**Response to Reviewer Comments**

*We thank the Editor and both Reviewers for their constructive criticisms of the paper, which we believe have helped us to strengthen the manuscript. We have responded to all of their comments and questions with changes to the manuscript, as described in our point-by-point response below (in blue, interspersed with the original reviewer comments). Line numbers in blue refer to line numbers in the new document (see also the Marked Manuscript: ‘fulltext\_trackedchanges.docx’). The main changes were some additions to Box 1, a new Supplementary Text section, and additional discussion text to address issues raised by Reviewer 2. To partially compensate for the additional text, we have edited to make the text more concise where possible.*

*Over the course of checking model residuals for studies that used the animal model, we identified two studies containing six heritability estimates that were misclassified as juveniles when they in fact were calculated using adult coral colonies. We therefore re-ran our models with the correct life stage categorization and found qualitatively identical results from previously for both model selection and parameter significance (Supplementary Code Appendix C, Tables S1-14, Figs. S2-8). The updated results are presented in the re-submission.*

Reviewer(s)' Comments to Author:

Reviewer: 1

Comments to the Author

The manuscript entitled “Coral adaptation to climate change: meta-analysis reveals high heritability across multiple traits” by Bairos-Novak et al. describes a meta-analysis of 95 heritability estimates from 19 previously published studies investigating coral traits under various climate change-related scenarios and at different life stages. I am not an expert on the statistical tools applied to perform the meta-analysis, but the analysis and interpretation of heritability estimates is clear and consistent. This work will benefit biological scientists broadly by demonstrating meta-analysis approaches to better model heritability estimates. Furthermore, this study highlights a critical need to study coral reproduction, fecundity, and estimates of thermal performance optima and limits. The results are novel and clearly presented. The figures, besides minor issues with Figure 3 (see below), are clearly interpretable. The authors have provided supplemental information with clear documentation of their analytical approach and findings.

*We thank Reviewer 1 for their positive appraisal of our manuscript.*

Minor comments:

General question- are total estimates of phenotypic variation available for these studies?

The conversation about how environmental heterogeneity affects selection and additive genetic variance is important. The heritability estimates shown here across different treatments are compelling but it would be useful to know how the estimates may be affected by total variation experienced under different environments.

*R1.1 Unfortunately, estimates of total phenotypic variation are only available for 3 of the 19 studies examined (Wright et al. 2019 and Zheng et al. 2019 where all data are available online, and Carlon et al. (2011) where the mean and coefficient of variation for all corallite traits is provided). Thus, estimating any effects of environmental heterogeneity on trait plasticity or variation would be limited to only these three studies; however, we agree it is an important question, and that reporting such statistics should be a priority for further work. We now make this point at lines 231-234.*

Figure 3: The top of the “survival” panel is cut-off and the “H” and “h” characters disappeared from the legend

*R1.2 We have modified the figure to ensure that survival and other top panels are not cut off in the new version.*

*We believe that the disappearance of ‘h’ characters in the legend of Fig. 3 only occurs in the Microsoft Word version of the file and not in the final attached .eps file of the figure (which appears at the end of the submission PDF). However, should the paper be accepted, we will re-check and correct as necessary during the final proofing stage.*

Reviewer: 2

Comments to the Author

The authors present a much-needed meta-analysis that compiles existing estimates of the heritability of existing traits in corals. This is of timely relevance given that corals are extremely vulnerable to climate change and local stressors and their ability to persist over the next several decades will largely depend on their capacity to adapt to changing environments.

I would first like to commend the authors on a well-written and interesting paper; as well as excellent documentation and code accessibility through the use of Rmarkdown files. I find no major flaws with the paper from a methodological standpoint, though as I've also mentioned to the editor, I certainly do not consider myself an expert on meta-analysis/model selection statistical methods.

*We appreciate the comments of Reviewer 2 regarding our manuscript and have endeavoured to address every comment.*

I do, however, have a much deeper understanding of evolutionary theory/quantitative genetics and, on this front, I believe your paper needs to include a more in-depth discussion and qualification of how it is that heritability is measured in most coral studies.

Estimating heritability by using the breeder’s equation and exerting some kind of selection on a population gives you realized heritability, not narrow sense heritability in the canonical sense, which is derived from the regression of the mid parent trait values on offspring values. This is what most coral studies are doing since no one really has the patience, funding, or luck to successfully rear corals across multiple generations and measure traits of parents and offspring in common garden conditions and calculate heritability in that way. Some studies do look at parents and their offspring, but usually only focus on larvae (e.g. Dixon et al. 2015) or at most early juveniles (e.g Quigley et al. 2020). Though they often don't directly measure parental traits and rely on their environment of origin as some proxy for, say, thermal tolerance (e.g. Quigley et al. 2020 again where they take the northern GBR parents to be more thermally tolerant because they are from warmer reefs).

