

# Sexual selection improves population fitness: a meta-analysis

## Response to Decision Letter

Dear Dr. Jones and colleagues,

Many thanks for your time, and for the very helpful comments on our manuscript. We have considerably reworked the manuscript in light of the many insightful comments and suggestions provided by the reviewers. Please see below for a detailed list of responses to each of the reviewers' points. We also attach a revised manuscript and a revised copy of the supplementary material, as well as a copy of the revised manuscript in which the significant changes and additions have been highlighted. Please let us know if we can do anything further to assist you.

In addition to the changes suggested by reviewers, the peer-review process highlighted some human errors on our behalf in the dataset with respect to effect size calculation, these were issues to a select few effect sizes. As such, we have thoroughly rechecked our dataset and re-ran the analyses. Ultimately the corrections to the dataset have altered our conclusions.

Yours Sincerely,

Justin Cally and co-authors

---

### Comments from Reviewer 1 (Prof. Jacek Radwan)

*The manuscript presents results of a meta-analysis assessing the effect of sexual selection on population fitness. This topic has been increasingly studied over the past decade or so, and the time seems ripe for a synthesis. The authors have done good job searching the literature – it includes all relevant papers I could remember, and the results should be of interest to a broad range of evolutionary biologists. I cannot expertly judge on state-of-the-art methodology, but I do have several general concerns about how the analyses were performed.*

Many thanks for your time and this valuable feedback.

*Firstly, it seems that several male traits like to be under sexual selection, but not related to population fitness were included. I don't think this is correct given the question being asked (i.e. whether sexual selection increases population fitness). I think traits which are directly under sexual selection (eg. attractiveness, reproductive success) should not be pooled with traits which may respond to manipulation of sexual selection indirectly (eg. male development time, survival) and can affect population fitness. Distinguishing between both types of trait could actually be revealing – e.g. could expose trade-offs between sexually selected traits and fitness components unrelated to reproductive competition (see eg. Radwan et al. 2015 Evol Biol), a thus potentially explain lower effect of sexual selection on (pooled) male traits than on female traits.*

The reviewer is correct that several traits are likely under trade-offs with other traits as sexual selection not only affects mean fitness but alters life history traits (i.e. sexual selection may increase male body size or attractiveness, but decrease development rate). In essence this is why our meta-analysis sought to investigate the *net* effect of sexual selection on population fitness across many traits, rather than one that may be traded off in a given direction. Importantly, to account for the variable and uncertain relationships certain traits have with fitness (as raised by the reviewer). We provide a table (Table S1) on how each trait is measured and their relationship with fitness. Given that this information was in the Supplementary Material we have **revised the manuscript to clarify the distinctions more thoroughly...** **Probably need to check this again.**

Additionally, the reviewers comment that male attractiveness may not be related to population fitness is correct. Because male attractiveness may be positively or negatively correlated with average fitness (although in many condition-dependent traits a positive association is assumed) we have re-classified *Male Attractiveness* as ambiguously related to fitness, rather than indirect. All subsequent models, statistics and figures now take into account this re-classification. However, given the small sample size for male attractiveness effect sizes ( $n = 6$ ), we find only marginal changes in the results and no key changes in the key findings of the study.

*Secondly, looking at Figure 1, one notices apparent anomalies, for example significantly positive slope for male attractiveness, based on studies with average effect size close to zero. I think this (and few others) surprising estimates may result from fitting random terms across all trait types (fitted as a fixed factor, second model); I guess fitting interaction (random slopes) would not be feasible for some categories including few data points, but some of them could easily be pooled in wider categories.*

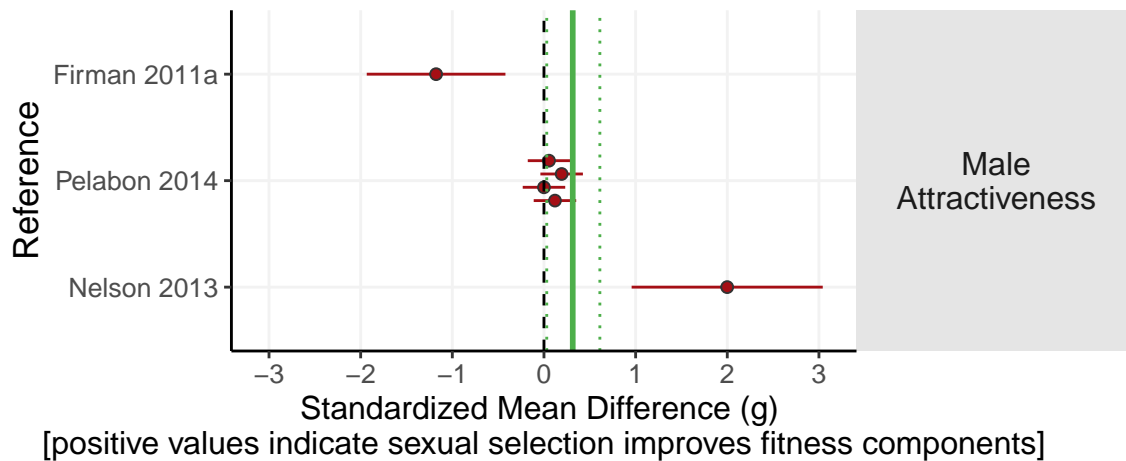
The reviewer raises questions of the analysis that produce seemingly suprising results. We agree that some of *significant* predictions in Figure 1 (whereby 95 % CIs do not overlap zero) appear surprising based on the distribution on effect sizes. In regards to the trait “male attractiveness”, the 95 % CIs do not overlap zero. This is the case even though the higher weighted studies are very close to zero. However, this seeming anomaly can be explained by various reasons.

