**Title: The predictability and magnitude of life-history divergence to ecological agents of selection: a meta-analysis in livebearing fishes**

Authors: Michael P. Moore1, Rüdiger Riesch2, and Ryan A. Martin1

1. Department of Biology, Case Western Reserve University, Cleveland, Ohio 44106, USA

2. School of Biological Sciences, Royal Holloway, University of London, Egham TW20 0EX, UK

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RAM conceived the study, all authors designed the study, MPM conducted the literature search and calculated effect sizes, MPM and RAM conducted all analyses, all authors discussed the results, MPM wrote the initial draft of the manuscript, and all authors contributed to revisions.

**Abstract**

Environments causing variation in age-specific mortality⎯ecological agents of selection⎯mediate the evolution of reproductive life-history traits. However, the relative magnitude of life-history divergence across selective agents, whether divergence in response to specific selective agents is consistent across taxa, and whether it occurs as predicted by theory remains largely unexplored. We evaluated divergence in offspring size, offspring number, and the trade-off between these traits, using a meta-analysis in livebearing fishes (Poeciliidae). Life-history divergence was consistent and predictable to some (predation, hydrogen sulfide) but not all (density, food limited, salinity) selective agents. In contrast, magnitudes of divergence among selective agents were similar. Finally, there was a negative, asymmetric relationship between offspring-number and offspring-size divergence, suggesting greater costs of increasing offspring size than number. Ultimately, these results provide strong evidence for predictable and consistent patterns of reproductive life-history divergence, and highlight the importance of comparing phenotypic divergence across species and ecological selective agents.

**Introduction**

An essential goal of life-history theory is to understand how demographic traits respond to natural selection (Stearns 1992; Roff 2002). Maternal investment in offspring size and number has received considerable attention because of the direct association between these traits and fitness, and the inherent trade-offs between them (e.g. Smith & Fretwell 1974; Lim *et al.* 2014). Specifically, as the resources available to invest in each reproductive event are finite, investment in one trait constrains investment in the other (van Noordwijk & de Jong 1986; Stearns 1992; Roff 2002). Selection acting directly on either trait is therefore predicted to lead to a response in both (e.g., Czesak & Fox 2003; Riesch *et al.* 2014). In general, populations experiencing divergent patterns of age-specific mortality are expected to evolve differential reproductive strategies (i.e. life-history divergence). When adult mortality rates are high relative to juvenile mortality rates, females investing in as many offspring as possible are expected to have the highest fitness, even if this investment comes at a cost of also producing smaller offspring (Stearns 1992; Roff 2002). Conversely, when juvenile stages experience high mortality rates relative to adult mortality rates, larger offspring may be more robust to unfavorable conditions, and maternal investment in larger, but potentially fewer, offspring is favored (Stearns 1992; Roff 2002).

The underlying cause of differences in age-specific mortality patterns is environmental variation (Wade & Kalisz 1990; MacColl 2011), and a suite of studies have evaluated how maternal investment in offspring size and number diverges in response to ecological agents of selection (e.g. Reznick 1982; Martin 1995; Badyaev & Ghalambor 2001; Duponchelle *et al.* 2008; Riesch *et al.* 2014). Such studies represent crucial tests for shared (i.e. replicated across taxa) and predictable (i.e. in accordance with theory) phenotypic responses to natural selection (Wilbur *et al*. 1974; Langerhans & DeWitt 2004; Losos 2011), and have greatly increased our understanding of how life histories respond to the causes of selection. Additionally, as many organisms face similar selective pressures (e.g. density, predators), simultaneously quantifying and comparing life-history divergence across selective agents and taxa provides broad insight into how the ecological causes of selection shape phenotypic diversity (Roff 2002; Losos 2011 MacColl 2011; Kingsolver *et al.* 2012). However, the relative effects of different selective agents on life-history divergence across taxa are largely unknown (Stearns 1992; Roff 2002).

Livebearing fishes (family:Poeciliidae) provide a unique opportunity to quantify and compare life-history divergence across multiple taxa and multiple selective agents. In addition to a wide global distribution and a well-resolved phylogeny, many species of these small, rapidly maturing fishes face similar selective agents across their ranges (Langerhans & DeWitt 2004; Riesch *et al.* 2014). Such patterns provide critical replication of reproductive life-history divergence both across and within species, and to multiple environments associated with variation in age-specific mortality regimes (Johnson & Bagley 2011). Moreover, live-bearing organisms are especially prone to strong constraints on the balance between offspring size and number due to finite body cavity space (e.g., Qualls & Shine 1995). In this study, we used a phylogenetic meta-analysis to evaluate the direction and magnitude of offspring-size and number divergence to multiple ecological agents of selection across 17 species of poeciliid fishes (Table S1). We reviewed the literature for studies that reported on life-history divergence to putative selective agents. Specifically, we then considered three primary questions:

1) *Is reproductive life-history divergence to selective agents consistent and predictable?*

Our literature search returned reproductive life-history responses to many putative selective agents (Table 1). Five of these agents (population density, food limitation, hydrogen-sulfide toxicity, predation, and salinity) were sufficiently replicated across studies to 1) estimate the overall direction of their effects (i.e. is there a consistent response across studies?), and 2) test the direction of their effects for accordance to *a priori* expectations based on key empirical results and theory (Table 1). Due to size-mediated competitive asymmetries for limited spatial and/or nutritional resources, high population density is predicted to select for larger offspring (e.g. Pianka 1970; Bashey 2008). Similarly, food limitation should most negatively affect the survivorship of small individuals, resulting in selection for larger, more robust offspring (e.g. Hamel *et al.* 2009; Jørgensen *et al.* 2011). The presence of toxic hydrogen sulfide in aquatic environments is predicted to select for larger offspring sizes, as smaller surface area to body volume ratios promote improved detoxification (Powell 1989; Riesch *et al.* 2014). In areas of high predation risk, adult mortality is high, and selection for many, small offspring occurs (e.g., Reznick 1982; Jørgensen *et al.* 2011). Finally, increased salinity causes osmotic stress with multiple subsequent metabolic and behavioral effects (e.g. Swanson 1998), and is therefore predicted to select for larger offspring sizes.

2) *How do the magnitudes of divergence in offspring size and number vary among selective agents?*

To assess if some selective agents elicit stronger life-history divergence than others, we evaluated the magnitudes of divergence to selective agents. Specifically, we compared the magnitudes of divergence between all abiotic and biotic selective agents, as well as among the five selective agents described above (Table 1). Additionally, to compare plastic, genetic, and a combination of plastic and genetic responses, we evaluated the magnitudes of divergence among females exposed to experimentally-manipulated selective agents within their lifetime (i.e. plastic), females from populations with historical exposure to the selective agent that were then reared in a common garden (i.e. genetic), and wild caught (i.e. plastic and/or genetic).

3) *What is the relationship between offspring-size and number divergence across selective agents?*

From all of the studies included in our meta-analysis, we considered the general relationship between offspring-size and number divergence. In addition to assessing whether the slope was significantly negative (indicating a trade-off), we also quantified whether the slope of this relationship differed from negative one. This would indicate that investment in one trait increases proportionally greater (i.e. more than -1) or less than (i.e. less than -1) the investment in the other. Finally, we asked whether the slope of this relationship differed among our five best-replicated selective agents.

**Methods**

*Study selection and effect size calculation*

We performed a comprehensive literature search for studies published through January 2015 that reported how offspring number and size (and also reproductive allocation, i.e., the ratio of reproductive organ mass to dry body mass; see *Supplemental Methods and Analyses*) varied with exposure to putative selective agents in species of the family Poeciliidae. We first searched for papers through *Google Scholar* using the keywords: “Poeciliidae, Reproductive Investment”; “Poeciliidae, Offspring Size”; “Poeciliidae, Offspring Number”; “Poeciliidae, Life history Evolution”; “Poeciliidae, Life history Plasticity”. We additionally searched for studies using the citations within each of these collected papers. In total, this initial search yielded 168 studies that potentially included information about how at least one of our focal traits diverged in response to selective agents. From this database, a study was retained if it unambiguously reported: at least one of the reproductive life-history traits in multiple levels of a selective agent for a single species; the sample sizes that were used at each level of the selective agent; and a measure of variability of the focal trait(s) about the means (i.e. standard error, standard deviation, confidence interval). A total of 54 studies across 17 species met these criteria (Table 1; see *Supplemental Methods and Analyses* for full citation list and Table S1 for species represented in each environment).

We calculated mean trait values for levels of the environment included within each study. For wild-caught females, mean trait values were calculated for females from each sampled area. For experimentally manipulated females, mean trait values were calculated for each level of the manipulation. For females reared in a common garden, mean trait values were calculated for each population originating from the different selective environments. Due to the small total number of divergence estimates in common garden studies (10), we statistically could not account for divergence differences between F1 and F2 generations. For all study designs, when multiple populations from a single environmental level were used, we weighted trait value means by population size when calculating the grand mean for that level. In these cases, we calculated the corresponding measurement error of those means by propagation. When trait values and variances were not reported in tables, we extracted values from digitized figures with ImageJ.

To provide a standardized estimate of life-history divergence, we used Hedge’s G and its corresponding error variance. We included the less intense environmental level as the baseline (i.e. [μmore selective–μless selective]/SDpooled). Thus, each effect size can be interpreted as “life-history divergence”, in standard deviations, between two levels of the selective agent. Four studies considered life-history variation along a gradient, and in such cases we include divergence only from the two ends of the gradient (e.g. Uller *et al.* 2013). This resulted in a total of 170 estimates of reproductive life-history divergence among the three traits (Table 1; Table S1). Additional details of our effect size calculations can be found in the *Supplemental Methods and Analyses*.

