Illustrating the importance of meta-analysing variances alongside means in ecology and evolution

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Abstract

Meta-analyses are increasingly used in biology to both quantitatively summarize available evidence for specific questions, and generate new hypotheses. While this powerful tool has mostly been deployed to study mean effects, there is untapped potential to study effects on (trait) variance. Here, we use a recently published dataset as a case study to show how meta-analysis of variance can provide insights into ecological and evolutionary processes. This dataset included 704 effect sizes from 89 studies, covering 56 animal species, and was originally used to test developmental stress effects on a range of traits. We found that developmental stress not only negatively affects mean trait values, but also increases trait variance, mostly in reproduction, showcasing how meta-analysis of variance can reveal previously overlooked effects. Furthermore, we show how meta-analysis of variance can be used as a tool to help meta-analysts make informed methodological decisions, even when the primary focus is on mean effects. We encourage meta-analysts in all disciplines to move beyond the world of means and start unravelling secrets of the world of variance.

Keywords: tyranny of averages, variability, variance ratio, coefficient of variation, early-life effects, opportunity for selection, parental effects, transgenerational effects

Introduction

"*Our preoccupation with averages has blinded us to biological realities*" (Hogben and Sim, 1953). Despite the exponential increase in the use of meta-analysis in recent years (Gurevitch et al., 2018; Stewart, 2009) almost all meta-analyses have exclusively focused on the study of mean effects (Koricheva and Gurevitch, 2014; Nakagawa and Santos, 2012). Meta-analysis is a powerful tool for integrating findings and generating new hypotheses, yet meta-analysts may be neglecting important biological realities by focusing on means alone.

Fortunately, recent statistical advances in the field of meta-analysis have made it possible to study variance effects (Nakagawa et al., 2015), and meta-analyses of variance are starting to emerge (electronic supplementary material 1). For example, meta-analyses of variance have shown that early-life dietary restriction not only affects mean longevity (English and Uller, 2016) but also increases variance in longevity (Senior et al., 2017); and that sexual selection on males not only increases mean but also decreases variance in fitness-related traits (Cally et al., 2019). Despite this, meta-analyses of variance are still rarely used, and thus, a large portion of biological realities remains to be discovered.

In this study, we aim to promote the use of meta-analysis of variance in biology and other disciplines. We used a recently published meta-analytic dataset of experimental studies (Eyck et al., 2019) as a case study to test the prediction that developmental stress not only negatively affects mean trait values, but also increases variance among individuals. Furthermore, we used meta-regression to test whether mean and variance effects differ across traits. Our meta-analysis of variance

revealed developmental stress effects on variance, mostly on reproduction, and highlighted the importance of shifting some of our meta-analytic attention to the raw material for natural selection: variation.

Methods

Data analyzed

Experimental data on the effects of developmental stress on phenotype and fitness were obtained from Eyck et al. (2019). Before the analyses, we made modifications to the dataset (see details in electronic supplementary material 2). In brief, we: (1) excluded effect sizes based only on inferential statistics (k = 145 effect sizes excluded) because the calculation of our effect size statistics requires raw means, standard deviations (SD), and sample sizes; (2) excluded measurements not bounded at zero because our effect size statistics assume ratio scale data (Houle et al., 2011) (k = 7); (3) excluded group-level proportional data from the meta-analysis of variance as they do not have associated SD (e.g. 25% vs. 40% survival between control and treatment group; Nakagawa et al., 2015) (k = 3); (4) revisited primary studies to confirm the calculation of effect sizes and their direction, and excluded 27 effects sizes from the meta-analysis of means because we could not assign a direction to them; (5) reclassified traits into six categories (behaviour, development, metabolism and physiology, morphology, reproduction, and survival) following Acasuso-Rivero et al. (2019); and (6) excluded two effect sizes that were identified as outliers by the function ‘escalc()’ from the R package ‘metafor’ v.2.1-0 (Viechtbauer, 2010) due to their large mean to SD ratio.

Effect size calculation

We calculated two types of effect sizes and their associated sampling variances using the function ‘escalc()’ from the R package ‘metafor’ v.2.1-0 (Viechtbauer, 2010). To study mean effects, we calculated the log response ratio (lnRR; Hedges et al., 1999). To study variance effects we calculated the log coefficient of variation ratio (lnCVR; Nakagawa et al., 2015; Senior et al., *in preparation*). In 23 studies (25.8% of all studies) involving 252 effect sizes (35.8% of all effect sizes), multiple treatment groups shared a common control group, leading to non-independence among effect sizes (Lajeunesse, 2011). To deal with this non-independence, we adjusted the sample size of the control groups to be equal to the original sample size of that control group divided by the number of times that control group was compared to a treatment group (Noble et al., 2017). For comparison with the original study, we conducted an additional meta-analysis of means based on a standardized mean difference effect size (see electronic supplementary material 3).