Firstly, although the effect size prediction for the trait has 95 % CIs not overlapping zero, the overall magnitude of the effect size is small (see Table excerpt), and the Bayes Factor (an estimate of the likelihood that the effect size is actually positive) is also small. The full table for all predicted effect sizes used in Figure S1 can be seen in **S8**. Below we provide the excerpt of this table and forest plot for “Male attractiveness”.

Secondly, the effect size predictions were made using a single model that incorporated all 459 effect sizes, thus model predictions for each trait have narrower confidence intervals as the fitted values do not incorporate measurement error. In regards to our R code and analysis, this means that the predictions that appeared in Figure 1 are sourced from using `fitted.brmsfit` as opposed to `predict.brmsfit`. In order to clarify this seeming anomaly in model predictions, some meta-analyses investigating the effect of a variable on more than one outcome model each outcome (in this case the *fitness component*) separately. Arguably, this method provides more variable model estimates as models will always have lower power due to reduced sample sizes and the incorporation of measurement error in the predictions. We have added a table to the Supplementary Material where models are independently conducted on all fitness components where  $n > 3$  (**Table S9**). This may be of particular value for researchers using our meta-analysis as a research tool, whereby they are interested in the effect sizes from only a single trait (as opposed to our focus on population fitness as a whole).

Given, the confusion with regards to Figure 1 as it originally appeared within the manuscript we have altered the figure to a generalized forest plot by grouping the effect sizes from each of the fitness classes (ambiguous, indirect and direct). The previous Figure 1 has now been moved to the Supplementary Material with corresponding tables.

Fitness Component	Bayes Prediction	Bayes SE	Bayes LCI	Bayes UCI	n	BF	REML Prediction	REML SE	REML LCI	REML UCI
Male Attractiveness	0.297	0.13	0.033	0.56	6	6.1e+01	0.296	0.110	0.0792	0.51



When the effect sizes ( $n = 6$ ) for male attractiveness are viewed isolated from others, one can see that the large effect size (Nelson 2013) shifts the overall predicted effect size to be marginally positive.

*Thirdly, type of trait measured explained 35% variance, but the authors do not explore this any further. However, examination of Fig. 1 suggest that some indirect/ambiguous fitness measures account for much of this heterogeneity and they generally have higher average effect sizes than direct measures (except for immunity). I'd like to see if the authors recover their main result if they only direct measures.*

**Add more in discussion about the variability amongst traits and why some might be subject to trade offs (e.g. immunity):** We do kind of talk about this and an earlier draft had some of Jaceks work with regards to sexual conflict maintaing genetic variance through trade-offs. Should we add this back in?

The reviewer provides an accurate shortcoming of discussion on the observed heterogeneity between fitness components. The sixth paragraph of our discussion is raises some potential reasons why heterogeneity may be high within our meta-analysis. Additionally, it may please the reviewer to find an addition to our Supplementary Material (Table S9), now conducts independent meta-analyses and obtains  $I^2$  for each of these traits. Even when metanalyses are conducted on a single trait, heterogeneity ( $I^2$ ) is still high  $> 90\%$ .

In regards to conducting a meta-analysis on just direct fitness components, the reviewer provides a valid question of our use of direct **and** indirect fitness components for the meta-analysis investigating the effects of sex and stress. Based on the question we asked we were interested in the effect of sexual selection on many components of fitness.

Nevertheless, we conducted our analysis using just direct fitness measures. We find the same key associations; that sexual selection generally elevates fitness, especially for females, with the effect magnified in stressful environments. Below we present the findings. **should we put this in the supp?**

Additionally, in order to further distinguish the effects of sexual selection on ambiguous, indirect and direct fitness components, we have structured the second paragraph of the results to more consistently reflect our classification system.

