The role of maternal effects on offspring performance in familiar and novel environments

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Abstract

Maternal effects are an important evolutionary force that may either facilitate adaptation to a new environment or buffer against unfavourable conditions. The degree of variation in traits expressed by siblings from different mothers is frequently sensitive to environmental conditions. This could generate a Maternal-by-Environment interaction (M×E) that could inflate estimates of Genotype-by-Environment effects (G×E). We aimed to test for environment-specific maternal effects (M×E) using a paternal full-sib/half-sib breeding design in the seed beetle *Callosobruchus maculatus*, where we split and reared offspring from the same mother on two different bean host types – original and novel. Our quantitative genetic analysis indicated that maternal effects were very small on both host types for all the measured life-history traits. There was also little evidence that maternal oviposition preference for a particular host type predicted her offspring's performance on that host. Further, additive genetic variance for most traits was relatively high on both hosts. While there was higher heritability for offspring reared in the novel host, there was no evidence for G×Es, and most cross-host genetic correlations were positive. This suggests that offspring from the same family ranked similarly for performance on both host types. Our results point to a genetic basis of host adaptation in the seed beetle, rather than maternal effects. Even so, we encourage researchers to test for

potential M×Es because, due to a lack of testing, it remains unclear how often they arise.

Keywords: genetic correlation, host adaptation, maternal effects, seed beetle, life history

Introduction

Maternal effects modify phenotypes that undergo selection and are therefore a potentially important evolutionary force (Mousseau and Fox, 1998; Räsänen and Kruuk, 2007; Moore *et al.*, 2019). They may either facilitate adaptation to novel environments (Fox and Savalli, 2000; Leftwich *et al.*, 2019), or buffer against changing conditions through trans-generational phenotypic plasticity (Shama *et al.*, 2014). Maternal effects have also been shown to have a range of other implications, such as moderating population dynamics (Plaistow and Benton, 2009), and increasing niche breadth (Van Asch *et al.*, 2010). Maternal effects, which can arise due to both genetic and environmental variation among mothers, can be defined as 'the causal influence of the maternal genotype or phenotype on the offspring phenotype' (Wolf and Wade, 2009). Genetic maternal effects might increase total heritability and facilitate evolution (Wilson *et al.*, 2005; Räsänen and Kruuk, 2007), as opposed to phenotypic (environmental) maternal effects. Teasing these two sources of maternal effects apart is often challenging, however (Kruuk and Hadfield, 2007). Irrespective of their genetic basis, maternal effects increase the degree of similarity between siblings and may thus bias estimates of direct genetic effects upward if ignored (Räsänen and Kruuk, 2007; McAdam *et al.,* 2014). This can lead to

an overestimation of the likely response to selection (McGlothlin and Galloway, 2014).

Maternal effects are often environment sensitive (Rossiter, 1998; Galloway, 2005; Räsänen and Kruuk, 2007; McAdam *et al.,* 2014). It is unclear, however, whether challenging or favourable conditions will result in stronger maternal effects (Charmantier and Garant, 2005; Rowiński and Rogell, 2017). A harsher environment is typically assumed to increase variation among offspring from different mothers (Charmantier and Garant, 2005; Räsänen and Kruuk, 2007). This may, for example, stem from differences in maternal ability to provision offspring (Parichy and Kaplan, 1992). On the other hand, marine sticklebacks showed weaker maternal effects under stressful conditions (warmer temperature) (Shama *et al.*, 2014). Similarly higher population densities reduced offspring differences attributable to variation in maternal age in soil mites (Plaistow and Benton, 2009). Environment-dependent variation in maternal effects like this represents a form of Maternal-by-Environment interaction, M×E (Figure 1B). Another form of M×E occurs, irrespective of change in variance across environments, if individual mothers differ in how they affect their offspring in an environment-specific manner (Figure 1C). In an experiment with great tits for instance (Berthouly *et al.*, 2008), mothers supplemented with carotenoids raised smaller nestlings than the (un-supplemented) control

95 mothers. When the brood size was increased, however, the result was
96 opposite and the offspring of carotenoid-supplemented mothers grew faster
97 compared to controls (Berthouly *et al.*, 2008). A similar interaction was also
98 observed for offspring immune response (Berthouly *et al.*, 2008). The level
99 of maternal carotenoids thus affects the fate and relative performance of
100 the great tit offspring depending on the brood size. This interaction would
101 cause cross-over of the maternal effects reaction norms because of the
102 change in rank of maternal siblings between the two environments (Figure
103 1C). In general, a quantitative genetic analysis of potential M×E can help us
104 to identify the mechanisms that increase similarity between siblings within
105 the same environment beyond genetic relatedness. That analysis would be
106 especially useful if such mechanisms themselves are undescribed, or their
107 role is not fully understood. Many cases probably involve a mixture of
108 changes in ranking and variances (as in Figure 1D), but the change in relative
109 phenotype of offspring (i.e. shift in the rank) due to maternal effects is less
110 often accounted for. In general, ignoring significant levels of M×E might bias
111 estimates of additive genetic effects in a host-specific way and inflate G×E
112 as shown by Vega-Trejo *et al.* (2018). This could partially explain
113 inconsistency in G×E estimation across different studies (Saltz *et al.*, 2018).