*General Modeling Approach*

We employed a linear mixed-effects model approach to evaluate reproductive life-history divergence using the *MCMCglmm* package (Hadfield 2010) with the statistical software R v.3.1.2 (R Development Core 2014). To account for uncertainty associated with the true divergence values included in our study, we used the squared standard error of the calculated effect sizes as our measurement error variance (Nakagawa & Santos 2012). As random effects in all models, we included study identity, species identity, and a covariance matrix based on the topology of an ultrametric Poeciliidae phylogeny (Pollux *et al.* 2014) assuming a Brownian motion model of evolution. Not all species were represented in all analyses, and thus the phylogeny was pruned for each analysis by dropping out non-represented species. While some models included additional random effects (see below), study type was never included as a random effect as it was perfectly confounded with some selective agents. We specified an inverse gamma prior with *V*=1.000 and *nu*=0.003 except where noted otherwise, however, our results were robust to 1000-fold increases to *nu*. For all models, we used 500,000 iterations, with a burn-in of 100,000 and thinning interval of 10, and subsequent tests indicated low autocorrelation. We ran all models in triplicate, and Gelman-Rubin diagnostics indicated model convergence (all potential scale reduction factors <1.1; Gelman & Rubin 1992). For each analysis, we evaluated the proportion of total variance accounted for by each random effect (I2; Nakagawa & Santos 2012; Table S2), and additionally calculated phylogenetic heritability (*H*2*p*; Lynch 1991). As the phylogeny was pruned for each analysis, thereby altering the phylogenetic covariance matrix among analyses, H2p estimates should be compared among analyses with caution.

Preliminary analyses indicated that three estimates of offspring-size divergence (two hydrogen-sulfide estimates, and one predation estimate) were very large outliers (|G|>10), and prevented adequate model estimation of the mean and variance of effects. However, in all cases, these divergence estimates were in the same direction as the mean divergence for their respective environments, thus their exclusion makes our analyses conservative. Additionally, very few studies reported on reproductive allocation, and no discernable patterns emerged from these analyses. Thus we report these methods and the results in the *Supplemental Methods and Analyses*. Lastly, visualization of funnel plots (Fig. S1) and Egger’s regression of meta-analytic residuals indicated no substantial publication bias (Table S3; Egger *et al.* 1997, Nakagawa & Santos 2012).

1) *Is reproductive life-history divergence to selective agents consistent and predictable?*

We compared reproductive life-history divergence to the selective agents included in our dataset by fitting separate models for each trait and comparing the responses to zero. For offspring size and offspring number, we included only selective agents that had at least five estimates of divergence (Table 1). For these analyses, we considered phenotypic divergence as consistent across studies and taxa when the 95% highest posterior density (HPD) intervals of the mean did not overlap zero. Additionally, divergence was considered predictable when its direction matched the *a priori* predictions (Table 1).

2) *How do the magnitudes of divergence in offspring size and number vary among selective environments?*

We quantified the magnitudes of reproductive life-history divergence (*i*) among study types (i.e. experimental manipulation, field collections, and common garden), (*ii*) among the five selective agents from Question 1, and (*iii*) between the abiotic and biotic selective agents in the database (Table 1). For the analysis of study type, we also included the selective agent as an additional random intercept, and thus specified our inverse gamma prior as V=1, *nu*=0.004. We used separate analyses for offspring-size and number divergence, and report the mean and 95% HPD intervals. Quantifying the magnitudes of divergence necessitates using absolute values (|G|), which upwardly bias small estimates with relatively large measurement error (see Hereford et al. 2004). To account for this bias, we corrected our divergence estimates by applying the posterior distributions of solutions and variance estimates to a folded normal distribution (see Kingsolver et al. 2012).

3) *What is the relationship between offspring-size and number divergence across selective agents?*

We assessed the relationship between offspring-size and offspring-number divergence. This analysis specifically evaluated whether increases to offspring number resulted in concurrent decreases to offspring size. We used a similar modeling approach as described above, but we fit offspring-size divergence as the dependent variable and offspring-number divergence as a fixed effect. Because standard errors for the offspring-size divergences tended to be larger, we used the squared standard errors of this trait as our measurement error variance. As variation in offspring-size divergence was observed among selective agents (see *Results*), we included a random intercept of selective agent (in addition to the random effects described in our general modeling approach) to ensure that variation in the intercepts was not driving any potential relationship. We specified an inverse gamma prior as V=1, *nu*=0.004 for this analysis. We considered the mean posterior estimate of the intercept and slope, and used the 95% HPD intervals to evaluate differences from zero and negative one.

To explicitly evaluate whether the slopes of this relationship differed among selective agents included in Questions 1 and 2, we fit models that included the selective agent, offspring-number response, and their interaction as fixed effects. We conducted separate analyses with each selective agent as the reference level and tested for significant differences among the slopes. With the exception of a random intercept for selective agent, we included the same set of random effects as described.

By quantitatively comparing life-history divergence in this way, we are likely making comparisons among very different degrees of environmental variation among and within selective agents. Quantitative comparisons of the variation of environmental intensity among selective agents would require a common scale, such as mortality rate. As no such scale was available for our analyses, we could not compare the variation of selection intensities among selective agents. To account for potential within-selective agent variation in the magnitude of the environmental change (e.g. 100% versus 300% increase in H2S), we calculated the relative increase of environment intensity for divergence estimates to the selective agents with quantitative scales (e.g. salinity, H2S; Table 1). As the relative increase of the environmental intensity is only comparable among divergence estimates within a selective agent, we conducted separate analyses for each environment including this variable as a fixed effect. We detail these analyses and results in the *Supplemental Methods and Analyses*. However, our results were qualitatively and quantitatively similar even after the inclusion of this covariate (Fig S5-S6), indicating that the observed patterns presented here are at least not strongly influenced by within-selective agent variation of environmental intensity.

**Results**

*1) Is reproductive life-history divergence to selective agents consistent and predictable?*

In general, mean offspring-size and number divergences were in the predicted directions for most selective environments, but were not always different from zero (Fig. 1). In response to elevated hydrogen sulfide concentrations, females significantly increased offspring size (mean, lower 95% HPD interval, upper 95% HPD interval hereafter: 2.81, 1.44 to 4.09), and decreased offspring number (-1.45, -2.69 to -0.29). When faced with high predation risk, females exhibited significantly decreased offspring size (-1.64, -2.53 to -0.69) coupled with increased offspring number (1.24, 0.28 to 2.13). Responses to food limitation, however, were mixed, as the direction of offspring-size divergence was not consistent across studies (0.02, -0.82 to 0.91), but offspring number significantly decreased (-0.98, -1.79 to -0.11). While the effects of population density were in the predicted direction, the mean estimated responses did not differ from zero (offspring size: 0.81, -0.20 to 1.82; offspring number: -0.53, -1.44 to 0.37). With elevated salinity, females exhibited no significant patterns of reproductive life-history divergence (offspring size: -0.63, -1.94 to 0.68; offspring number: 0.85, -0.42 to 2.24), and patterns for offspring size were opposite to the predicted direction (Table 1). *H*2*p* was modest for both offspring-size (0.23, 1.26x10-4 to 0.73; I2Total: 0.97, 0.95 to 0.98) and offspring-number (0.04, 7.65x10-5 to 0.18; I2Total: 0.98, 0.97 to 0.99) divergence.

2) *How do the magnitudes of divergence in offspring size and number vary among selective agents?*

Among study types (Fig. S2), experimental manipulations (size: 1.04, 0.64 to 1.97; number: 0.74, 0.47 to 1.35) and common garden experiments (size: 1.07, 0.65 to 2.03; number: 0.80, 0.56 to 1.44) tended to exhibit stronger responses than field collections (size: 0.82, 0.58 to 1.47; number: 0.51, 0.35 to 0.92). *H*2*p* was low for both the magnitude of offspring-size (0.05, 0.02 to 0.10; I2Total: 0.99, 0.99 to 1.0) and offspring-number (0.04, 0.02 to 0.09) divergence.

Offspring-size divergence tended to be greater to abiotic (0.92, 0.42 to 1.68) than biotic selective agents (0.52, 0.28 to 0.92; Fig.2). In contrast, offspring-number responses were similar between abiotic (0.61, 0.43 to 1.08) and biotic (0.54, 0.33 to 1.03) selective agents. *H*2*p* of offspring-size divergence was moderate (0.30, 0.20 to 0.45; I2Total: 0.905, 0.88 to 0.94), but was low for offspring-number divergence (0.13, 0.09 to 0.24; I2Total: 0.96, 0.96 to 0.97).

Considering the specific selective agents used in Question 1, offspring-size divergence was the greatest in response to hydrogen-sulfide toxicity (2.81, 1.47 to 4.10) and the smallest in response to food-limited environments (0.48, 0.35 to 0.87). Offspring-size divergences were also fairly large as a result of variation in predation risk (1.64, 0.76 to 2.56), while divergences in response to population density and salinity were similar (density: 0.90, 0.40 to 1.64; salinity: 0.91, 0.53 to 1.72). The largest mean offspring-number divergences were observed to hydrogen sulfide (1.49, 0.48 to 2.43) and predation risk (1.25, 0.37 to 1.99), while the smallest was observed for population density (0.68, 0.36 to 1.28). The magnitudes of offspring-number divergence to food limited (1.01, 0.34 to 1.67) and high salinity (1.05, 0.54 to 1.97) environments were similar. For the magnitude of offspring-size divergence, we observed the greatest *H*2*p* of any analysis (0.58, 0.42 to 0.79; I2Total: 0.91, 0.88 to 0.94). *H*2*p* was low for offspring-number responses (0.03, 0.02 to 0.06; I2Total: 0.922, 0.90 to 0.94).

However, nearly all estimates of the magnitudes of divergence exhibited overlapping 95% credible intervals, and thus the results of these particular analyses should be interpreted cautiously.