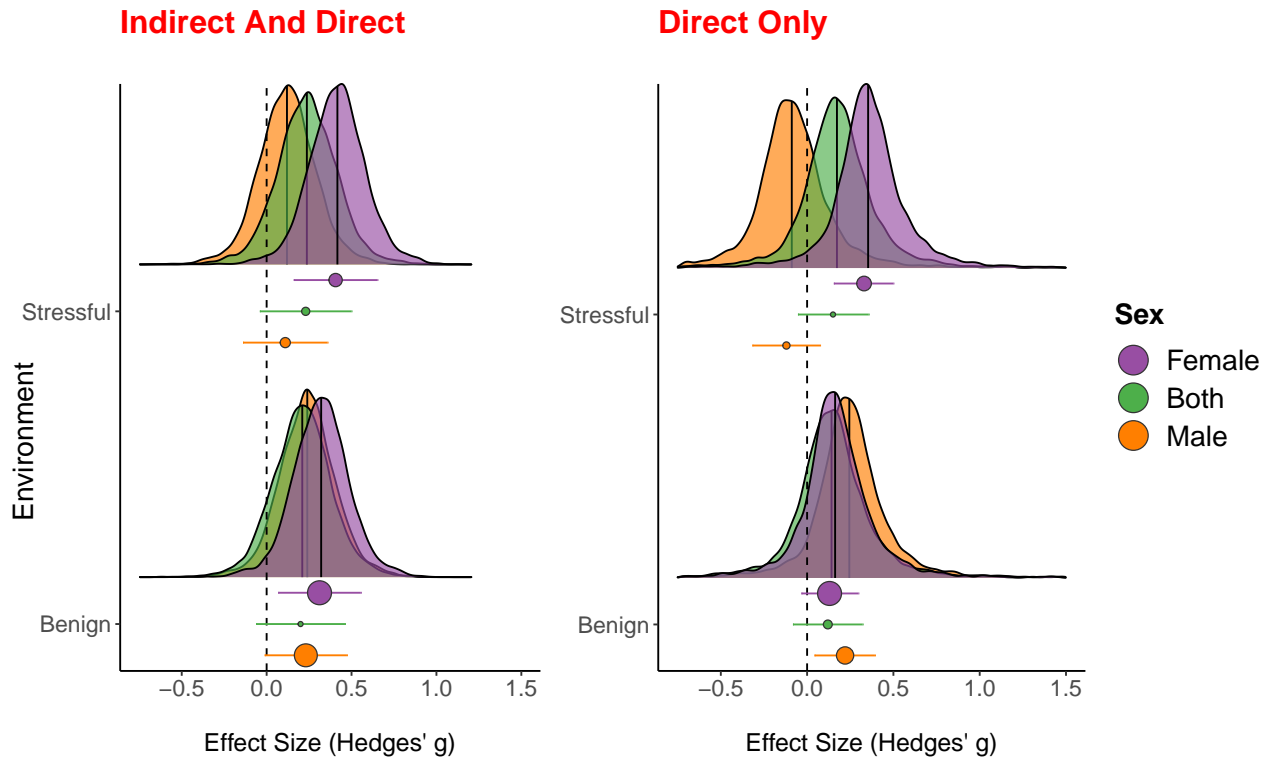


Table 2: Model using only direct measures of fitness

Sex	Environment	Prediction	SE	CI.lb	CI.ub	n
Male	Benign	0.22	0.089	0.043	0.393	43
Both	Benign	0.12	0.103	-0.082	0.322	15
Female	Benign	0.13	0.084	-0.033	0.297	86
Male	Stressful	-0.12	0.100	-0.317	0.075	13
Both	Stressful	0.15	0.105	-0.053	0.357	12
Female	Stressful	0.33	0.088	0.155	0.5	31

Another major problem I have with the manuscript concerns interpretation of the very intriguing finding that the response to manipulation of sexual selection was stronger for female traits compared to male traits. I'm confused by the authors' explanation: do they assume sexual selection acted directly on females, and not only indirectly, via males? Only then things like mother to daughter heritability, or hard selection on females, should matter.

Leave this for Luke

Good suggestion!

Perhaps the effect on females is indeed direct, and results from stress imposed by polygamous treatment, which magnifies direct, hard selection on females? This would be an important finding, and perhaps the authors could test it with their dataset by contrasting middle-class-neighborhood-like studies from those which allowed for female evolution. But if correct, this explanation is not exactly the effect of sexual selection, but rather enhanced selection of females due to enhanced (male induced) stress, so the interpretation of results should change.

Not too sure what he means.

Answer

**Other comments:**

*l. 30 – reviews on sexual conflict are OK to cite here, but there are empirical papers actually demonstrating correlation between male sexual selected traits (Harano et al. 2011; Plesnar et al. 2014) which should also be cited.*

Thank you, we now cite those papers as suggested in line 31. Additionally, they are especially pertinent to experimental evolution studies using species such as the bulb mite (*Rhizoglyphus robini*) (Plesnar Bielak et al., n.d.) and flour beetles (*Gnatocerus cornutus*) (Harano et al. 2010).

*l. 151 – the authors discuss beneficial effects of sexual selection on direct fitness measures such as reproductive success or offspring viability, but estimates for both of these measures actually overlapped zero! Perhaps joint analysis of direct fitness measures, as I suggested above, could support this conclusion, but currently this is an overstatement.*

The reviewer is correct in that the 95 % CI overlap zero for the three direct fitness components (extinction rate, offspring viability and reproductive success) have 95 % CI overlapping zero. Additionally, our analysis reveals that the predicted effect size for direct fitness components has 95 % CIs that overlap zero for Bayesian, but not REML models (REML  $\beta = 0.13$ , 95% CIs: 0.022 to 0.24; Bayesian  $\beta = 0.13$ , 95% CIs: -0.068 to 0.30,  $BF_{>0} = 4.9$ ). In this respect we have tapered and clarified our statement that we find some evidence that sexual selection increases mean values of traits directly related to fitness. However, we retain our statement that sexual selection generally elevates the mean of fitness components directly related to fitness as a two-way 95 % confidence limit is an arbitrary cut-off and the Bayes Factors suggest that there is a high likelihood that the effect size for direct fitness components is greater than zero.

*In the discussion the authors say they included the number of experimental evolution generations, but I could not find this information in methods.*

It is correct that we did not use the number of generations in our main analysis. The manuscript (Methods section) states that the number of generations. In the supplementary material we investigate the role of number of generations (the lineage is evolved for) has on fitness in the section *Meta-analyses including many moderator variables* as well as in Figure S12 and S13. Generations (specifically, log-Generations) had minimal effect on the effect sizes and was removed for the models that appeared in the main text.

