, because mean standardized
83 ratios have not typically been reported in behavioral studies, it is not possible to determine
84 how these results translate to magnitudes of behavioral differences among individuals.
85 Whether traits differ in the magnitude of individual differences consequently remains an
86 important open topic for behavioral ecologist to tackle. More generally, the use of mean-

87 standardization means researchers can ask new and exciting questions about how different
88 types of behaviors differ and the magnitude of effects on behavioral variation.

89 As an example of how mean standardization complements repeatability, we can
90 revisit data collected (simulated) by Wilson (2008) for a variety of morphological and
91 behavioral traits of unicorns (see also de Villemereuil, Morrissey et al., 2017). Two
92 populations of unicorns exhibited the same average aggression and the same repeatability
93 of aggression ($r = 0.80$, Fig 1). However, unicorns in Population 1 exhibited less variability
94 both among individuals and across repeated measurements of the same individuals than
95 observed for Population 2 (Fig 1 C&D). This difference in variability is apparent when
96 directly comparing variance components (Fig 2A) but obscured under variance
97 standardization (Fig 2B). The use of I values recaptures this difference between the two
98 populations at both the among-individual and within-individual levels (Fig 2C). The use of I
99 therefore highlights that while the unicorns of both populations were equally aggressive
100 and exhibited the same repeatability, individual unicorns in Population 2 differ from each
101 other to a greater degree than did those in Population 1 (Fig 2C). This is an inference that
102 could not have been drawn from the comparison of repeatabilities and suggests interesting
103 future questions regarding the contribution of genetic and environmental factors to
104 aggression in unicorns.

105 There are, of course, caveats to the use of mean standardization. First, it only applies
106 to traits on ratio or log scales (though the evolutionary implications discussed above and
107 by Hansen, Pélabon et al. (2011) are not applicable on log scales). Ratio scale does not refer
108 to values expressed as ratios but rather to whether how something has an objective zero

109 value and if the comparison of two measurements of the same kind estimates the ratio of
110 the difference in their magnitude (Houle, 1992; Hansen, Pélabon et al., 2011). This issue of
111 a trait having a real zero is particularly important as researchers frequently standardize
112 measures based on their standard deviations and centered to their mean prior to analysis
113 (e.g. Hadfield, 2010). This approach can facilitate statistical model fitting but prohibits
114 mean standardization and thus limits the inferences that can be made. Finally, while mean
115 standardization can be conducted on the data scale for non-normally distributed traits
116 following de Villemereuil, Schielzeth et al. (2016), its interpretation in such cases is not
117 clear.

118 The use of variance standardized measures like repeatabilities versus mean
119 standardization has been discussed a great deal in the evolutionary literature, as have the
120 points that we make above (e.g. Houle, 1992; Hansen & Houle, 2008; Hansen, Pélabon et al.,
121 2011; Holtmann, Lagisz et al., 2017). However, given the manner in which repeatability is
122 frequently discussed in animal behavior studies, these points require continued emphasis
123 (see also Wilson, 2018). Importantly, we are not suggesting that behavioral ecologists stop
124 using repeatability, but rather want to emphasize that variance ratios like repeatability *and*
125 mean standardized estimates allow for different inferences. The study of “animal
126 personality” and behavioral variation continues to ask increasingly sophisticated questions
127 regarding when and why behavioral variation is manifested. This expanding range of
128 questions necessitates an expanded quantitative toolbox as not all questions will be
129 properly addressed with repeatability. Mean standardization is one such tool. Which tool
130 should be used fundamentally comes down to the questions being asked.

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193

194 Tables and Figures

195

196 Table 1. Variance and mean standardized measurements of variation and example interpretations for which each might be

197 appropriate.

Metric		Interpretation	Reference
Variance Standardized Measures			
Adjusted Repeatability	$\frac{V_I}{V_I + V_R}$	Proportion of variation due to intrinsic differences among individuals (i.e. due to genetic and permanent environmental effects)	(Nakagawa & Schielzeth, 2013; de Villemereuil, Morrissey et al., 2017)
Unadjusted Repeatability	$\frac{V_I}{V_I + V_F + V_R}$	Proportion of total variation that is attributable to differences among individuals conditioned on measurable, fixed effects (VF). Fixed effects might include either procedural/experimental controls or biological	(Nakagawa & Schielzeth, 2013; de Villemereuil, Morrissey et al., 2017)
Mean Standardized Measures			
Mean-Scaled Individual Variation (I_I)	$100 \times \frac{V_I}{\bar{x}^2}$	Percentage of variation relative to the mean explained by differences in trait expression among individuals	this manuscript
Mean-Scaled Fixed Effect Variation (I_F)	$100 \times \frac{V_F}{\bar{x}^2}$	Percentage of variation relative to the mean explained by differences in trait expression due to fixed effects	this manuscript
Mean-Scaled Residual Variation (I_R)	$100 \times \frac{V_R}{\bar{x}^2}$	Percentage of variation relative to the mean explained by differences in trait expression due to unmeasured sources of variation	(Houle, 1992; Hansen, Pélabon et al., 2011)