For the meta-analysis of means, effect sizes were coded such that negative values indicate that developmental stress negatively affects fitness. That is, effect sizes were coded based on the expected relationship between the trait and fitness. For example, since fitness was expected to positively associate with body mass and immune response, the sign of those effect sizes were left unchanged. However, since fitness was expected to negatively associate with latency to reproduce and corticosterone levels, the sign of those effect sizes were inverted (all decisions are available in the R script “003_data_preparation.R” in Sánchez-Tójar et al., 2019). For the meta-analysis of variance, effect sizes were left unchanged as we expected an increase in variance across traits.

Meta-analyses and meta-regressions

We ran two multilevel meta-analytic (i.e. intercept-only) models, one for each type of effect size, to test whether developmental stress generally affects phenotype and fitness both at the mean (lnRR) and at the variance level (lnCVR), and two multilevel meta-regression models to test whether developmental stress effects differed across different types of traits. For meta-analytic models we investigated unexplained variation across studies (after accounting for sampling variance) by estimating total and separate relative heterogeneity for each random effect (I^2; Nakagawa and Santos, 2012), and absolute heterogeneity (Q) using the R package 'metafor' v.2.1-0 (Viechtbauer, 2010). For meta-regressions, we estimated the percentage of variance explained by the moderators ($R^2_{marginal}$; Nakagawa and Schielzeth, 2013).

Publication bias

We assessed publication bias at the mean level only because virtually all studies included in our dataset focused on mean effects, i.e. we do not expect publication bias at the variance level. We ran a variant of Egger's regression using the meta-analytic residuals as the response variable, and the precision (i.e. the square root of the inverse of the sampling variance) as the moderator (Nakagawa and Santos, 2012). Additionally, we assessed potential temporal trends in effect sizes that could indicate a time-lag bias (Jennions and Møller, 2002; Koricheva and Kulinskaya, 2019) by running a multilevel meta-regression that included year of publication as a z-transformed moderator (Nakagawa and Santos, 2012; Sánchez-Tójar et al., 2018).

Random effects

All models included the following random effects: (i) observation ID, which represents the observational or residual variance that needs to be explicitly modelled in a meta-analytic model, (ii) study ID, which encompassed those estimates obtained within each specific study, (iii) species ID, which encompassed those estimates obtained for each species, and (iv) phylogeny, which consisted of a phylogenetic relatedness correlation matrix. To build the phylogeny, we searched for our species in the Open Tree Taxonomy (Rees and Cranston, 2017) and retrieved the phylogenetic relationships from the Open Tree of Life (Hinchliff et al., 2015) using the R package 'rotl' v.3.0.5 (Michonneau et al., 2016). We estimated branch lengths following Grafen (1989) as implemented in the function 'compute.brlen()' of the R package 'ape' v.5.2 (Paradis and Schliep, 2019). The single polytomy encountered was dealt with via randomization using the function 'multi2di()' from the R package 'ape' v.5.2 (Paradis and Schliep, 2019).

We used the R programming language v.3.5.1 (R Core Team, 2018) throughout. All analyses were run in a Bayesian framework based on Stan programming language using the R package 'brms' v.2.9.0 (Bürkner, 2017; model parameters available in the R code provided). Figures and tables were created using the R package 'ggplot2' v.3.1.0 (Wickham, 2016), and the R package 'gt' v.0.1.0 (Iannone et al., 2019), respectively. All data and code are available in Sánchez-Tójar et al. (2019).

Results

Our final dataset consisted of 704 effect sizes from 89 studies covering 56 animal species (Aves = 12 sp., Reptiles = 12 sp., Arthropods = 11 sp., Fishes = 9 sp., Amphibians = 6 sp., Mammals = 6 sp.; Figure S2).

Meta-analysis of variance

Overall, developmental stress increased variance by around 4% on average, albeit uncertainty was high (Table 1, Figure 1). The effect of developmental stress on variance differed depending on the trait studied, with reproduction showing the largest increase in variance (ca. 21% on average) (Figure 2). However, the percentage of variance explained by the trait moderator was less than 1% (Table 2), indicating that most of the heterogeneity remains unexplained.

Table 1. Results of the meta-analyses testing the effect of developmental stress on mean (lnRR) and variance (lnCVR) in phenotype and fitness. The results of the Egger's regression test are also shown (see section 'Publication bias').