*Fig. S1 is not referred to in the main texts, is it different from Fig. 2, except that the latter contains predicted average values for fitness components?*

**No difference...** kind of there for documentation on how we created it (transparency). We now get rid of the forest plot in the manuscript. However our supp info has a few plots that are in the manuscript. I think it is good to show the code we used to create it... for reproducibility

---

## Comments from Reviewer 2

*This meta-analysis investigated the consequences of sexual selection experiments on trait mean and variance (comparing sexually selected groups vs control groups). Overall, the authors observe sexual selection usually increase mean and reduce variance (especially in females). The authors conclude sexual selection's benefits outweigh its detrimental effects. This meta-analysis is extremely well conducted (the use of both likelihood-based and Bayesian models for robustness), and although I am not an expert on this topic, I really enjoyed reading it, and it was very clear. Especially, I am impressed with the detailed supplement which showed the code and analysis. However, I have several comments regarding their analysis, which will increase the robustness of results and thus conclusions.*

Many thanks for your time and attention, and for the valuable feedback.

*1 – The use of Hedges' g. I understand that Hedges' g was probably used because it can take interval measurements as well as ratio measurements (lnCVR can only take ratio measurements).*

However,  $g$  cannot really deal well with heterogeneity between two groups (i.e. experimental and control groups having different variances). This is why Hedges'  $g$  (Cohen's  $d$ ) was criticized earlier.

Osenberg, C. W., O. Sarnelle, and S. D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. *American Naturalist* 150:798-812.

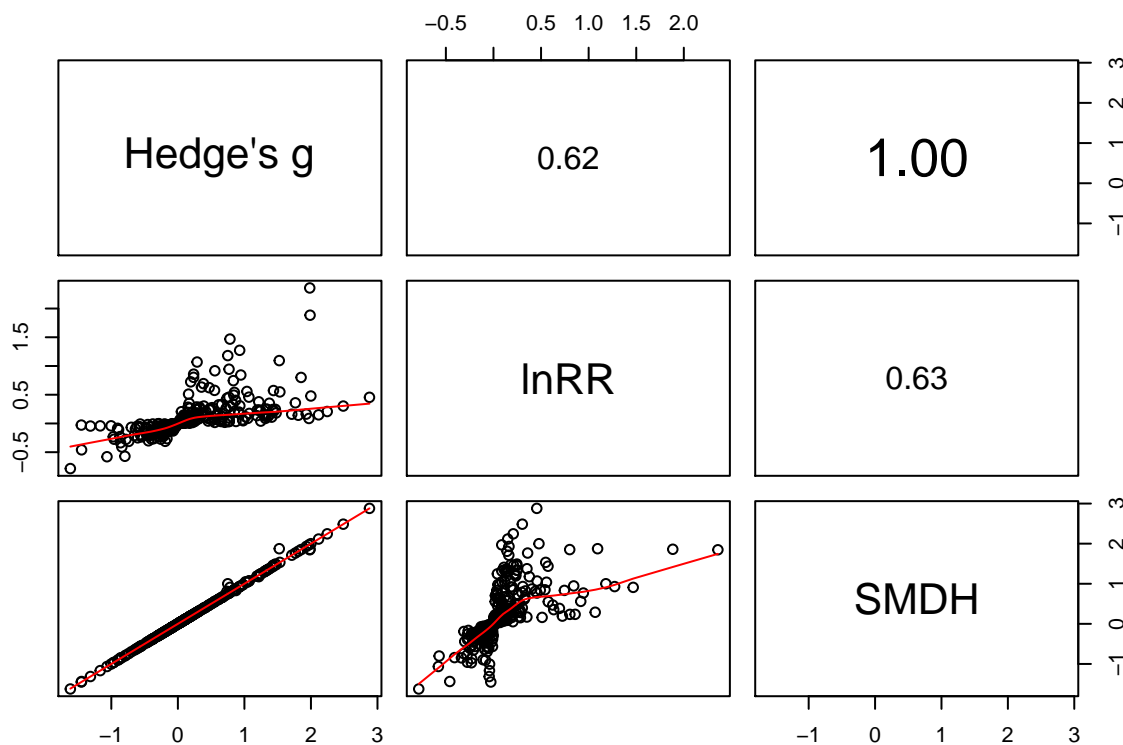
As a response, they come up with log response ratio ( $\ln RR$ ) - see

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150-1156.

I recommend that the authors use  $\ln RR$  for their effect size for mean comparison as well as Hedges'  $g$  to see the robustness of their conclusions for the mean.

Reviewer 2 has rightly pointed out that the use of Hedges'  $g$  has been criticized for its ability to account for heterogeneity between the control and treatment groups [Osenberg\_1997]. We extended our meta-analysis by including the log response ratio ( $\ln RR$ ) as well as a modified version of Hedges'  $g$  that attempts to account for this heterogeneity, this modified statistic (Bonett 2009) can be derived from the `metafor` package for meta-analysis (Viechtbauer 2010), where it is named SMDH (standardized mean difference with heteroscedastic population variances in the two groups). There are several key findings from the use of  $\ln RR$  and SMDH:

Firstly, Hedges'  $g$  and SMDH are highly correlated (in means and variance). This suggests that unequal variance between the treatment and control groups (heteroscedasticity) is unlikely to impact the effect size of Hedges'  $g$ .