*3) What is the relationship between offspring-size and number divergence across selective agents?*

Increased offspring number was associated with decreased offspring size (intercept: 0.11, -1.12 to 1.38; slope: -0.25, -0.48 to -0.03; Fig. 3), indicating a significant trade-off. As the 95% credible intervals of the slope also did not overlap negative one, it suggests that, on average, an increase in offspring number by one standard deviation results in a decrease of offspring size by less than one standard deviation. Moreover, we found that there were no differences in the slopes of this relationship among the selective agents (all 95% HPD intervals of contrasts overlapped 0). *H*2*p* was low (0.07, 5.62x10-5 to 0.33; I2Total: 0.99, 0.98 to 1.0).

**Discussion**

Ecological agents of selection drive adaptive phenotypic divergence (Wade & Kalisz 1990; MacColl 2011), and identifying parallel phenotypic responses across taxa to these selective agents has broad implications for resolving patterns of local adaptation and speciation (Rundle & Nosil 2005; Losos 2011). We quantitatively assessed reproductive life-history divergence to multiple selective agents in the poeciliid family of livebearing fishes. While divergence to some selective agents was not consistent or predictable across studies, we found consistent and predictable divergence in reproductive strategies to predators and hydrogen sulfide. Additionally, within selective agents, traits, and experimental designs, we found considerable variation in the magnitudes of divergence. We also found that a one standard deviation increase in offspring number was associated with only, on average, a 0.25 decrease in standard deviations of offspring size. Notably, these effects were robust to the weak-to-moderate phylogenetic-level variance observed in our analyses. Overall, these results reveal the parallel nature of life-history divergence to some, but not all, selective agents, and further highlight the importance of quantifying and comparing life-history divergence to the ecological causes of selection.

*Is reproductive life-history divergence to selective agents consistent and predictable?*Even after controlling for phylogeny, offspring-size and number divergence was consistent and predictable to predation and hydrogen sulfide (Fig. 1), which indicates strong convergence of life-history patterns in response to these environments. This supports the findings of other comparative studies that suggest that the evolution of life-history strategies is consistent and predictable across taxa in some environments (e.g., Duponchelle *et al.* 2008), even if the convergent traits are not the direct target of selection in all cases (e.g. Riesch *et al.* 2014). In contrast, divergences to population density and salinity were not significantly different from zero across taxa (Fig. 1). Such a finding highlights that even closely related, ecologically similar organisms may respond to the same selective agent with differing life-history strategies. Variation in the strength of viability selection offers one possible explanation for this result. While predation and hydrogen-sulfide toxicity strongly mediate mortality variation (e.g. Reznick *et al.* 1996; Plath *et al.* 2013), differences in population density may primarily affect other fitness-related traits, such as growth (e.g. Bashey 2008). In such cases, offspring receiving seemingly suboptimal investment may not only survive, but may eventually minimize fitness differences through mechanisms such as compensatory growth and reproduction (e.g. Lindholm *et al.* 2006; Moore *et al.* 2015, but see Auer *et al.* 2010). Such patterns may mitigate the strength of selection on investment in offspring size, for example, and may lead to the evolution of multiple, optimal life-history strategies across populations or species (Wilbur *et al.* 1974; Losos 2011). Future research into how each environment mediates variation in offspring fitness remains necessary, but our analysis provides substantial evidence of parallel, predictable reproductive life-history divergence to selective agents associated with strong variation in age-specific mortality.

Convergent responses across taxa to various selective agents, like those observed here, provide strong evidence for the repeated evolution of reproductive life histories under certain environmental conditions (Langerhans & DeWitt 2004; Losos 2011). While substantial evidence in poeciliid fishes exists for evolved genetic differences to some selective agents (e.g. Reznick 1982; Riesch *et al.* 2013), we cannot rule out plasticity as a factor in generating at least some of the observed divergence. Indeed, when considering divergence among experimental designs, studies isolating the effects of plastic and genetic effects tended to find similar magnitudes (Fig. S2). However, evidence for plasticity’s role in mediating evolved differences is rapidly growing (West-Eberhard 2003; Lind et al. 2015), and, in many cases, genetic divergence to selective agents may have begun as plastic responses before becoming fixed via genetic accommodation (e.g., Schlichting & Wund 2014). Thus, even divergence mediated by developmental plasticity may often reflect the initial stages of evolved divergence (Lind *et al.* 2015; but see Ghalambor *et al.* 2015). Future research should nonetheless evaluate the relative roles of plastic and genetic differences underlying predictable divergence to multiple selective agents. Irrespective of the underlying mechanism, our data provides strong support for shared patterns of phenotypic divergence to similar selective agents across taxa.

*How do the magnitudes of divergence in offspring size and number vary among selective agents?*

Despite differences in the consistency of divergence among traits and environments, we did not detect strong variation in the magnitudes of divergence among the selective agents, traits, and study designs. This likely reflects the substantial variation in the magnitudes of divergence *within* each of these factors (Fig. 2). Interestingly, controlling for the relative increase in the intensity of the environment did not account for this variation within selective agents (Figs S5-S6). Moreover, species- and phylogenetic-level effects occasionally explained a moderate proportion of the residual variation in the magnitudes of divergence (Table S2), however these effects were rarely strong enough to suggest that shared evolutionary history is solely responsible for this pattern. Consequently, it seems likely that unique aspects of each population’s selective regime may contribute to this variation. In particular, within each focal environment, multiple selective agents may be acting on offspring size and number either concurrently or with some temporal variability. In such cases, population-specific interactions among selective agents may constrain the degree of divergence in any one direction, with consequent effects on the observed magnitudes (e.g., MacColl 2011; Langerhans & Riesch 2013). Indeed, certain environments may often be correlated (e.g. increased predation with reduced density; MacColl 2011), and future research should disentangle how shared and unique aspects of population-specific selective regimes affect the magnitude of life-history divergence (*sensu* Langerhans & DeWitt 2004).

*What is the relationship between offspring-size and number divergence across selective agents?*

Broad investment trade-offs between offspring size and number across species and environments are expected from theory (Smith & Fretwell 1974), and a recent meta-analysis indicates their near ubiquity (Lim *et al.* 2014). However, quantifying the slopes of these size-number relationships across multiple species and environments may provide important, additional insight into life-history evolution. In this study, we observed that the slope of the relationship significantly differed from both zero and negative one. While there is tremendous interspecific variation in the absolute sizes and numbers of offspring produced (Johnson & Bagley 2011; Olivera-Tlahuel *et al.* 2015), increasing the number of offspring by one standard deviation should generally be more energetically and ecologically costly than increasing the sizes of each offspring by one standard deviation. For example, consider a hypothetical fish with the mean and standard deviation of embryo size (1.9±0.6 mg) and number (10.5±4.7 offspring) estimated from the dataset. A one standard deviation increase in embryo size to an average number of offspring is an additional 6.1 mg, while a one standard deviation increase in offspring number to an average embryo size would result in an additional 8.9 mg. Consequently, we might expect that an increase of one standard deviation of number requires more than one standard deviation decrease to offspring size, and therefore a slope less than negative one is predicted. Yet, across taxa, a one standard deviation increase in offspring number was associated with only, on average, a 0.25 standard deviation decrease to offspring size (Fig. 3).

Two explanations of this intriguing result seem most plausible: (1) high energetic costs of per-capita offspring size maintenance associated with viviparity, and (2) strong importance of trade-offs between current and future reproduction. As some poeciliid species provision offspring throughout embryonic development (Pollux *et al.* 2009; Olivera-Tlahuel *et al.* 2015), the costs of provisioning a few large offspring may be proportionally greater than the costs of provisioning many small offspring. This could bias the magnitude of the slope, and further research should investigate the energetic requirement of per-capita provisioning among different sizes of clutches and different levels of maternal provisioning. A slope with a magnitude less than one is also consistent with energetic trade-offs between current and future reproduction mediated through shifts in reproductive allocation. For example, when adult mortality is high relative to juvenile mortality, females are expected to increase offspring number via shifting energetic allocation away from future reproduction and towards current reproduction. Indeed, the life-history predictions for high adult mortality environments are specific to trade-offs between current and future reproduction (Stearns 1992; Roff 2002), and are only indirectly associated with increases to offspring number. An increased overall allocation to current reproduction may then alleviate some of the energetic costs imposed on offspring-size investment, and females may not need to greatly reduce investment in offspring size. However, if energetic trade-offs between current and future reproduction alone explained this relationship, a size-number trade-off may not have been observed at all, and thus our results are suggestive of trade-offs both between and within reproductive events. Ultimately, very little is currently known about the magnitude of the slope of this nearly ubiquitous trade-off, and quantifying this relationship across taxa may provide general insight into the energetic and ecological constraints mediating the evolution of maternal-investment patterns.

*Ecological agents of selection and the predictability of phenotypic divergence*

A fundamental goal of biology is to understand the predictability and consistency of phenotypic divergence to shared selective pressures, and life-history theory provides a wealth of testable predictions for how phenotypes should respond to variation in age-specific mortality. Importantly, it is the ecological agents of selection that are the causes of variation in age-specific mortality (Wade & Kalisz 1990; MacColl 2011). While many studies have identified selective agents driving phenotypic divergence (e.g. Grant & Grant 2002; Martin & Pfennig 2009; Calsbeek & Cox 2010), comparisons of phenotypic responses to multiple ecological agents of selection are scant. As many organisms face similar general selective agents (e.g. density, predators), such studies provide valuable insight into the factors that globally shape phenotypic diversity. Our study has revealed consistent, predictable patterns of divergence in reproductive life-history strategies to toxic environments and predation risk in livebearing fishes. These selective agents are likely to influence mortality variation for many organisms, and future inquiry may quantify and compare their effects on divergence to assess their general importance over a broader taxonomic sampling. As our understanding of the patterns of selection continues to improve (Kingsolver *et al.* 2012), studies assessing the generality of phenotypic responses to the ecological causes of selection are also necessary (MacColl 2011). Quantifying divergence across species and selective agents enables direct estimation of the direction, and magnitude of evolutionary responses, and our study provides strong evidence for parallel evolutionary responses to ecological agents of selection.