Effect size	k	Meta-analytic mean	$I^2_{Obser.}$ (%)	I^2_{Study} (%)	$I^2_{Species}$ (%)	I^2_{Phylo} (%)	I^2_{Total} (%)	Q_{test}	Egger's test
lnRR	677	-0.12 [-0.26,0.02]	36.7 [25.1,45.2]	32.5 [18.5,43.4]	12.2 [0.0,25.5]	19.4 [0.7,38.9]	99.9 [99.9,100.0]	14993	-0.13 [-0.18,-0.06]
lnCVR	701	0.04 [-0.08,0.14]	45.9 [35.6,55.7]	21.5 [7.6,31.2]	19.3 [4.4,28.3]	4.1 [0.0,25.7]	91.7 [90.2,93.5]	1963	NA

k = number of estimates; I^2 = heterogeneity; Q_{test} = Cochrane's Q test; NA = not applicable; Obser. = Observational or residual variance; Phylo = Phylogeny. Egger's test = intercept of an Egger's regression following Nakagawa and Santos (2012). Estimates shown correspond to modes and 95% Highest Posterior Density Intervals. N = 89 studies.

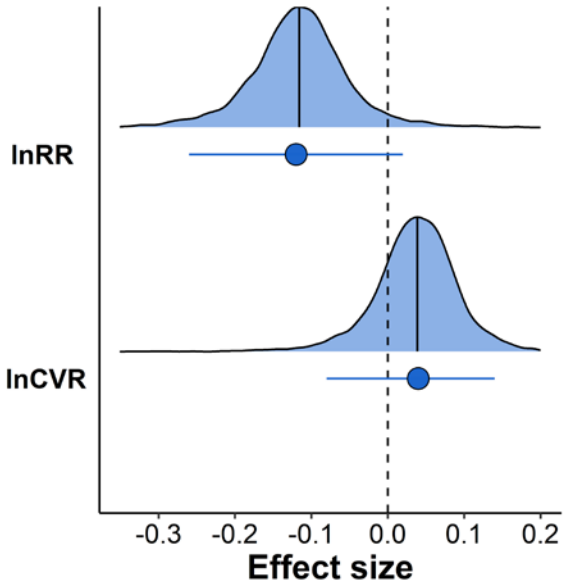

Figure 1. Developmental stress affects negatively mean, and slightly increases variance in trait values. Points and associated error bars correspond to posterior modes and 95% highest posterior density intervals (HPDI) from the meta-analyses (see section 'Methods'). The posterior distributions with vertical lines indicating the median are plotted on top of their respective modes and 95% HPDI.

Meta-analysis of mean

Our results showed that, on average, developmental stress negatively affected mean trait values by around 13% (Table 1, Figure 1). The meta-regression showed that developmental stress affected all traits negatively, with the strongest effects being on reproduction (ca. 21% on average) and behaviour (ca. 16% on average; Table 2, Figure 2). Nonetheless, heterogeneity remained high even after including the trait moderator (Table 2).

Table 2. Results of the meta-regressions testing whether the effect of developmental stress on mean (lnRR) and variance (lnCVR) differ across traits. The results of a meta-regression assessing temporal trends in effect sizes are also shown (see section 'Publication bias').

Estimates	Mode [95% HPDI]	N	k
lnRR (k = 677)			
Behaviour	-0.16 [-0.30,-0.01]	33	95
Development	-0.13 [-0.29,0.01]	17	55
Metabolism and Physiology	-0.12 [-0.27,0.02]	26	118
Morphology	-0.09 [-0.22,0.06]	51	308
Reproduction	-0.18 [-0.34,-0.04]	14	62
Survival	-0.10 [-0.28,0.10]	7	39
$R^2_{marginal}$ (%) =	0.58 [0.07,1.50]	-	-
lnRR (k = 677; time-lag bias test)			
Intercept	-0.12 [-0.25,0.01]	-	-
Year of publication	0.01 [-0.02,0.06]	-	-
$R^2_{marginal}$ (%) =	0.00 [0.00,0.51]	-	-
lnCVR (k = 701)			
Behaviour	0.03 [-0.15,0.17]	33	100
Development	-0.01 [-0.19,0.15]	17	55
Metabolism and Physiology	0.03 [-0.11,0.20]	26	122
Morphology	0.03 [-0.11,0.14]	51	325
Reproduction	0.18 [0.01,0.36]	14	60
Survival	0.10 [-0.18,0.34]	7	39
$R^2_{marginal}$ (%) =	0.72 [0.05,2.63]	-	-

N = number of studies; k = number of estimates; $R^2_{marginal}$ = percentage of variance explained by the moderators (Nakagawa and Schielzeth 2013). Year of publication was z-transformed. Estimates shown correspond to posterior modes and 95% Highest Posterior Density Intervals (HPDI).