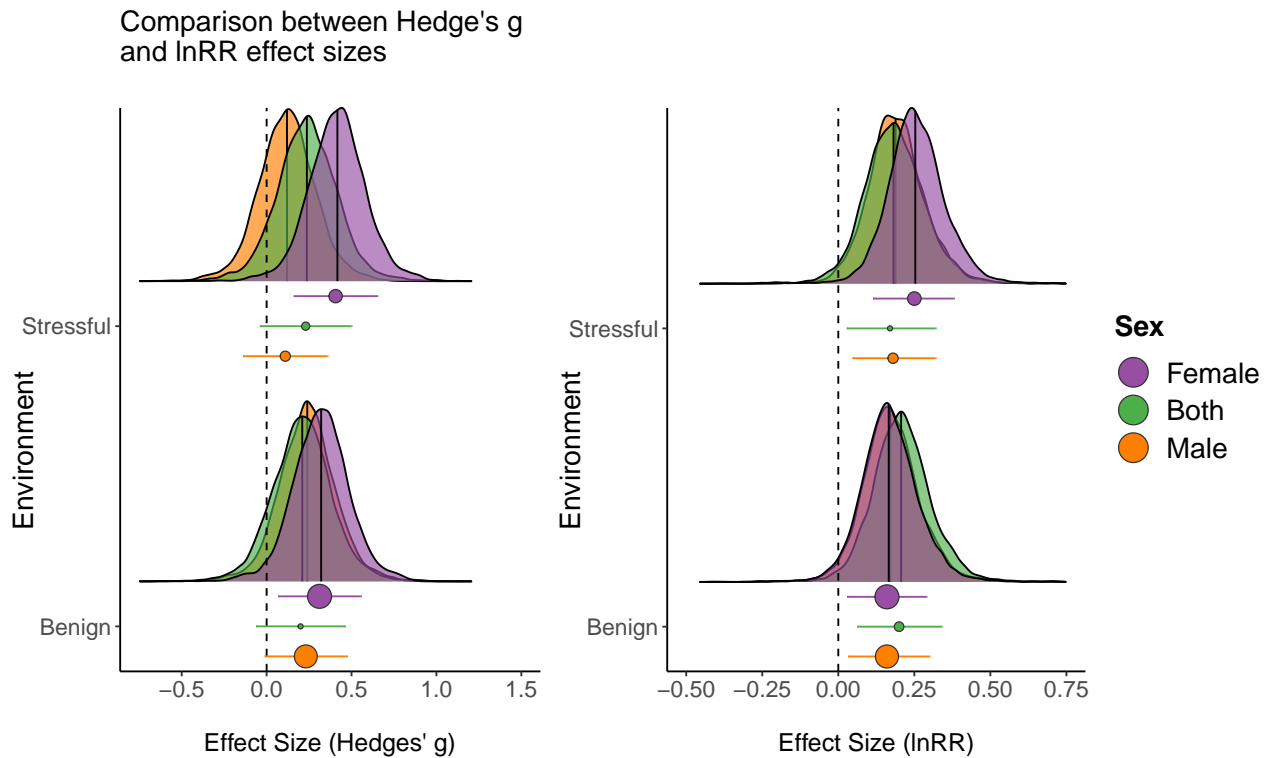
Secondly, The calculation of  $\ln RR$  and SMDH can only be calculated for effect sizes where the study reported means, standard deviations and sample sizes (352 out of 459). This is a limitation as in our analysis we investigate the effects of sex and stress on a further restricted dataset (direct and indirect fitness traits only). Specifically, fewer effect sizes from stressful conditions are able to be calculated; making Hedges'  $g$  an advantageous effect size in comparison to  $\ln RR$ .

Sex	Environment	Hedge's $g$ sample size	$\ln RR$ sample size
Male	Benign	113	100

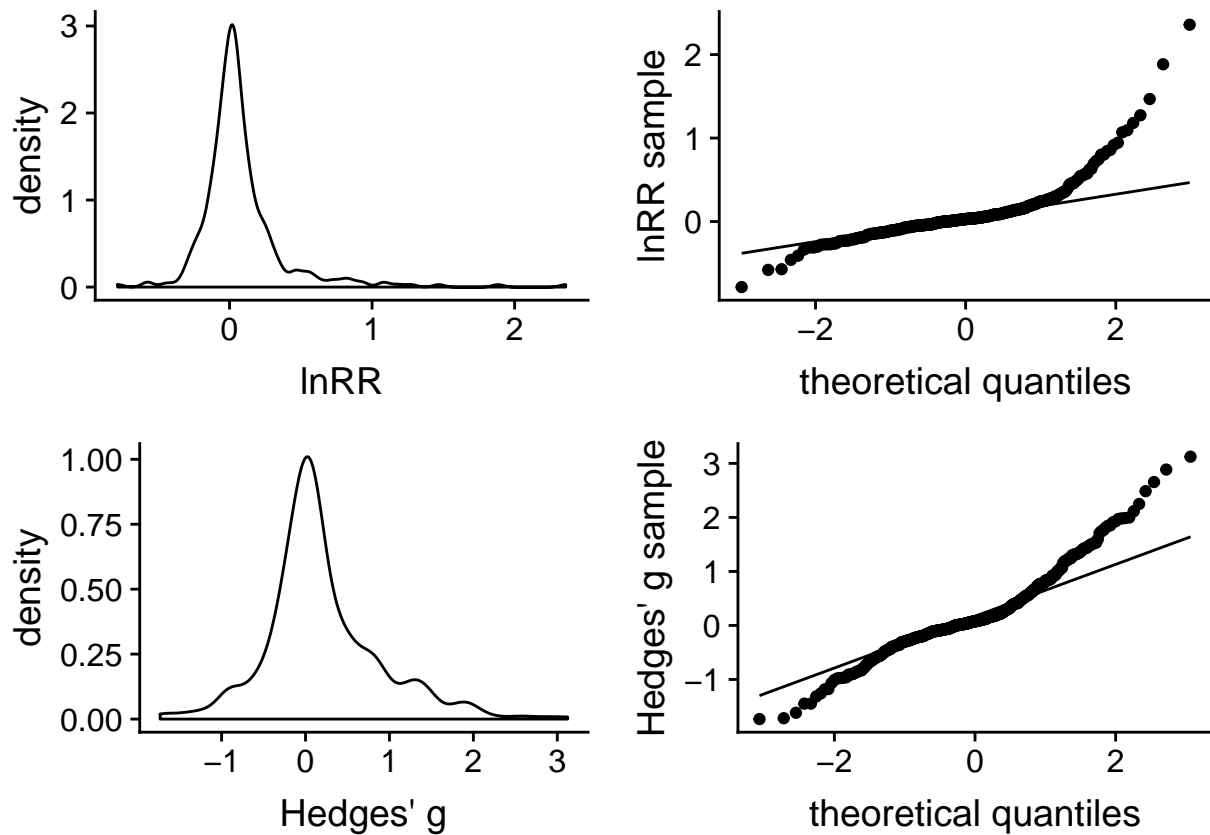
Sex	Environment	Hedge's g sample size	lnRR sample size
Both	Benign	15	12
Female	Benign	125	110
Male	Stressful	23	14
Both	Stressful	18	6
Female	Stressful	36	27
Total	-	330	269