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**Tables**

Table 1. Summary of ecological agents of selection. Bolded agents had sufficient replication for individual estimation of the consistency and predictability of life-history divergence. Arrows signify the direction of the *a priori* predictions for phenotypic divergence in response to increases in the selective agents. Percent increase of each selective agent was calculated by dividing the highest level of the selective agent by the lowest (+1 when the lowest magnitude had a value of 0) for each divergence estimate and multiplying by 100. For this calculation, we include only studies where the quantitative value for each level of the selective agent was listed. Here, we report the mean and standard deviation of the increase.

**Table 1.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Selective agent**  **(mean % increase ± SD)** | **Abiotic/**  **Biotic** | **Offspring size replicates** | **Offspring number replicates** | **Reproductive allocation replicates** |
| ash input  (-) | abiotic | 0 | 1 | 0 |
| darkness  (-) | abiotic | 0 | 2 | 1 |
| **density**  (311 ± 284) | biotic | 15 ↑ | 13 ↓ | 3 |
| **food limitation**  (232 ± 142) | biotic | 20 ↑ | 15 ↓ | 9 |
| **hydrogen sulfide**  (2830 ± 1827) | abiotic | 9 ↑ | 13↓ | 3 |
| pollution  (-) | biotic | 0 | 1 | 0 |
| **predation**  **(-)** | biotic | 16 ↓ | 12 ↑ | 13 |
| **salinity**  (1122 ± 536) | abiotic | 5 ↑ | 6 ↓ | 1 |
| temperature variability  (-) | abiotic | 3 | 1 | 0 |
| water depth average  (-) | abiotic | 1 | 1 | 0 |
| water depth variability  (-) | abiotic | 1 | 1 | 1 |

**Figures**

Figure 1. Offspring-size (a) and offspring-number (b) divergence to selective agents. The black diamonds represent mean divergence ± 95% credible intervals for each selective agent as estimated by the meta-analysis. Individual circles illustrate unique estimates of divergence, and the size of the circle corresponds to the inverse of the standard error. Phenotypic divergence to selective agents was considered significant (i.e. consistent) when the 95% credible intervals from the meta-analysis did not overlap zero. Both offspring-size and offspring-number divergence are significantly different from zero, and match *a priori* predictions for divergence to increased hydrogen sulfide and predation. Offspring-number divergence to food limitation is also significantly different from zero and matched *a priori* predictions.

Figure 2. Magnitudes of offspring-size (green circles) and offspring-number (blue circles) divergence to abiotic and biotic selective agents (a), as well as the five selective agents that met the inclusion criteria in Question 1 (b; see Methods). The black diamonds represent the mean magnitude of divergence ± 95% credible intervals for each selective agent as estimated by the meta-analysis. Individual circles illustrate the absolute values of the unique estimates of divergence, and the size of the circle corresponds to the inverse of the standard error.

Figure 3. Relationship between divergence in offspring size and offspring number investment. Each circle represents an estimate of divergence for both offspring size and number, and the size of the circle corresponds to the inverse of the standard error of the value for offspring-size divergence. The dotted line illustrates a hypothetical relationship between offspring size and number divergence with a slope of negative one. The solid black line is the fitted relationship between offspring-size and number divergence from the meta-analysis. The estimated slope is 0.25, and is significantly different from both zero and negative one (see Results).



Figure 1.



Figure 2.



Figure 3.

**Supplemental Methods and Results**

*Detailed description of effect size calculation*

Experimental designs differed among studies, and thus were necessarily handled differently. Many studies reported on the mean trait values of wild-caught individuals from each environmental level (i.e. “field collections”). When mean trait values for multiple populations within each environmental level were reported, we pooled the means within each environmental level, and calculated a grand mean for that environmental level. Many other studies reported on experimental manipulations of each environmental level in the laboratory or in mesocosms (i.e. “experimental manipulations”). Lastly, some studies considered trait divergence of individuals from populations at each environmental level when reared in a common environment (i.e. “common garden”). As the number of studies employing these methods was small, we treated studies the same irrespective of whether they measured the divergence of individuals whose parents were wild-caught or individuals whose parents were lab-born. Many studies reported trait values and corresponding measurement variances in tables, however, when necessary, we extracted values from digitized figures with ImageJ.

From each of these mean trait values at the environmental levels, we calculated Hedge’s G and the corresponding measurement error variance as our measure of phenotypic divergence. We used Hedge’s G instead of Cohen’s D because we did not want to assume that the population means shared a common standard deviation. We included the less strongly selective environment as the baseline mean (i.e. [μmore selective – μless selective]/SDpooled). We used the author’s characterization of each environment to determine the level with stronger selection when possible. Thus, each effect size can be interpreted as the “life-history divergence”, in standard deviations, of the phenotypic difference between the two extremes of the selective agent considered. When more than two levels of the selective agents were reported, we only used the mean trait values from the highest and lowest reported levels. For each calculated divergence, we recorded: the study identity; the species; the study type (i.e. experimental manipulation, field collected individuals, common garden); the potential selective agent; whether the agent was abiotic or biotic; and the identity of the relevant life-history trait. This resulted in a total of 170 estimates of reproductive life-history divergence among the three traits (Table 1; Table *S2*).

*Reproductive allocation – Consistency and Predictability* *Analysis*

Relatively few studies in our dataset considered reproductive-allocation divergence across selective agents (Table 1). For this analysis, only two selective agents met the sample size criterion that were used for inclusion in the offspring size and number analyses (i.e. five estimates of divergence), and thus we reduced the minimum number of divergence estimates necessary for inclusion to three. The selective agents that met this new criterion were: population density, food limitation, hydrogen sulfide concentration, and predation risk. For this analysis, we considered phenotypic divergence as consistent when the 95% highest posterior density (HPD) intervals about the estimated mean did not overlap zero. Heterogeneities for variance components (I2) are reported in Table S4.

*Reproductive Allocation – Magnitude Analyses*

We quantified the magnitudes of reproductive-allocation divergence: across experimental designs (i.e. experimental manipulation, field collections, and common garden); across the five selective agents from Question 1); and between abiotic and biotic selective agents across all the environments considered (Table 1). For the analysis of experimental designs, we included the selective agent as an additional random intercept to our general modeling approach, and thus specified our inverse gamma prior as V=1, *nu*=0.004. As quantifying the magnitudes of divergence necessitates the use of the absolute values of the effect sizes, our analyses and subsequent calculations of mean divergence implemented the folded normal distribution, and we report mean divergences as absolute values (e.g. |G|).

*Consistency, predictability, and magnitude analyses after accounting for relative environmental variation - Methods*

By calculating life-history divergence as the phenotypic difference between the least and most extreme environments, we may be equating very different levels of environmental variation both within and across selective agents. Without a common scale, such as mortality rate, it is logistically difficult to quantitatively compare intensity of selection among environments, such as predation (e.g. low or no predation vs high predation risk) and hydrogen sulfide concentration (e.g. μM H2S) or salinity (ppt Salinity). However, to account for the possibility that environmental variation within selective agents is mediating the extent of the observed divergence, we calculated the relative increase of environmental intensity (% change) between the least and most extreme environment for each effect size. We added a one to environmental levels that were quantified as zero. As some studies did not report quantitative detail about the environmental variation in the study, we only could calculate this value for a subset of the data. Additionally, as predation risk was always measured as no or low predation risk versus the presence of predators or high predation, we could not calculate relative increase of environmental intensity for this selective agent. We centered this variable to a mean of 0 within selective agents and scaled by one standard deviation (i.e. z-transformed), so that the estimated intercepts from subsequent analyses were directly comparable to analyses without this covariate.

Even after Z-transformation of the relative increase of environmental intensity within selective agents, it is still unclear how biologically appropriate it is to compare values among selective environments. For example, a 100% increase in density and a 7% increase in salinity have similar Z-transformed relative increase of environmental intensity values in our dataset (-0.74 and -0.64, respectively) but its difficult to assume that those environmental intensity increases are biologically comparable. Consequently, to avoid making this assumption, we conducted individual analyses of the predictability and magnitude of life-history divergence for each putative selective agent using a similar framework as described for the other analyses. However, instead of fitting an intercept-only model, we also included the standardized relative increase of environmental intensity as a fixed effect. In analyses of predictability, a significant intercept indicates that, at the average increase of environmental intensity within a selective environment, there is consistent direction of divergence. Additionally, in these analyses, a significant slope would support an association between estimated phenotypic divergence and the increase of environmental intensity considered by the study. For the magnitude analyses, significant slopes would indicate a relationship between the magnitude of life-history divergence and the degree of environmental intensity. Our random effects structure was generally the same as for our other analyses with a few exceptions. As our sample size for each analysis was considerable smaller due to the subsetting of the data, and our inability to calculate values for the covariate for some studies, we could not include all of the random effects from our other models into all of these analyses. For offspring-size divergence to density, there were fewer than four species that were represented in the analysis, and we could not include a covariance matrix based on the topology of the Poeciliidae phylogeny. Additionally, when there were fewer than six total estimates of divergence for a selective agent/trait combination, models either resulted in extremely wide credible intervals or did not converge even after increasing the chain length to 4,000,000 iterations. Consequently, we could not run models for the following combinations of selective agents and traits: Density (RA), hydrogen sulfide (offspring size, RA), and salinity (offspring size, offspring number, RA).

*Reproductive-Allocation Divergence: Consistency and Predictability Results*

Credible intervals of estimated means all overlapped 0 (Figure S3), and thus divergence in reproductive allocation was not consistent in direction or predictable for any of the selective agents. There was modest *H*2*p* of divergence across selective agents (Table S4).