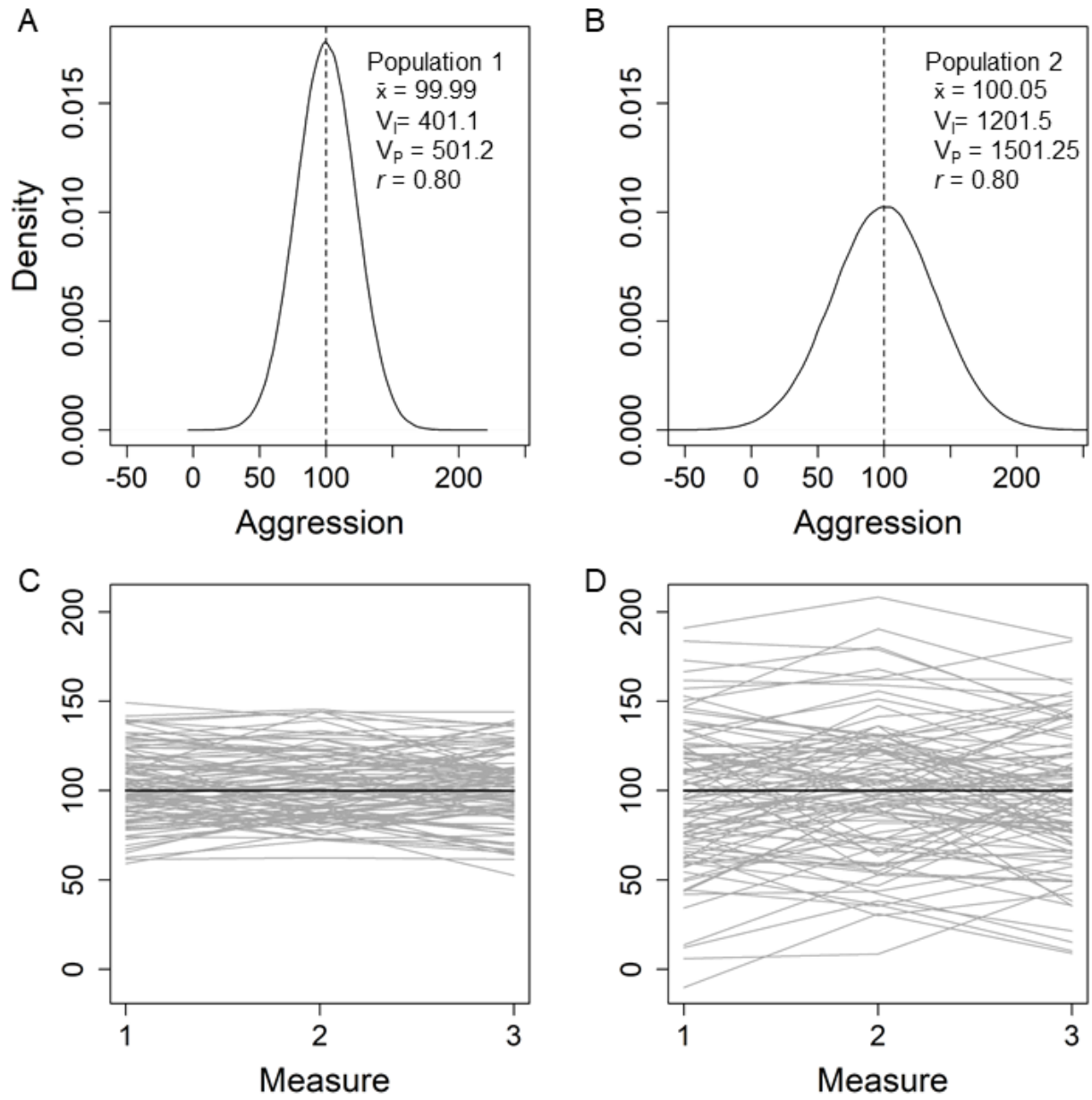
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199 Figure 1. Populations can have the same repeatability yet have drastically different
200 magnitude of among-individual variance relative to their means. For example, two
201 populations of unicorns studied by Wilson (2008) had the same average aggression and the
202 same repeatability despite different amounts of variability (A versus B). This can be more
203 clearly observed (C versus D) if one hundred randomly selected individuals from
204 population 1 have their aggression measured three times (lines in C) and one hundred
205 randomly selected individuals from population 2 are likewise measured three times (lines
206 in D). The comparison of individuals from population 1 (C) and from population 2 (D)
207 demonstrates that, despite the equal repeatability, individuals from population 2 exhibit
208 much larger differences from each other than do unicorns in the first population.