Thirdly, if we conduct a meta-analysis using lnRR as the effect size we obtain very similar results with all major conclusions unchanged, keeping in mind that lnRR and Hedge's are on different scales; (further model results can be found within the Supplementary Material):

+ The effect of sexual selection on population fitness is generally positive. + This effect is magnified for females in stressful environments with a significantly positive interaction term (stress\*females).



Fourthly, Hedges' g appears more normally distributed than lnRR, which to some extent may come as a surprise as  $lnRR$  should usually be more normally distributed around zero. However, given that our meta-analysis combines multiple traits, with different scales of magnitude lnRR may lead to some erroneous and biased effect sizes. Specifically, Lajeunesse (2015) showed that  $lnRR$  is problematic when quantifying the outcome of studies with small sample sizes, and can yield unsuitable variance estimates when the parameter scale of the study are close to zero. The more normal distribution of the Hedges' g is anticipated to increase model fit.



The  $\ln RR$  is a commonly used effect size when the trait of interest has a natural zero point. Given that we did not extract the data with this in mind, it may be a further limitation of  $\ln RR$ .

For these reasons we have decided to use Hedges'  $g$  as the main effect size throughout the manuscript but reference and provide equivalent statistical analysis for  $\ln RR$  in the supplementary material.

2 — The authors may consider also doing another set of meta-analyses using  $\ln VR$  (log variability ratio - proposed in Nakagawa et al. 2015).

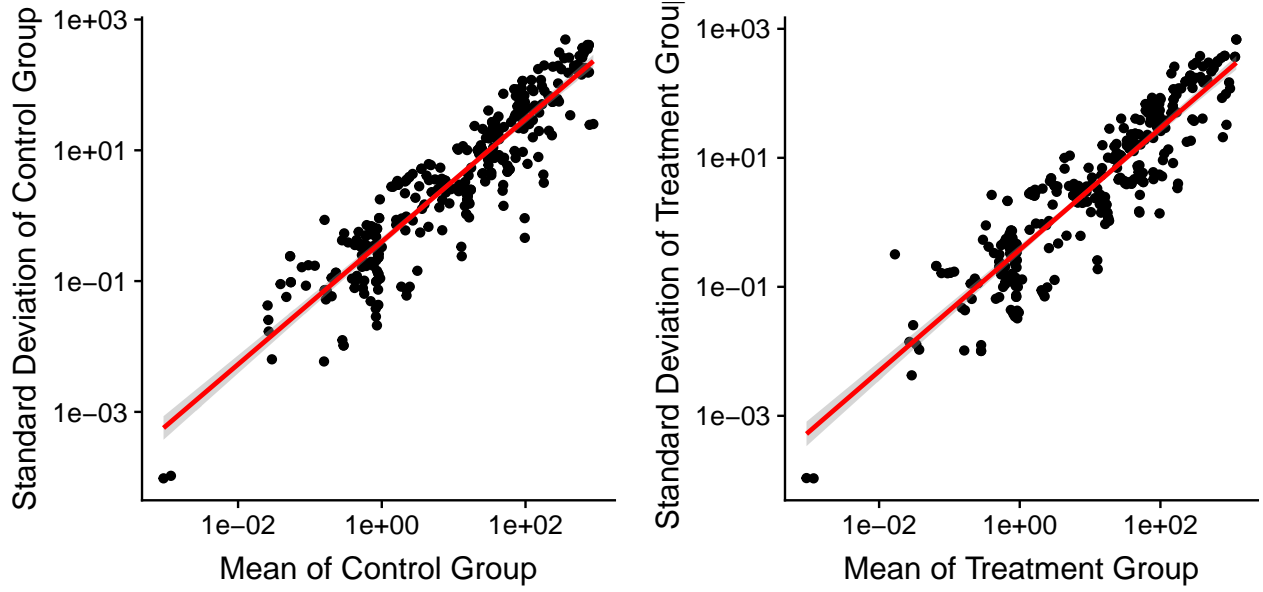
Nakagawa, S., R. Poulin, K. Mengersen, K. Reinhold, L. Engqvist, M. Lagisz, and A. M. Senior. 2015. Meta-analysis of variation: ecological and evolutionary applications and beyond. *Methods in Ecology and Evolution* 6:143-152.

As one can see in Figure 2, the mean results (Hedges'  $g$ ) are a mirror image of the variance results (this makes sense CV controls for means). I would like to see what the absolute change in variances. Probably the authors can put the analysis using  $\ln VR$  in the supplement. The results of this analysis can be discussed. Also, the mean-variance relationship between mean and variance ( $sd$ ) should be verified (e.g. plot log mean and log  $sd$  or log variance).