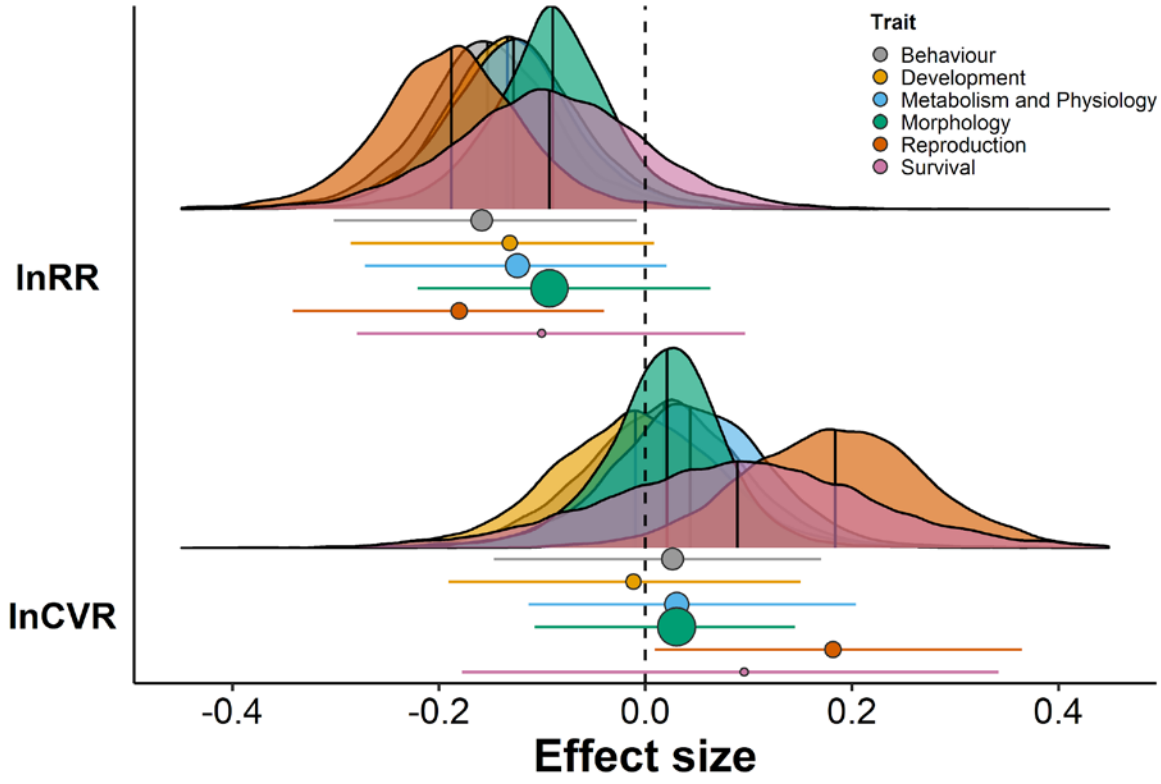

Figure 2. Developmental stress affects mean and variance differently across traits, with the strongest effects being on reproduction. Points and associated error bars correspond to posterior modes and 95% highest posterior density intervals (HPDI) from the meta-regressions (see section 'Methods'). The posterior distributions with vertical lines indicating the median are plotted on top of their respective modes and 95% HPDI. Point size is proportional to the number of effect sizes (see Table 2).

Publication bias

The intercept of the Egger's regression was negative and the 95% HPDI did not overlap zero, thus, highlighting some evidence for the existence of publication bias in this dataset (Table 1). The meta-regression testing for temporal trends in effect sizes showed a small effect size reduction over time, but the trend was uncertain and the percentage of variance explained by the moderator was essentially zero (Table 2).

Discussion

Combining a recent advance in meta-analytic methodology and a case study, we demonstrate how meta-analysis of variance can shed light on important biological processes. We showed that developmental stress not only negatively affects mean trait values, but also increases trait variance among individuals. Our results have also revealed that developmental stress affects reproduction most strongly, both at the mean and at the variance level. Overall, we encourage meta-analysts to start focusing on both mean and variance effects to unearth previously overlooked effects.