*Reproductive-Allocation Divergence: Magnitude Results*

All sample sizes were small for these analyses, and credible intervals exhibited substantial overlap among comparisons. Consequently, we report trends here. Across experimental designs (Fig. S4a), magnitudes of divergence were similar, although field collections (0.46, 0.35 to 0.91) tended to have a smaller magnitude of divergence than experimental manipulations (0.81, 0.47 to 1.51) or common garden (0.75, 0.52 to 1.37). *H*2*p* was modest (Table S30). Abiotic selective agents (0.60, 0.39 to 1.14) tended to have larger magnitudes of divergence than biotic selective agents (0.54, 0.25 to 0.95; Fig. S4b). *H*2*p* of reproductive-allocation divergence was moderate (Table S30). Divergence to predation risk (0.61, 0.35-1.13) tended to be the smallest of any of the four selective agents considered, while all other selective agents were similar (Fig. S4c). Moderate *H*2*p* was also detected for reproductive-allocation divergence in this analysis (Table S4).

*Consistency, predictability and magnitude analyses after accounting for relative environmental variation - Results*

In all cases, analyses accounting for the relative increase of environmental intensity did not qualitatively differ from analyses that did not consider this variable (Fig. S5). Additionally, the slope of this covariate was not significantly different from zero in any model (Tables S19-S30, S32-33). While this quantitative result may have been driven by low power to detect any such effects, graphical assessment of the relationship between the magnitude of life-history divergence and the relative increase of environmental intensity also strongly indicated little support for any pattern (Fig. S6).

*Full citation list of the 54 studies included in the final database*

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**Supplemental Tables**

Table S1. Species represented in each environment included in our dataset. Numbers in parentheses after species codes correspond to the number of estimates of divergence. Species coding: B.rha = *Brachyraphis rhabdophora*; B.ros = *Brachyraphis roseni*; G.aff = *Gambusia affinis*; G.gei = *Gambusia geiseri;* G.hol = *Gambusia holbrooki*;G.hub *= G. hubbsi;* G.sex = *Gambusia sexradiata;* H.for = *Heterandria formosa;* P.fes = *Priapichthys festae*; P.gra = *Poecilopsis gracilis;* P.lat = *Poecilia latipinna;* P. mex = *Poecilia mexicana;* P.mon = *Poeciliopsis monacha*; P.pro = *Poeciliopsis prolifica*;P.occ = *Poeciolopsis occidentalis*; P.ret = *Poecilia reticulata;* P.tur = *Poeciliopsis turneri*.

Table S2. Heterogeneity statistics (I2; proportion of the total variance explained) for each analysis. Values of 0.25, 0.50, and 0.75 correspond low, medium, and high proportions of the total variance explained by each random factor (*H*2*p*; proportion of total heterogeneity explained by phylogeny). See Methods for specific model specification, and footnote and Nakagawa & Santos (2012) for calculation of values.

Table S3. Model results from Egger’s regression of meta-analytic residuals. A significant intercept indicates evidence of publication bias.

Table S4.Heterogeneity statistics (I2; proportion of the total variance explained) for reproductive-allocation analyses. Values of 0.25, 0.50, and 0.75 correspond low, medium, and high proportions of the total variance explained by each random factor (*H*2*p*; proportion of total heterogeneity explained by phylogeny). See Methods for specific model specification, and footnote and Nakagawa & Santos (2012) for calculation of values.

|  |  |  |  |
| --- | --- | --- | --- |
| Selective Agent | Offspring Size | Offspring Number | Reproductive Allocation |
| ash input | - | G.hol (1) | - |
| darkness | - | P.mex (2) | P.mex (1) |
| density | P.ret (2), H.for (10), P.mon (3) | P.ret (3), H.for (4), P.mon (5), G.aff (1) | P.ret (2) |
| food limitation | P.ret (6), P.lat (2), P.fes (1), H.for (1), P.mon (2), P.pro (2), P.occ (2), P.tur (1), P.gra (1), G.gei (1) | P.ret (5), P.lat (1), P.mon (2), P.pro (2), P.occ (2), P.tur (1), P.grac (1), G.gei (1) | P.ret (3), P.lat (1), P.mon (1), P.pro (2), P.gra (1), G.gei (1) |
| hydrogen sulfide | P.ret (1), P.lat (1), P.mex (2), G.sex (2), G.hol (1), G.aff (1), G.hub (1) | P.ret (1), P.lat (1), P.mex (6), G.sex (2), G.hol (1), G.aff (1), G.hub (1) | P.mex (2), G.sex (1) |
| pollution | - | G.aff (1) | - |
| predation | P.ret (10), P.lat (1), B.rha (1), B.ros (2), G.aff (1), G.hub (2) | P.ret (6), P.lat (1), B.rha (1), G.aff (1), G.hubb (3) | P.ret (10), P.lat (1), B.ros (1), G.hub (1) |
| salinity | P.lat (1), H.for (1), G.aff (3) | P.lat (2), H.for (2), G.aff (3) | G.aff (1) |
| temperature variability | G.hol (1), G.aff (2) | G.hol (1) | - |
| water depth average | G.hub (1) | G.hub (1) |  |
| water depth variability | G.aff (1) | G.aff (1) | G.aff (1) |

Table S1

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Offspring Size | | | Offspring Number | | |
| **Analysis** | Mean | L95% HPD | U95% HPD | Mean | L95% HPD | U95% HPD |
| **Consistency** |  | | |  | | |
| H2p | 0.233 | 0.000 | 0.733 | 0.040 | 0.000 | 0.183 |
| Study I2 | 0.190 | 0.000 | 0.413 | 0.421 | 0.000 | 0.778 |
| Species I2 | 0.272 | 0.000 | 0.641 | 0.031 | 0.000 | 0.128 |
| Phylogeny I2 | 0.227 | 0.000 | 0.721 | 0.038 | 0.000 | 0.172 |
| Residual I2 | 0.283 | 0.048 | 0.615 | 0.488 | 0.146 | 0.963 |
| Total I2 | 0.972 | 0.953 | 0.989 | 0.977 | 0.965 | 0.988 |
| **Study Type** |  | | |  | | |
| H2p | 0.052 | 0.022 | 0.104 | 0.042 | 0.022 | 0.085 |
| Study I2 | 0.006 | 0.002 | 0.010 | 0.285 | 0.144 | 0.460 |
| Species I2 | 0.017 | 0.007 | 0.034 | 0.018 | 0.009 | 0.037 |
| Phylogeny I2 | 0.045 | 0.019 | 0.091 | 0.041 | 0.022 | 0.082 |
| Selective Agent I2 | 0.917 | 0.867 | 0.961 | 0.430 | 0.265 | 0.597 |
| Residual I2 | 0.007 | 0.003 | 0.010 | 0.190 | 0.108 | 0.277 |
| Total I2 | 0.992 | 0.989 | 0.995 | 0.965 | 0.954 | 0.975 |
| **Abiotic vs Biotic** |  | | |  | | |
| H2p | 0.279 | 0.202 | 0.454 | 0.131 | 0.093 | 0.236 |
| Study I2 | 0.389 | 0.311 | 0.439 | 0.673 | 0.559 | 0.748 |
| Species I2 | 0.104 | 0.058 | 0.191 | 0.052 | 0.031 | 0.096 |
| Phylogeny I2 | 0.251 | 0.184 | 0.417 | 0.128 | 0.091 | 0.231 |
| Residual I2 | 0.160 | 0.113 | 0.192 | 0.110 | 0.062 | 0.158 |
| Total I2 | 0.904 | 0.891 | 0.925 | 0.964 | 0.955 | 0.970 |
| **Selective agents** |  | | |  | | |
| H2p | 0.577 | 0.416 | 0.794 | 0.032 | 0.019 | 0.058 |
| Study I2 | 0.023 | 0.009 | 0.039 | 0.578 | 0.403 | 0.733 |
| Species I2 | 0.330 | 0.121 | 0.461 | 0.012 | 0.007 | 0.023 |
| Phylogeny I2 | 0.511 | 0.383 | 0.761 | 0.030 | 0.018 | 0.056 |
| Residual I2 | 0.042 | 0.027 | 0.057 | 0.301 | 0.170 | 0.444 |
| Total I2 | 0.905 | 0.880 | 0.936 | 0.922 | 0.899 | 0.940 |
| **Trade-Off** |  | | |  |  |  |
| H2p | 0.072 | 0.000 | 0.327 |  |  |  |
| Study I2 | 0.150 | 0.000 | 0.345 |  |  |  |
| Species I2 | 0.095 | 0.000 | 0.295 |  |  |  |
| Phylogeny I2 | 0.516 | 0.179 | 0.855 |  |  |  |
| Selective Agent I2 | 0.073 | 0.000 | 0.326 |  |  |  |
| Residual I2 | 0.154 | 0.016 | 0.345 |  |  |  |
| Total I2 | 0.988 | 0.978 | 0.996 |  |  |  |

Table S2

e.g. I2study = σ2study / (σ2study + σ2species + σ2phylogeny + σ2residual + σ2measurement error)

e.g. H2p = σ2phylogeny / (σ2study + σ2species + σ2phylogeny + σ2residual)

Table S3.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Offspring Size** | | | | | |
| **Effect** | **Estimate** | **Standard Error** | **t** | **df** | ***P*** |
| Intercept | 0.449 | 0.682 | 0.658 | 1, 60 | 0.513 |
| Precision | -0.022 | 0.137 | -0.160 | 1, 60 | 0.873 |
|  |  |  |  |  |  |
| **Offspring Number** | | | | | |
| **Effect** | **Estimate** | **Standard Error** | **t** | **df** | ***P*** |
| Intercept | -0.245 | 0.772 | -0.318 | 1, 57 | 0.752 |
| Precision | 0.101 | 0.155 | 0.651 | 1, 57 | 0.518 |
|  |  |  |  |  |  |
| **RA** | | | | | |
| **Effect** | **Estimate** | **Standard Error** | **t** | **df** | ***P*** |
| Intercept | -0.124 | 0.823 | -0.151 | 1, 26 | 0.881 |
| Precision | 0.036 | 0.133 | 0.268 | 1, 26 | 0.791 |