The reviewer suggestions have been included in our meta-analysis as Supplementary Material in order to maintain transparency in our conclusions. Several key points arise from the meta-analysis of variation:

Firstly, as the reviewer suggested we justify the use of  $\ln CVR$  by assessing the mean-variance relationship. The major limitation of  $\ln VR$  is that it does not account for the mean-variance relationship and that is why  $\ln CVR$  was suggested as the favourable correction (Nakagawa et al. 2015). Given this finding the use of  $\ln CVR$  is preferred over  $\ln VR$ , as  $\ln VR$  does not account for the mean-variance relationship.



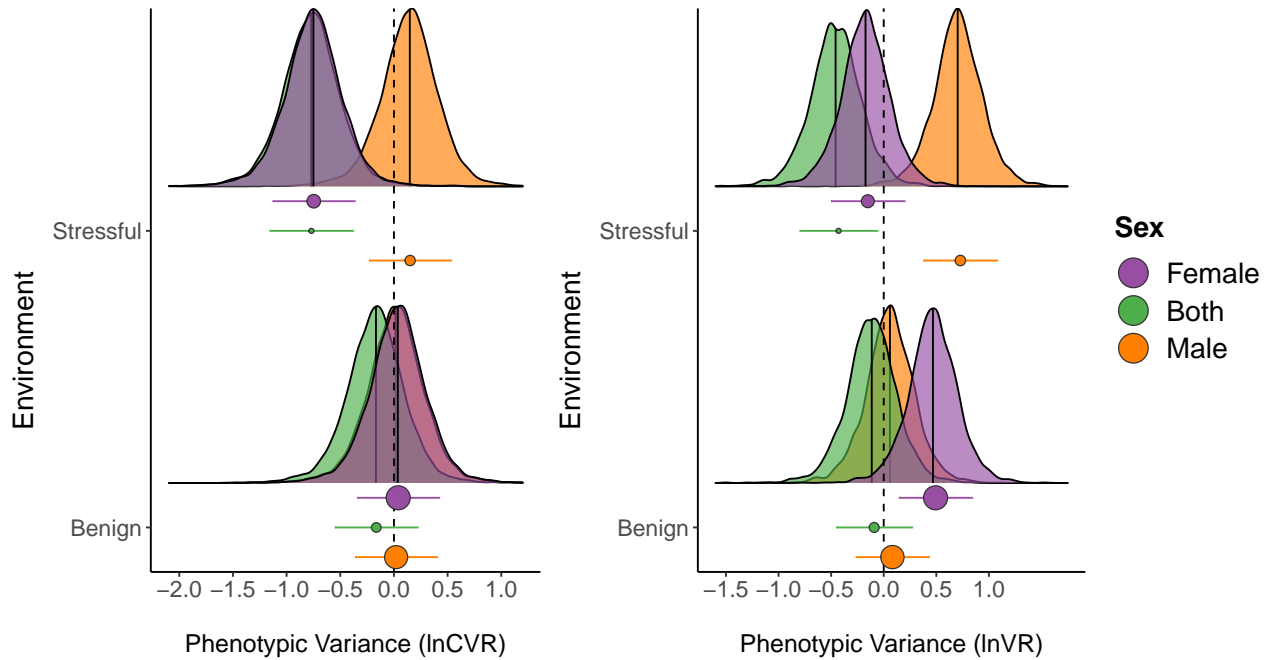


Secondly, We conducted both Bayesian and REML meta-analyses for  $\ln VR$ , which we present in the supplementary material and briefly discuss in the manuscript. We found a similar trend for the meta-analysis of variance using  $\ln CVR$  and the meta-analysis of variance using  $\ln VR$ , These are:

- In stressful environments sexual selection leads to a decrease in the variance for females, relative to benign environments.
- Sexual selection reduces variance in females compared to males.

However, when using  $\ln VR$ , the variability of fitness traits for males under sexual selection increased,  $\ln VR$  for females in stressful environments was not statistically different from zero, and sexual selection in benign environments increased phenotypic variance for females. Model results and predictions (from the REML model) can be found within the Supplementary Material.

### Comparison between InCVR and InVR effect sizes



3 —  $I^2$  needs to be explained.  $I^2$  is proposed originally here:

Higgins, J., and S. Thompson. 2002. Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine* 21:1539 - 1558.

But later expanded in here for mixed models (hierarchical models)

Nakagawa, S., and E. S. A. Santos. 2012. Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* 26:1253-1274.

This is what the authors use. Also, it will be good to put the degree in  $I^2$  in the context. To do this see this paper:

Senior, A. M., C. E. Grueber, T. Kamiya, M. Lagisz, K. O'Dwyer, E. S. A. Santos, and S. Nakagawa. 2016. Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and implications. *Ecology* 97:3293-3299.

We value the reviewers feedback and have incorporated all the suggestions within a paragraph within the methods of our manuscript.

4 — Publication tests have been conducted on, I think, “meta-analytic” residuals results as suggested in Nakagawa and Santos 2012. One could use such residuals to conduct the trim and fill method and see how much the mean could move (see Nakagawa and Santos 2012). One should remember the funnel asymmetry could be caused by the presece of heterogeneity. See:

Egger, M., G. Smith, M. Schneider, and C. Minder. 1997. Bias in metaanalysis detected by a simple, graphical test. *Br Med J* 315:629 - 634.