114 Phytophagous insects are a valuable model group to study life-history
115 evolution, especially when interested in trade-offs arising from

specialization to a preferred host (Via and Lande, 1985; Agrawal, 2000). At the same time, phytophagous insects exhibit a variety of maternal effects that influence key life-history traits (Fox and Dingle, 1994; Rossiter, 1996; Fox and Czesak, 2000; Van Asch *et al.*, 2010), including host-specific maternal effects (Fox *et al.*, 1997; Cahenzli and Erhardt, 2013). In the current study, we investigated the presence of maternal effects, and the potential for an interaction between maternal effects and offspring rearing host environment, on general offspring life-history traits, as well as daughters' egg laying preferences for different host types in the seed beetle, *Callosobruchus maculatus* (Coleoptera: Chrysomelidae). This beetle is a common pest of stored legumes worldwide. The larvae feed on multiple legume species (family Fabaceae) with varying degrees of success (Gompert and Messina, 2016; Price *et al.*, 2017; Messina *et al.*, 2018). Females lay eggs on host beans shortly after copulation (Mitchell, 1975). Host choice is crucial as larvae cannot move between beans. Incorrect decisions about where a female chooses to lay her eggs inevitably lead to lower quality, or even dead, offspring (Mitchell, 1975; Messina and Fry, 2003; Messina *et al.*, 2007). Larvae hatch 4-5 days after oviposition and burrow into the bean to feed on the endosperm. A single seed commonly harbours multiple larvae. The variable level of larval competition within seeds results in different sized adult beetles, which affects their condition, female reproductive

137 performance and egg size (Fox and Savalli, 1998). Depending on the
138 temperature and host species, adults typically emerge within 26-36 days of
139 oviposition (Fox *et al.*, 2003; Messina, 2004a). *Callosobruchus maculatus*
140 shows large sexual dimorphism in life-history traits with males emerging
141 earlier, being smaller and having a shorter lifespan than females (Guntrip *et*
142 *al.*, 1997; Fox, Bush, *et al.*, 2004; Iglesias-Carrasco *et al.*, 2020).

143 We used a full-sib/half-sib split brood design to tease apart the role of
144 additive genetic and maternal effects on *C. maculatus* life-history traits
145 when larvae develop on two host types – original (cowpea) and novel (mung
146 bean). We hypothesised that:

147 1) There are strong maternal effects on offspring life-history traits
148 (Fox, 1993; Messina and Fry, 2003). This led us to predict that a considerable
149 component of offspring phenotypic variation, beyond that due to additive
150 genetic effects, would be due to offspring having different mothers.

151 2) Maternal effects are environment-specific (M×E). Specifically, we
152 predicted that the maternal effects variance would differ between offspring
153 host environments (Figure 1B), and/or that the rank of offspring from the
154 same mother will change between the two host types decreasing the cross-
155 environmental maternal correlation (Figure 1C, D).

3) Novel host type will be more challenging for offspring. Hence, offspring developing in the novel host would suffer reduced performance compared to those developing in the original host type (i.e. lower larval survival, longer larval development, lower body mass at emergence, and shorter adult lifespan).

4) Maternal host preference will predict offspring performance. We predicted that offspring would perform better on the host type preferred by their mother when she laid her eggs.

Methods

Experiment overview. We aimed to estimate genetic and maternal effects for four life-history traits and host egg laying preference. To do this we used a half-sib/full-sib split brood design with offspring reared on two different host types - original or novel. We created the parental generation for our experiment by mating beetles from our stock population. We mated parents and tested mother egg laying preference for the two host types. We then let them lay eggs on both host types and measured offspring life-history traits and the daughters' host preference. We used animal mixed-effects models to test our predictions.

176

177 **Origin and maintenance of stock beetles.** Beetles used as the parental
178 generation for our experiment were obtained from a large stock population
179 originally sourced from the University of Western Australia (Perth, Australia)
180 in 2017 where they had been bred on cowpea (*Vigna unguiculata*, Fabaceae)
181 for at least 90 generations. We maintained this stock in our lab at the
182 Australian National University on cowpea for another 9 generations before
183 we began this experiment. Our stock was maintained in four, regularly mixed
184 (every 5 generations) populations of over 500 individuals, each kept on
185 cowpea at 25-26 °C.