Developmental stress effects on phenotype and fitness have been studied often. For example, studies have investigated the effects of different developmental stressors on morphology and coloration (Tschirren et al., 2009), attractiveness (Kahn et al., 2012), social network position (Boogert et al., 2014), telomere dynamics (Grunst et al., 2019), and fitness (Arbuthnott and Whitlock, 2018). Perhaps not surprisingly, several reviews and meta-analyses have attempted to synthesize how different developmental stressors influence phenotype and fitness, however the majority focused on mean effects (e.g. English and Uller, 2016; Eyck et al., 2019; Macartney et al., 2019; Nakagawa et al., 2012), with only a few exploring the effects of some developmental stressors on variance (O'Dea et al., 2019; Senior et al., 2017, 2015). Here we confirm the results of Eyck et al. (2019), showing that developmental stress negatively affects mean trait values, with the strongest effects on reproduction (ca. 21%) and behaviour (ca. 16%). Additionally, our meta-analysis of variance revealed that developmental stress also increases trait variance, and that this effect is mostly driven by an increase in variance of around 21% in reproduction. This increase in variance in experimental *versus* control treatments is in agreement with previous

meta-analyses showing that dietary restriction increases variance in longevity (Senior et al., 2017), that single-food diets increase variance in fitness (Senior et al., 2015), and that increasing developmental temperature leads to larger phenotypic variance in fish (O'Dea et al., 2019). Furthermore, our results also agree with a recent meta-analysis showing that environmental stress can increase both genetic and residual variances (Rowiński and Rogell, 2017). Overall, our study shows that developmental stress may lead to increased opportunity for (natural) selection via increasing its raw material, i.e. variation.

Calculating lnCVR for a meta-analysis of variance requires essentially the same information needed to estimate other commonly used effect size statistics such as Cohen's *d* (Cohen, 1988), Hedges' *g* (Hedges, 1981) and lnRR (Hedges et al., 1999). Specifically, one simply needs the mean, SD and sample size for the two groups being compared (Nakagawa et al., 2015). Nonetheless, there are some limitations that meta-analysts need to be aware of when conducting a meta-analysis of variance. First, as in the case of lnRR, only ratio scale data can be used to calculate lnCVR, and equations to derive lnCVR from other statistics such as *F* or *t* statistics are not available. Furthermore, lnCVR cannot be calculated for group-level proportional data (Nakagawa et al., 2015). Second, absolute error variance will generally be larger for lnCVR than for mean-based effect size statistics. This large sampling variance will generally lead to lower levels of absolute heterogeneity in lnCVR compared to mean-based effect size statistics (e.g. Table 1), and overall highlights that meta-analysing variances will usually be more data-hungry than meta-analysing means. Despite these limitations, meta-analysis of variance is rather uncomplicated, making it easy for meta-analysts to start shifting some of their

preoccupations with averages to more variance-driven hypothesis testing and development.

Meta-analysis of variance not only can reveal important biological realities, but can also help making informed methodological decisions. By identifying whether the compared groups show unequal variances (i.e. whether there is heteroscedasticity), meta-analysis of variance can help meta-analysts choose between effect sizes that assume homoscedasticity (e.g. Cohen's *d*, Cohen, 1988; Hedges' *g*, Hedges, 1981), and those that incorporate heteroscedasticity (e.g. SMDH, Bonett, 2009, 2008; see electronic supplementary material 3 for an example). This is important because not accounting for heteroscedasticity can cause parameter misestimation in meta-analysis (Bonett, 2009, 2008). Overall, we suggest that even when variance-based hypotheses are of no interest to the researcher, meta-analysis of variance can still be used as a powerful methodological tool helping to choose the correct effect size statistic.

Conclusion

Our analyses on the effects of developmental stress on both mean and variance in phenotype and fitness showcases how meta-analysing variances alongside means can help unravel crucial processes. Importantly, meta-analysing variances is not limited to ecology and evolution, and can also advance disciplines such as agriculture (Knapp and Heijden, 2018), social sciences (O'Dea et al., 2018) and medicine (Senior et al., 2016). We have also shown how meta-analysis of variance can be used as a methodological tool to make informed decisions on how to choose effect size statistics for the study of mean effects. Overall, a holistic understanding of

the world requires moving beyond the world of means to incorporate the world of variance.

Authors' contributions

Contributorship following CRediT taxonomy (Allen et al., 2014; https://www.casrai.org/credit.html). AST: *Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing - original draft, Writing - review & editing*. NPM: *Investigation, Methodology, Validation, Writing - review & editing*. REO: *Conceptualization, Writing - review & editing*. KR: *Funding acquisition, Supervision, Writing - review & editing*. SN: *Conceptualization, Methodology, Funding acquisition, Supervision, Writing - review & editing*.

Competing interests

We declare no competing interests.

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Data accessibility

All data and code are available at the Open Science Framework (Sánchez-Tójar et al., 2019).

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