**No in-buit functionality for trim-and-fill for rma.mv in metafor... could figure out a way to do it I suppose, not sure if worth it**

5 — Figure 3 - are these grey envelopes 95% CI?

Yes they are, we have now included this information in the figure caption. Thank you for highlighting this.

6 — the title - do the authors include “a systematic review” - so “a systematic review and meta-analysis” - these two things are different - see:

Nakagawa, S., and R. Poulin. 2012. Meta-analytic insights into evolutionary ecology: an introduction and synthesis. *Evolutionary Ecology* 26:1085-1099.

Our study does not involve a systematic review. The scope of a systematic review was larger than this meta-analysis entailed. However, we did use a systematic literature search strategy and PRISMA framework of inclusion/exclusion. **I think there is some unsureness here on what counts as a systematic review... I remember in medicine a meta-analysis MUST be part of a systematic review, but I guess ecology and evolution is more flexible.**

*Hope my comments are useful.*

They were extremely useful, many thanks!

---

### Comments from Reviewer 3

This manuscript addresses the question of whether, on average, sexual selection has a net beneficial or detrimental effect on population fitness, using a meta-analysis of experimental evolution studies comparing the fitness of populations under different intensities of sexual selection. The analyses consider the effects of sexual selection on both the mean and variance of population fitness, and test whether these effects differ for stressful vs. benign environments, or depend on the measure of population fitness.

These are issues of longstanding interest, and as there is now quite a wealth of experimental evolution studies addressing these questions a meta-analysis synthesising their findings is timely.

Many thanks for your time and attention, and for the valuable feedback.

The results of this meta-analysis broadly concur with current theoretical predictions, and are likely to interest a wide readership. Across all studies, environment types and fitness measures there was a small positive effect of sexual selection on mean population fitness, although effect sizes varied with the fitness measure used. The positive effect of sexual selection on fitness was strongest for females in stressful environments, who also showed reduced variance in fitness under sexual selection.

Answer

The authors discuss these findings thoughtfully, although they focus more on the (weaker) effects found for ‘direct’ measures of fitness while somewhat neglecting the effects seen for ‘indirect’ fitness measures (e.g. of attractiveness, mating latency, lifespan, ejaculate traits). These potentially deserve more consideration, especially as many appear to be male-limited traits or measured mainly in males, that would appear to have a direct bearing on male mating success (if an indirect link to overall fitness), yet despite this the overall effect of sexual selection on male fitness is not significant.

Need to answer this in a similar line to Jaceks comments.

**I have only a few more specific comments:**

**Does your approach consider variation in the intensity of sexual selection exclusively on males? This is worth noting (e.g. statements such as that on line 98-99 might be amended to “Sexual selection on males significantly improved female fitness.”)**

Answer

Experiments manipulating the sex ratio to alter sexual selection might simultaneously decrease sexual selection on males while increasing sexual selection on females. Would this be classified as reduced sexual selection in your analyses? I don't think you included this aspect of study design as a moderator variable in any of your analyses – given that close to half of the effects you include come from “alternative manipulations” (line 70) perhaps you could test whether this affects effect size?

Answer

It seems possible that sexual selection on females, and not only on males, could affect population fitness – potentially even more directly than sexual selection on males. And might differing extents of sexual selection in each sex interact with the differences you saw in fitness measured in males vs. females?

Answer

L111-118 It seems a little odd that there is no residual heterogeneity in your  $I^2$  estimates. From the supplemental information it is not entirely clear to me how you have adapted the function that is under development in “metaAidR”, but can you double check that you have appropriately incorporated the residual variance into these estimates?

Answer

L307-311 Please clarify here that  $\ln\text{CVR}$  was calculated as the ratio  $\ln(CV\text{fitness}_{SS}/CV\text{fitness}_{noSS})$

Answer

**Fig. 3** Please explain the dashed red and black lines in the figure caption.

Answer

**Tables 1, 2** Please check – the parameter estimates for ‘Female sex’ and test for ‘Female > Male’ are bolded inconsistently between the REML and Bayesian models where these estimates are identical.

Answer

## References

- Bonett, Douglas G. 2009. “Meta-Analytic Interval Estimation for Standardized and Unstandardized Mean Differences.” *Psychological Methods* 14 (3). American Psychological Association: 225.
- Harano, Tomohiro, Kensuke Okada, Satoshi Nakayama, Takahisa Miyatake, and David J Hosken. 2010. “Intralocus Sexual Conflict Unresolved by Sex-Limited Trait Expression.” *Current Biology* 20 (22). Elsevier: 2036–9.
- Lajeunesse, Marc J. 2015. “Bias and Correction for the Log Response Ratio in Ecological Meta-Analysis.” *Ecology* 96 (8). Wiley Online Library: 2056–63.
- Nakagawa, Shinichi, Robert Poulin, Kerrie Mengersen, Klaus Reinhold, Leif Engqvist, Malgorzata Lagisz, and Alistair M Senior. 2015. “Meta-Analysis of Variation: Ecological and Evolutionary Applications and Beyond.” *Methods in Ecology and Evolution* 6 (2). Wiley Online Library: 143–52.
- Plesnar Bielak, Agata, Anna M. Skrzynecka, Krzysztof Miler, and Jacek Radwan. n.d. “Selection for Alternative Male Reproductive Tactics Alters Intralocus Sexual Conflict.” *Evolution* 68 (7): 2137–44. doi:10.1111/evo.12409.
- Viechtbauer, Wolfgang. 2010. “Conducting Meta-Analyses in R with the Metafor Package.” Journal Article. *Journal of Statistical Software* 36 (3): 1–48.