Table S4.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Reproductive Allocation | | |
| **Analysis** | Mean | L95% HPD | U95% HPD |
| **Consistency** |  |  |  |
| H2p | 0.194 | 0.000 | 0.773 |
| Study I2 | 0.037 | 0.000 | 0.155 |
| Species I2 | 0.389 | 0.000 | 0.834 |
| Phylogeny I2 | 0.190 | 0.000 | 0.763 |
| Residual I2 | 0.352 | 0.023 | 0.843 |
| Total I2 | 0.969 | 0.939 | 0.994 |
| **Study Type** |  |  |  |
| H2p | 0.376 | 0.242 | 0.624 |
| Study I2 | 0.006 | 0.003 | 0.012 |
| Species I2 | 0.364 | 0.201 | 0.557 |
| Selective Agent I2 | 0.181 | 0.101 | 0.301 |
| Phylogeny I2 | 0.357 | 0.232 | 0.600 |
| Residual I2 | 0.042 | 0.020 | 0.068 |
| Total I2 | 0.950 | 0.937 | 0.964 |
| **Abiotic vs Biotic** |  |  |  |
| H2p | 0.458 | 0.290 | 0.674 |
| Study I2 | 0.044 | 0.019 | 0.077 |
| Species I2 | 0.415 | 0.220 | 0.617 |
| Phylogeny I2 | 0.418 | 0.263 | 0.654 |
| Residual I2 | 0.079 | 0.033 | 0.135 |
| Total I2 | 0.956 | 0.945 | 0.969 |
| **Selective Environments** |  |  |  |
| H2p | 0.463 | 0.283 | 0.701 |
| Study I2 | 0.005 | 0.002 | 0.010 |
| Species I2 | 0.449 | 0.244 | 0.653 |
| Phylogeny I2 | 0.431 | 0.267 | 0.667 |
| Residual I2 | 0.055 | 0.028 | 0.085 |
| Total I2 | 0.940 | 0.925 | 0.959 |

**Supplemental Figures**

Figure S1. Funnel plots of standardized meta-analytic residuals for models of offspring-size (a), offspring-number (b), and reproductive-allocation (c) divergence across the selective agents. Each point represents a unique estimate of divergence. Egger’s regression indicated no strong evidence for publication bias (Table S2).

Figure S2. Magnitudes of offspring-size (green circles) and offspring-number (blue circles) divergence across the experimental designs included in our analyses. The black diamonds represent the mean magnitude of divergence ± 95% credible intervals for each environment as estimated by the meta-analysis. Individual circles illustrate the absolute values of unique estimates of divergence, and the size of the circle corresponds to the inverse of the standard error.

Figure S3. Reproductive-allocation divergence to the four selective agents included in the analysis (see Supplemental Methods). The black diamonds represent mean divergence ± 95% credible intervals for each selective agent as estimated by the meta-analysis. Individual circles illustrate unique estimates of divergence, and the size of the circle corresponds to the inverse of the standard error. Phenotypic divergence to selective agents was considered repeatable when the 95% credible intervals from the meta-analysis did not overlap zero.

Figure S4. Magnitudes of reproductive-allocation divergence across experimental designs (a), abiotic and biotic selective agents (b), and the selective agents used in the repeatability analysis. The black diamonds represent the mean magnitude of divergence ± 95% credible intervals for each selective agent as estimated by the meta-analysis. Individual circles illustrate the absolute values of unique estimates of divergence, and the size of the circle corresponds to the inverse of the standard error.

Figure S5. Estimated intercepts from the models including all selective agents (“full”; filled points) and from the environment-specific models including the covariate of relative environmental increase (“single”; open points) for the predictability analyses (a) and the magnitude analyses (b). Each point represents the mean-estimated model intercept and the error bars indicate the 95% credible intervals. Estimated intercepts of both models are qualitatively and quantitatively similar, suggesting no strong effect of including a covariate of relative increase of environmental intensity.

Figure S6. The magnitudes of estimated life-history divergence plotted against the relative increase of environmental intensity for each of the four selective agents with quantitative levels of environmental variation. Each point represents an estimate of divergence, and the size of the points corresponds to the inverse of the standard error. Relative increases of environmental intensity are not standardized to a mean of 0 for this figure, but are natural-log transformed to enhance visual clarity. Points are jittered horizontally by 0.2. In general, there is not a strong relationship between the relative increase of environmental intensity and the magnitude of life-history divergence.



Figure S1.



Figure S2.



Figure S3.



Figure S4.



Figure S5.



Figure S6.

Supplemental Model Outputs

As there are 30 tables in this section, captions are provided above tables.

Table S5. Model results from the analysis of the consistency and predictability of offspring-size divergence to all selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-size divergence to each selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **Mean** | **L95% HPD** | **U95% HPD** |
| Density | 0.81354 | -0.20172 | 1.81511 |
| Food Limitation | 0.01839 | -0.82115 | 0.91128 |
| Hydrogen Sulfide | 2.80861 | 1.43848 | 4.09104 |
| Predation | -1.63691 | -2.53289 | -0.69341 |
| Salinity | -0.63461 | -1.94281 | 0.67854 |
|  |  |  |  |
| **Random Effects** | **Mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.2933 | 0.0003934 | 0.6361 |
| Species | 0.4416 | 0.0001677 | 1.29 |
| Phylogeny | 0.475 | 0.0001817 | 1.91 |
| Residual | 0.4173 | 0.1195 | 0.7944 |

Table S6. Model results from the analysis of the consistency and predictability of offspring-number divergence to all selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-number divergence to each selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Density | -0.5325 | -1.4422 | 0.3706 |
| Food Limitation | -0.9823 | -1.7925 | -0.1122 |
| Hydrogen Sulfide | -1.4523 | -2.6924 | -0.2928 |
| Predation | 1.2371 | 0.2774 | 2.1301 |
| Salinity | 0.8538 | -0.4232 | 2.2373 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.903 | 0.0002918 | 2.121 |
| Species | 0.06325 | 0.0001723 | 0.2658 |
| Phylogeny | 0.08773 | 0.0002139 | 0.3866 |
| Residual | 0.8835 | 0.2538 | 1.732 |

Table S7. Model results from the analysis of the consistency and predictability of reproductive-allocation divergence to all selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of reproductive-allocation divergence to each selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Density | -0.3363 | -1.4965 | 0.7397 |
| Food Limitation | -0.8137 | -1.7266 | 0.0416 |
| Hydrogen Sulfide | -0.6624 | -2.1784 | 0.8197 |
| Predation | 0.4395 | -0.4383 | 1.2768 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.03827 | 0.0001653 | 0.1522 |
| Species | 0.5137 | 0.0002377 | 1.629 |
| Phylogeny | 0.3025 | 0.0002343 | 1.418 |
| Residual | 0.3115 | 0.05571 | 0.6634 |

Table S8. Model results from analysis of the magnitude of offspring-size divergence among different study designs. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-size divergence for each study design.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Experimental Manipulation | 1.036894 | 0.6385313 | 1.965992 |
| Field Collection | 0.8166081 | 0.5808711 | 1.474953 |
| Common Garden | 1.070337 | 0.6490564 | 2.025943 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.02498743 | 0.01225061 | 0.03322895 |
| Species | 0.07549184 | 0.04848258 | 0.1322411 |
| Selective Agent | 4.01988 | 2.52414 | 6.297314 |
| Phylogeny | 0.2152253 | 0.1489912 | 0.40521 |
| Residual | 0.02982025 | 0.02161273 | 0.03309747 |

Table S9. Model results from analysis of the magnitude of offspring-number divergence among different study designs. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-number divergence for each study design.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Experimental Manipulation | 0.7362066 | 0.4681977 | 1.346107 |
| Field Collection | 0.5055178 | 0.3547549 | 0.9179555 |
| Common Garden | 0.8020736 | 0.561817 | 1.436206 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.2755923 | 0.1643827 | 0.4494315 |
| Species | 0.01809843 | 0.01376576 | 0.03681129 |
| Selective Agent | 0.4145248 | 0.2525214 | 0.6884118 |
| Phylogeny | 0.03779012 | 0.03032793 | 0.07893789 |
| Residual | 0.1746123 | 0.1197055 | 0.193749 |

Table S10. Model results from analysis of the magnitude of reproductive-allocation divergence among different study designs. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of reproductive-allocation divergence for each study design.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Experimental Manipulation | 0.8102017 | 0.4680178 | 1.513977 |
| Field Collection | 0.455628 | 0.319521 | 0.8227785 |
| Common Garden | 0.754391 | 0.5189011 | 1.3662 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.004652416 | 0.003286945 | 0.008921165 |
| Species | 0.1105836 | 0.07610413 | 0.2062544 |
| Selective Agent | 0.1016282 | 0.08520312 | 0.1911822 |
| Phylogeny | 0.1150924 | 0.09384901 | 0.2417273 |
| Residual | 0.02691287 | 0.01452035 | 0.03411826 |

Table S11. Model results from analysis of the magnitude of offspring-size divergence to abiotic and biotic selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-size divergence to each category of the selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| abiotic | 0.9187036 | 0.4152325 | 1.681928 |
| biotic | 0.491064 | 0.2774142 | 0.9196307 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.1460171 | 0.07411944 | 0.199257 |
| Species | 0.03982972 | 0.02853999 | 0.07735786 |
| Phylogeny | 0.09779624 | 0.1242896 | 0.1521627 |
| Residual | 0.05887378 | 0.04954905 | 0.06158944 |