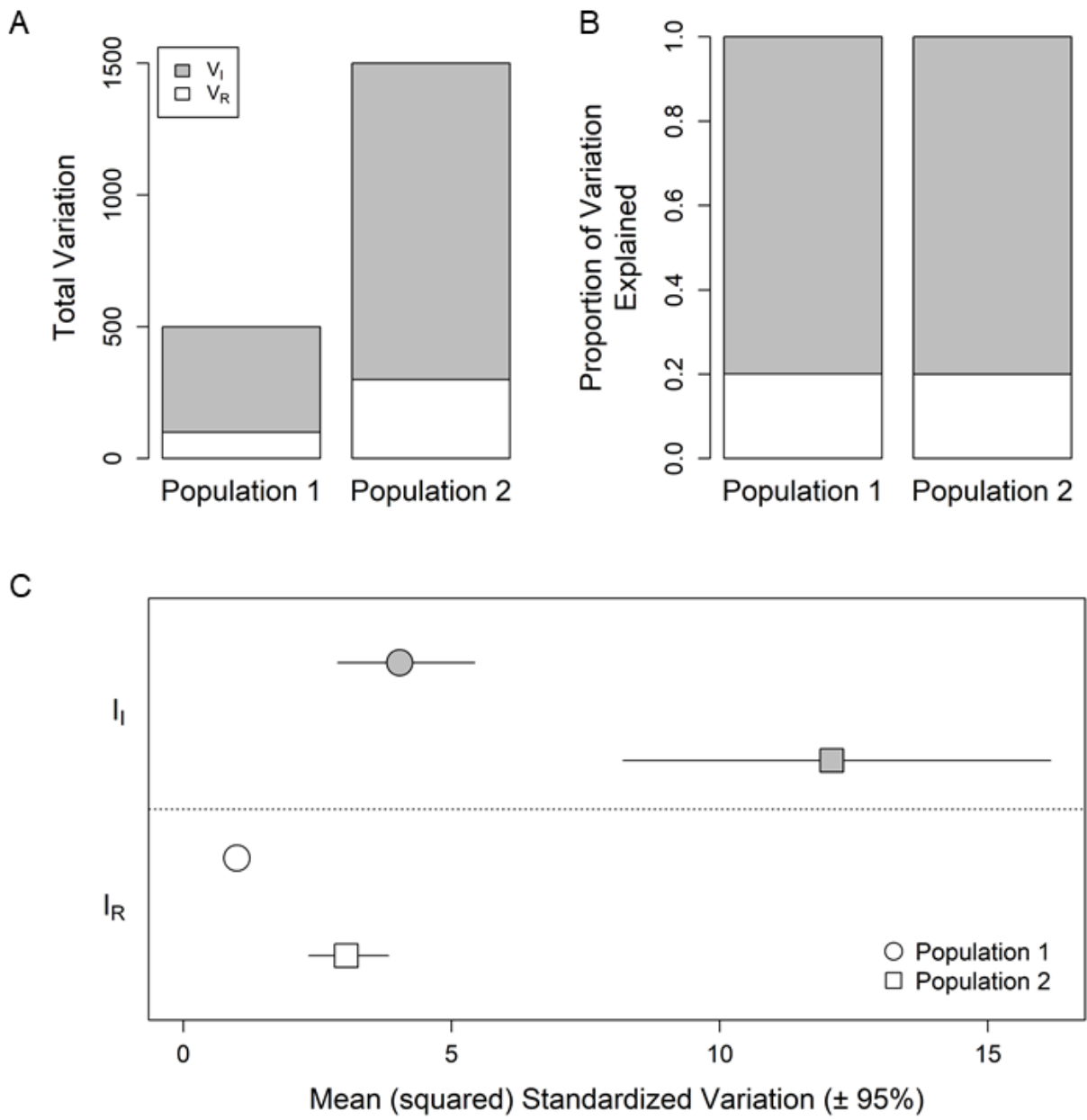
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210 Figure 2. Total (A) and proportional (B) variation explained by among- and within-
211 individual sources of variation (C) mean standardized estimates (error bars are the middle
212 95% of estimates based on resampling from Figure 1 A and B) in each population of
213 unicorns from Figure 1. Despite equal repeatability (B), population 2 has a greater
214 magnitude of among-individual variation relative to its mean (C). Thus, variation in this
215 trait for this population is expected to be more strongly influenced by genetic and
216 permanent environment sources of variation.

217



218
 219 Figure 1.
 220



221
222 Figure 2.