*R2.1 We agree with Reviewer 2 that realized heritability is limited in many ways relative to narrow-sense and broad-sense heritabilities. However, we believe that our too-brief description of the application of the breeder’s equation in the studies meta-analyzed here inadvertently led the reviewer to believe that the majority were measuring realized and not narrow-sense heritability. To be specific, from the studies examined in this meta-analysis, no studies calculated heritability using the realized heritability method (i.e. imposing a selection differential and measuring the resulting response in offspring, then using the Breeder’s equation to calculate realized heritability, h2R). Instead, the majority of studies (14/19) used the so-called ‘animal model’ method for estimating heritability* (Kruuk, 2004; Wilson et al., 2010)*, which uses relatedness information from a known pedigree (or using genetic markers to infer the pedigree) as a random effect in order to estimate the additive genetic variance, VA, associated with the breeding values of individuals.*

*To help clarify this, we have added a new section in the Supplementary Information file (Supplementary Text S1) regarding which heritability model studies used to estimate heritability. This text will ensure that readers know which heritability method was used (animal model, ANOVA-design, or Ritland’s regression) and the specific caveats of each method.*

Measuring realized heritability, especially if it is only done within one generation/population is going to over-estimate heritability, since it would also capture other things like plasticity in response to the selection pressure for instance. That may be partially accounted in some of the studies that report broad-sense instead of narrow sense heritability, but again even when studies are claiming to report broad-sense heritability (e.g. Wright et al. 2019) by taking fragmenting corals to control for genotype and measuring differences in response, one cannot fully disentangle the impact of canalization or preconditioning that might have occurred in that individual’s native environment and could be influencing their response under experimental conditions. In addition, as corals are holobionts, there is a whole other can of worms that comes into play in consider differences in symbionts or microbiome members between parents/offspring, or even different parts of the same colony. This is not to say that all these studies are wrong or useless, they are extremely important, and the coral field could benefit from more of these.

However, you should take these imperfections into consideration, when you present your meta-analysis as finding support for high heritability in important traits such as survival – a complicated trait to measure in a quantitative genetic context to begin with – and conclude this means that corals have more adaptive capacity than we might have thought. The heritability estimates you are analyzing are all very likely vast overestimates. Case-in-point, most of your heritability estimates for survival are close to 1, which even common sense would tell us cannot be the true value.

*R2.2 On the first sentence regarding realized heritability, please see the above response R2.1 regarding the absence of studies reporting realized heritability.*

*For the second point regarding individuals originating from different native environments, thus resulting in biased heritability estimates, we agree with Reviewer 2 in that “… one cannot fully disentangle the impact of canalization or preconditioning that might have occurred in that individual’s native environment and could be influencing their response under experimental conditions”. However, this is more likely in some cases than others. To address these points, we have added a new section on the confounding sources of phenotypic variation that may bias narrow-sense heritability (lines 463-495):*

*“Our review of the literature highlights some potential sources of bias in heritability estimates that are not well-controlled in coral studies to date. Studies that do not use shared common environments may overestimate heritability by confounding environment-driven phenotypic variation with additive genetic variation, such as when related individuals occur in the same environment and thus acclimatize similarly. Importantly, no studies examining adult corals raised corals to adulthood in a shared common environment, and thus do not control for preconditioning or canalization differences among colonies (Putnam and Gates 2015). However, coral larvae and juveniles were almost always raised in shared common environments during spawning and fertilization, thus larvae and juvenile heritability estimates are less likely to be overestimated due to this phenomenon. Despite this, there are a number of traits with higher heritability for larvae and/or juveniles relative to adults, such as survival, gene expression, nutrient content, and morphology (Fig. 3). This suggests that, at least for these traits, the variation associated with preconditioning and plasticity is unlikely to be particularly large relative to the additive genetic variance. Moreover, visual inspection of residuals suggested no additional unexplained variation that might be associated with whether or not a shared common environment was used (Fig. S9 in Supplementary Code C).*