Table S12. Model results from analysis of the magnitude of offspring-number divergence to abiotic and biotic selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-number divergence to each category of the selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| abiotic | 0.6087066 | 0.4316746 | 1.08063 |
| biotic | 0.540737 | 0.3287019 | 1.032035 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.6284863 | 0.3940504 | 0.6882425 |
| Species | 0.04670856 | 0.03338556 | 0.09025366 |
| Phylogeny | 0.1195926 | 0.09199409 | 0.2460935 |
| Residual | 0.1140659 | 0.08001459 | 0.138656 |

Table S13. Model results from analysis of the magnitude of reproductive-allocation divergence to abiotic and biotic selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of reproductive-allocation divergence to each category of the selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| abiotic | 0.6006887 | 0.3947658 | 1.139117 |
| biotic | 0.5381539 | 0.2539368 | 0.9507103 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.004712254 | 0.003264283 | 0.008881112 |
| Species | 0.08516787 | 0.05941225 | 0.1607796 |
| Phylogeny | 0.09876617 | 0.08115821 | 0.2058467 |
| Residual | 0.02567863 | 0.01393055 | 0.03127341 |

Table S14. Model results from the analysis of the magnitude of offspring-size divergence to all selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-size divergence to each selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Density | 0.9018127 | 0.4030796 | 1.644038 |
| Food Limitation | 0.4824078 | 0.3454365 | 0.873648 |
| Hydrogen Sulfide | 2.812912 | 1.465769 | 4.10291 |
| Predation | 1.644288 | 0.7575539 | 2.556533 |
| Salinity | 0.9082468 | 0.5269983 | 1.719794 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.02712187 | 0.01331318 | 0.03633587 |
| Species | 0.1255556 | 0.07596893 | 0.2075184 |
| Phylogeny | 0.2677913 | 0.1925363 | 0.5215902 |
| Residual | 0.03141243 | 0.02210791 | 0.03537172 |

Table S15. Model results from the analysis of the magnitude of offspring-number divergence to all selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of offspring-number divergence to each selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Density | 0.6778684 | 0.3646656 | 1.287301 |
| Food Limitation | 1.00712 | 0.3365418 | 1.66935 |
| Hydrogen Sulfide | 1.485663 | 0.4779208 | 2.430742 |
| Predation | 1.252457 | 0.3740778 | 1.99138 |
| Salinity | 1.046728 | 0.5388391 | 1.969808 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.3311571 | 0.173498 | 0.475642 |
| Species | 0.006338139 | 0.004935601 | 0.01310006 |
| Phylogeny | 0.01585247 | 0.01290341 | 0.0328141 |
| Residual | 0.158468 | 0.1056048 | 0.1859182 |

Table S16. Model results from the analysis of the magnitude of reproductive-allocation divergence to all selective agents. As the intercept was suppressed in this analysis, estimated mean values of fixed effects are the estimated mean values of reproductive-allocation divergence to each selective agent.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Density | 0.6849746 | 0.448374 | 1.287966 |
| Food Limitation | 0.8691994 | 0.3548209 | 1.536862 |
| Hydrogen Sulfide | 0.9967133 | 0.5978634 | 1.933719 |
| Predation | 0.6090089 | 0.345427 | 1.127385 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.002229092 | 0.00170841 | 0.004525417 |
| Species | 0.2158171 | 0.1431287 | 0.3874705 |
| Phylogeny | 0.2090245 | 0.1687815 | 0.4401236 |
| Residual | 0.02481803 | 0.01508396 | 0.03098065 |

Table S17. Model results for the analysis of the relationship between offspring number and offspring size across all selective agents. The slope of this relationship can be interpreted as a one standard deviation increase in offspring number results in a 0.251 standard deviation decrease to offspring size.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.11073 | -1.12402 | 1.38705 |
| Offspring number | -0.2535 | -0.48106 | -0.03021 |
|  |  |  |  |
| **Random Effects** | mean | L95% HPD | U95% HPD |
| Study | 0.3486 | 0.0004256 | 0.7888 |
| Species | 0.3374 | 0.0003256 | 1.001 |
| Selective Agent | 1.962 | 0.001239 | 5.182 |
| Phylogeny | 0.2491 | 0.0003592 | 1.139 |
| Residual | 0.478 | 0.1328 | 0.9219 |

Table S18. Results from models testing for differences in the slopes of the relationship between offspring size and offspring number among selective agents. Mean values for fixed effects are the mean differences in the slopes between one selective agent (baseline) and each of the other selective agents. As credible intervals for all comparisons overlapped 0, there is little support for variation in the slope of the relationship among selective agents.

|  |  |  |  |
| --- | --- | --- | --- |
| **Analysis** | **mean** | **L95% HPD** | **U95% HPD** |
| **Baseline - Density** |  |  |  |
| Food | 0.12501 | -1.12765 | 1.27808 |
| H2S | -0.72029 | -2.19879 | 0.72444 |
| Predation | -0.09348 | -1.3685 | 1.12373 |
| Salinity | 0.10892 | -1.22278 | 1.50642 |
| **Baseline - Food** |  |  |  |
| Density | -0.12186 | -1.29639 | 1.1042 |
| H2S | -0.84788 | -1.84758 | 0.1156 |
| Predation | -0.21459 | -0.79792 | 0.3854 |
| Salinity | -0.01343 | -0.82189 | 0.77259 |
| **Baseline - H2S** |  |  |  |
| Food | 0.84523 | -0.11704 | 1.83484 |
| Density | 0.72008 | -0.73795 | 2.17898 |
| Predation | 0.6322 | -0.37604 | 1.60788 |
| Salinity | 0.83433 | -0.33423 | 1.95644 |
| **Baseline - Predation** |  |  |  |
| H2S | -0.62799 | -1.63334 | 0.36918 |
| Food | 0.21817 | -0.38036 | 0.80189 |
| Density | 0.09394 | -1.18172 | 1.30864 |
| Salinity | 0.20209 | -0.67797 | 1.06301 |
| **Baseline - Salinity** |  |  |  |
| Predation | -0.20078 | -1.07437 | 0.66387 |
| H2S | -0.82987 | -1.9637 | 0.34732 |
| Food | 0.01239 | -0.77754 | 0.80892 |
| Density | -0.11152 | -1.45039 | 1.27099 |
| **Random Effects** |  |  |  |
| Study | 0.6014 | 0.000421 | 1.217 |
| Species | 0.3563 | 0.0002537 | 1.159 |
| Phylogeny | 0.2668 | 0.0002103 | 1.296 |
| Residual | 0.3968 | 0.05574 | 0.8661 |

Table S19. Model results from the analysis of consistency and predictability of offspring-size divergence to density. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.3627 | -0.5046 | 1.1492 |
| Percent increase | 0.2042 | -0.136 | 0.5099 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.05071 | 0.0001356 | 0.2046 |
| Species | 1.508 | 0.000158 | 2.106 |
| Residual | 0.02907 | 0.0001664 | 0.1148 |

Table S20. Model results from the analysis of the magnitude of offspring-size divergence to density. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.7771622 | 0.6249501 | 1.058152 |
| Percent increase | 0.2576972 | 0.133945 | 0.4602203 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.005394934 | 0.004342779 | 0.01087884 |
| Species | 2356.498 | 2348.471 | 2350.083 |
| Residual | 0.001292314 | 0.000992275 | 0.002612071 |

Table S21. Model results from the analysis of consistency and predictability of offspring-number divergence to density. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | -0.67462 | -2.04786 | 0.7007 |
| Percent Increase | -0.05266 | -1.68855 | 1.65448 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.6472 | 0.0002232 | 1.953 |
| Species | 0.5652 | 0.0001873 | 1.639 |
| Phylogeny | 0.6129 | 0.000229 | 1.691 |
| Residual | 0.08511 | 0.0002114 | 0.41 |

Table S22. Model results from the analysis of the magnitude of offspring-number divergence to density. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.9638989 | 0.577549 | 1.77366 |
| Percent Increase | 0.9204427 | 0.663926 | 1.68126 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.4462331 | 0.3199621 | 0.8285995 |
| Species | 73.83258 | 73.13121 | 74.09259 |
| Phylogeny | 5.927961 | 5.679266 | 6.629118 |
| Residual | 0.01782467 | 0.01476516 | 0.03776408 |

Table S23. Model results from the analysis of consistency and predictability of offspring-size divergence to food limitation. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.896518 | 0.4054304 | 1.615431 |
| Percent Increase | 0.47391 | 0.1287027 | 0.3256539 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.265918 | 0.2231909 | 0.5298028 |
| Species | 0.1763822 | 0.1534475 | 0.331552 |
| Phylogeny | 0.402482 | 0.3514631 | 0.7495466 |
| Residual | 0.407888 | 0.2492931 | 0.5893835 |

Table S24. Model results from the analysis of the magnitude of offspring-size divergence to food limitation. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.5021162 | 0.3010392 | 0.9470063 |
| Percent Increase | 0.1801689 | 0.1287027 | 0.3256539 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.004548217 | 0.00368471 | 0.009091508 |
| Species | 0.07425235 | 0.05403458 | 0.1445684 |
| Phylogeny | 0.1643788 | 0.1112521 | 0.2996347 |
| Residual | 0.005421159 | 0.004058137 | 0.01087538 |

Table S25. Model results from the analysis of consistency and predictability of offspring-number divergence to food limitation. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | -0.8067 | -1.8201 | 0.1945 |
| Percent Increase | 0.1392 | -0.6699 | 0.9709 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.2924 | 0.0001928 | 1.295 |
| Species | 0.2032 | 0.0002309 | 0.9017 |
| Phylogeny | 0.3014 | 0.0002246 | 1.335 |
| Residual | 1.027 | 0.1354 | 2.404 |