*Our results are also affected by other sources of phenotypic variation not accounted for in present studies, such as parental and epigenetic effects. Parental effects may have a larger influence on heritability than previously assumed (Noble et al. 2014; Kenkel et al. 2015b), and may be especially important for brooding corals in which the offspring develops within the parent colony as well as for species inheriting their symbiont communities directly from parents (i.e. vertical transmission) (Kenkel et al. 2015b; Quigley et al. 2017). Vertically-transmitting brooders and broadcast spawning species make up a minority of species examined (3/19 and 9/19, respectively), with the remaining being horizontally-transmitting spawners. Similarly, the number of heritability estimates from vertical transmitters made up only 9/95 and 16/95 heritability estimates, respectively, and thus parental effects via brooding and/or vertical transmission would have impacted a minority of estimates. Epigenetic effects may also inflate heritability estimates (Putnam and Gates 2015). In studies of multicellular animals, there has been little support for epigenetic inheritance via CgP methylation (Torda et al. 2017), although at least one recent study in corals has found such evidence (Liew et al. 2020). Further evidence is needed to determine if epigenetic changes confer fitness benefits similar to additive genetic effects (Torda et al. 2017), thus future studies aiming to separate phenotypic variation specific to parental effects, symbiont composition, epigenome, and additive genetic effects would be especially valuable.”*

On these points, I think you in your box on heritability you should: (1) explain the caveats/differences between estimating narrow sense heritability using the breeder equation and a selection pressure, aka realized heritability, and from midparent regression, (2) also discuss broad sense heritability since this comes up through the paper and will be helpful for a reader less familiar with quantitative genetics. Additionally, I think you should discuss these points more fully in your discussion as well as moderate your conclusion that corals are more adaptable than we might otherwise think. I don’t necessarily disagree with this conclusion, but I don’t think these data are the strongest argument for it.

*R2.3 In regard to the first point, we have added a new supplementary section on the differences and caveats (Supplementary Text S1; see reply R2.1: we had to put this in the Supplementary, rather than adding all this text to Box 1, to avoid going over the word limit). In regard to the second point, we have added further discussion to the differences between broad-sense and narrow-sense heritability in Box 1 as suggested (see Box 2 at line 72, first paragraph after equations), but note that the original submission discussed these differences already (see former Box 1 at line 72 of the original submission). Finally, we have added a new section discussing the confounding sources of phenotypic variation that are important to consider in the context of our review’s conclusions (see reply 2.2, lines 463-495).*

I have a few other minor comments:

In figure 2 it is not clear if these are broad or narrow sense.

*R2.4 Figure 2 presents the results of the overall dataset analysis that selected the trait type only model as optimal (selected based on the lowest AICc), and thus is pooling across heritability type and life stage (in contrast to Figure 3). To make this clearer, we have changed the first line of the caption to:*

*“Heritability estimates ± SE for the trait type-only model, not accounting for differences due to (i.e., pooled across) life stage and heritability type.” (lines 355-356)*

Lines 430 -432. I’m not following this logic. If there is stabilizing selection occurring at the juvenile stage, then heritability wouldn’t magically bounce back somehow at the adult stage. The juveniles that were selected for would continue to adult stages. Again, given that these studies are mostly all measuring realized heritability there may simply be less response to selection at the juvenile stage

*R2.5 We concede Reviewer 2’s first point, that stabilizing selection is likely to occur similarly both for juveniles as well as adults. We therefore have modified this statement to apply to only larvae to juvenile stages (lines 430-435 From juvenile to adults, we now suggest the following potential explanation (lines 437-443):*

*“There is also evidence that increases in additive genetic variance (VA) may occur via mutation accumulation across an organism’s lifetime (Wilson et al. 2008b). Moreover, reduced importance of local environment with age can result in reduced relative total variation, VP (e.g., the Wilson effect, Bouchard Jr. 2013). Both of these processes can therefore result in older life stages having higher heritability estimates. Making the distinction between these processes requires examining changes in VA and VP across an organism’s lifetime, which no coral studies have done to date.”*

Line 126: suggest adding in Logan et al. 2021 and briefly mentioning symbiont evolution.

*R2.6 We have added the above reference suggested by Reviewer 2 (lines 124-127 and 621-623) and now mention the potential for rapid symbiont evolution at lines 129-131.*

Lin 372 gene expression is also a more stochastic measurement some of this should be discussed.

*R2.7 We have added a this as a potential reason why gene expression is often observed to have low heritability (lines 373-376).*

Line 418-420 repeated what has been previously stated, remove

*R2.8 We have made this suggested removal.*

H and h seem to be missing in Fig 3 legend

*R2.9 As mentioned in R1.2, we believe this disappearance only occurs in the Microsoft Word version of the file, as it does not recur for the .eps attachment version of the figure (which appears at the end of the submission PDF). However, should the paper be accepted, we will re-check and correct as necessary during the final proofing stage.*

L 584 typo

*R2.10 The ‘predicts’ typo has been changed to ‘predictions’.*

**References**

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