Table S26. Model results from the analysis of the magnitude of offspring-number divergence to food limitation. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.896518 | 0.4054304 | 1.615431 |
| Percent Increase | 0.47391 | 0.1287027 | 0.3256539 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.265918 | 0.2231909 | 0.5298028 |
| Species | 0.1763822 | 0.1534475 | 0.331552 |
| Phylogeny | 0.402482 | 0.3514631 | 0.7495466 |
| Residual | 0.407888 | 0.2492931 | 0.5893835 |

Table S27. Model results from the analysis of consistency and predictability of reproductive-allocation divergence to food limitation. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | -0.7402 | -2.0018 | 0.5685 |
| Percent Increase | -0.1944 | -1.0883 | 0.6837 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.249 | 0.0002039 | 0.9792 |
| Species | 0.4306 | 0.000228 | 1.754 |
| Phylogeny | 0.5126 | 0.0002044 | 2.344 |
| Residual | 0.9924 | 0.000512 | 2.772 |

Table S28. Model results from the analysis of the magnitude of reproductive-allocation divergence to food limitation. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 0.9481819 | 0.521655 | 1.767469 |
| Percent Increase | 0.5161523 | 0.3561706 | 0.964985 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.5698322 | 0.5247947 | 0.8138086 |
| Species | 4.06831 | 3.863771 | 4.892402 |
| Phylogeny | 1.684642 | 1.508747 | 2.902663 |
| Residual | 0.742292 | 0.488382 | 1.307999 |

Table S29. Model results from the analysis of consistency and predictability of offspring-number divergence to hydrogen sulfide. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | -1.4906 | -3.1831 | 0.3866 |
| Percent Increase | 0.1963 | -0.7092 | 1.1004 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 0.4534 | 0.0001872 | 1.933 |
| Species | 0.6074 | 0.0002124 | 2.394 |
| Phylogeny | 1.122 | 0.0001731 | 4.603 |
| Residual | 1.332 | 0.2166 | 3.176 |

Table S30. Model results from the analysis of the magnitude of offspring-number divergence to hydrogen sulfide. “Percent increase” is the relative increase of environmental intensity, which was standardized to a mean of 0 to facilitate comparisons with life-history divergence models not including this covariate. The mean value for the intercept represents the mean divergence at the average degree of the relative increase of environmental intensity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Fixed Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| intercept | 1.662111 | 0.7492838 | 2.782691 |
| Percent Increase | 0.5324392 | 0.3630068 | 0.9782627 |
|  |  |  |  |
| **Random Effects** | **mean** | **L95% HPD** | **U95% HPD** |
| Study | 1.691206 | 1.540212 | 2.602305 |
| Species | 5.436367 | 5.100224 | 6.953073 |
| Phylogeny | 15.67133 | 14.58251 | 21.21045 |
| Residual | 0.7497772 | 0.4653045 | 1.118205 |

Table S31. Heterogeneity statistics (I2; proportion of the total variance explained) for analyses of variation in slopes the relationship of offspring size and number among selective agents (see Table S18). Values of 0.25, 0.50, and 0.75 correspond low, medium, and high proportions of the total variance explained by each random factor (*H*2*p*; proportion of total heterogeneity explained by phylogeny). See Methods for specific model specification, and footnote (Table S2) and Nakagawa & Santos (2012) for calculation of values.

|  |  |  |  |
| --- | --- | --- | --- |
|  | **mean** | **l95** | **u95** |
| H2p | 0.128 | 0.065 | 0.702 |
| Study I2 | 0.378 | 0.000 | 0.559 |
| Species I2 | 0.201 | 0.000 | 0.508 |
| Phylogeny I2 | 0.128 | 0.000 | 0.564 |
| Residual I2 | 0.263 | 0.026 | 0.587 |
| Total I2 | 0.969 | 0.949 | 0.988 |

Table S32. Heterogeneity statistics (I2; proportion of the total variance explained) for analyses of consistency and predictability of life-history divergence to each selective agent when accounting for variation in the relative increase of environmental intensity (see Tables S19-S30). Values of 0.25, 0.50, and 0.75 correspond low, medium, and high proportions of the total variance explained by each random factor (*H*2*p*; proportion of total heterogeneity explained by phylogeny). See Methods for specific model specification, and footnote (Table S2) and Nakagawa & Santos (2012) for calculation of values.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Offspring Size** | | | **Offspring Number** | | | **Reproductive Allocation** | | |
| **Analysis** | **Mean** | **L95% HPD** | **U95% HPD** | **Mean** | **L95% HPD** | **U95% HPD** | **Mean** | **L95% HPD** | **U95% HPD** |
| **Density** |  | | | | | | | | |
| H2p |  |  |  | 0.177 | 0.000 | 0.737 |  |  |  |
| Study I2 | 0.151 | 0.000 | 0.591 | 0.496 | 0.000 | 0.905 |  |  |  |
| Species I2 | 0.426 | 0.001 | 0.948 | 0.166 | 0.000 | 0.699 |  |  |  |
| Phylogeny I2 |  |  |  | 0.168 | 0.000 | 0.710 |  |  |  |
| Residual I2 | 0.104 | 0.000 | 0.432 | 0.086 | 0.000 | 0.490 |  |  |  |
| Total I2 | 0.681 | 0.261 | 1.000 | 0.917 | 0.798 | 1.000 |  |  |  |
| **Food Limitation** |  | | | | | | | | |
| H2p | 0.506 | 0.000 | 0.963 | 0.118 | 0.000 | 0.556 | 0.158 | 0.000 | 0.727 |
| Study I2 | 0.054 | 0.000 | 0.219 | 0.134 | 0.000 | 0.567 | 0.083 | 0.000 | 0.395 |
| Species I2 | 0.275 | 0.000 | 0.812 | 0.086 | 0.000 | 0.408 | 0.164 | 0.000 | 0.688 |
| Phylogeny I2 | 0.434 | 0.000 | 0.878 | 0.111 | 0.000 | 0.523 | 0.150 | 0.000 | 0.699 |
| Residual I2 | 0.090 | 0.000 | 0.390 | 0.601 | 0.158 | 0.949 | 0.523 | 0.038 | 0.929 |
| Total I2 | 0.853 | 0.709 | 0.972 | 0.932 | 0.861 | 0.992 | 0.919 | 0.813 | 0.996 |
| **H2S** |  | | | | | | | | |
| H2p |  |  |  | 0.166 | 0.000 | 0.764 |  |  |  |
| Study I2 |  |  |  | 0.110 | 0.000 | 0.545 |  |  |  |
| Species I2 |  |  |  | 0.137 | 0.000 | 0.618 |  |  |  |
| Phylogeny I2 |  |  |  | 0.159 | 0.000 | 0.749 |  |  |  |
| Residual I2 |  |  |  | 0.565 | 0.092 | 0.974 |  |  |  |
| Total I2 |  |  |  | 0.970 | 0.934 | 0.999 |  |  |  |

Table S33. Heterogeneity statistics (I2; proportion of the total variance explained) for analyses of the magnitude of life-history divergence to each selective agent when accounting for variation in the relative increase of environmental intensity (see Tables S19-S30). Values of 0.25, 0.50, and 0.75 correspond low, medium, and high proportions of the total variance explained by each random factor (*H*2*p*; proportion of total heterogeneity explained by phylogeny). See Methods for specific model specification, and footnote (Table S2) and Nakagawa & Santos (2012) for calculation of values.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Offspring Size** | | | **Offspring Number** | | | **Reproductive Allocation** | | |
| **Analysis** | **Mean** | **L95% HPD** | **U95% HPD** | **Mean** | **L95% HPD** | **U95% HPD** | **Mean** | **L95% HPD** | **U95% HPD** |
| **Density** |  |  |  |  |  |  |  |  |  |
| H2p |  |  |  | 0.074 | 0.065 | 0.088 |  |  |  |
| Study I2 | 0.000 | 0.000 | 0.000 | 0.002 | 0.001 | 0.003 |  |  |  |
| Species I2 | 0.998 | 0.998 | 0.998 | 0.967 | 0.963 | 0.969 |  |  |  |
| Phylogeny I2 |  |  |  | 0.031 | 0.029 | 0.035 |  |  |  |
| Residual I2 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |  |  |  |
| Total I2 | 0.998 | 0.998 | 0.998 | 1.000 | 1.000 | 1.000 |  |  |  |
| **Food Limitation** |  |  |  |  |  |  |  |  |  |
| H2p | 0.649 | 0.428 | 0.832 | 0.320 | 0.206 | 0.474 | 0.237 | 0.154 | 0.385 |
| Study I2 | 0.012 | 0.006 | 0.023 | 0.235 | 0.133 | 0.379 | 0.200 | 0.137 | 0.243 |
| Species I2 | 0.207 | 0.105 | 0.374 | 0.118 | 0.068 | 0.203 | 0.479 | 0.349 | 0.551 |
| Phylogeny I2 | 0.483 | 0.325 | 0.668 | 0.303 | 0.195 | 0.451 | 0.226 | 0.148 | 0.354 |
| Residual I2 | 0.016 | 0.008 | 0.036 | 0.280 | 0.177 | 0.391 | 0.082 | 0.052 | 0.146 |
| Total I2 | 0.719 | 0.658 | 0.802 | 0.937 | 0.922 | 0.953 | 0.988 | 0.987 | 0.991 |
| **H2S** |  |  |  |  |  |  |  |  |  |
| H2p |  |  |  | 0.952 | 0.923 | 0.959 |  |  |  |
| Study I2 |  |  |  | 0.021 | 0.013 | 0.034 |  |  |  |
| Species I2 |  |  |  | 0.021 | 0.014 | 0.037 |  |  |  |
| Phylogeny I2 |  |  |  | 0.951 | 0.922 | 0.958 |  |  |  |
| Residual I2 |  |  |  | 0.006 | 0.004 | 0.009 |  |  |  |
| Total I2 |  |  |  | 1.000 | 1.000 | 1.000 |  |  |  |