186

187 **Establishing the parental generation (P).** To obtain virgin males and females
188 for the parental generation (P), we exposed approximately 2000 un-infested
189 cowpea beans to stock beetles for a period of 48 h. Each bean, which had 5-
190 8 eggs on its surface (a density which is usual for our stock), was then placed
191 in an individual Eppendorf tube (with a pinhole for airflow). Once isolated,
192 we monitored these beans until adults began to emerge. We collected virgin
193 beetles each morning and used them in our experiment on the same day.
194 We knew that beetles were virgins as they were either the only beetle to
195 have emerged that day, or all beetles that had emerged were of the same

196 sex. Every evening, we discarded any extra beetles that had emerged during
197 that day to aid in the collection of virgins the following day. Using the beetles
198 that emerged each morning, we mated males and females according to a
199 full-sib/half-sib breeding design: each male was sequentially mated with
200 four random females over the day and the mating order was noted (similar
201 to Fox *et al.* (2003)). Pairs that did not copulate within 30 min were
202 separated for half an hour before being placed together for another mating
203 attempt. Each female was weighed (to the nearest 0.001 mg) prior to mating
204 (Cubis Ultra-Micro balance, Sartorius Lab Instruments GmbH., Goettingen,
205 Germany). All matings took place over six days ('day mated', range 1-6, see
206 *Model comparison and partitioning of phenotypic variance*). There is
207 therefore a positive correlation between parental developmental duration
208 (egg to adulthood) and 'day mated', but it is imperfect because parents
209 emerged from eggs initially laid over two days (i.e. 48 hours; see above).
210 There is no correlation between 'day mated' and adult parental age because
211 all matings occurred on the day that the parents emerged.

212

213 **Maternal host preference.** We used mung bean (*V. radiata*) as the novel
214 host type. We define the host as novel in that it was 'unlikely to have been
215 experienced by the study population within an evolutionary timescale'

216 (Rowiński and Rogell, 2017), approximately 100 generations in our case (see
217 also Kawecki (1995). Cowpea and mung are both suitable hosts for *C.*
218 *maculatus* (Messina, 2004a; Fox and Messina, 2018), but populations kept
219 on a specific host for multiple generations usually show better performance
220 on their usual host than a novel host (Messina, 2004a).

221 Once females had mated, we conducted choice trials to determine
222 their preferred host type for egg laying. We considered females ready to lay
223 eggs once the pair dismounted (Wilson and Hill, 1989). For the host
224 preference trials, we mixed cowpeas (original host) and mung beans (novel
225 host) in covered Petri dish (ø 5.5 cm). We used proportionally more mung
226 than cowpea beans (8:4) to roughly equalise the available surface area of
227 each bean type (similar to 10:5 used by Messina and Slade (1997)). Cowpea
228 beans have an approximately 1.6-times larger surface area (Paukku and
229 Kotiaho, 2008) and are 4-times heavier than mung beans (in our study the
230 average ± SD bean mass was 294±45 mg for cowpea, and 72±8 mg for mung
231 bean). Females were left to lay eggs for two hours, after which they were
232 removed and the number of eggs on each bean was counted. Relative
233 preference was calculated as the proportion of the eggs that a female laid
234 on the original host type (cowpea). The values for relative host preference
235 therefore ranged between 0 and 1.

236

237 **Generation of offspring (F1).** Directly after the host preference trial, we
238 transferred individual dams to plastic containers (ø 4 cm, height 6 cm) with
239 10-13 mung beans and left them to lay eggs for 14-18 h. We then moved
240 dams to new containers with 10-13 cowpea beans for 9-10 h. This difference
241 in laying time was required because initial trials showed that more time was
242 necessary for females to lay a sufficient number of eggs on the novel host
243 (mung beans), than on cowpea (the original host). Females were presented
244 with mung beans first to prevent them from laying all their eggs on what we
245 expected to be the preferred host type (cowpea) (Messina and Slade, 1997).
246 Maternal age and/or laying order effects are unlikely to have influenced
247 differences between mung and cowpea-reared offspring due to the short
248 period of time we allowed females to lay eggs (i.e. <24 h). Previous studies
249 have shown no effect of female age (hence laying order) on offspring quality
250 during the first days of laying after emergence (Wasserman and Asami, 1985;
251 Fox, 1993; Fox and Dingle, 1994; Iglesias-Carrasco *et al.*, 2018). Further, one
252 of the authors (MLH) found, in a separate experiment looking at oviposition
253 preferences and offspring traits over the same time frame, that the order in
254 which host beans are presented does not have any observable effect on
255 offspring survival, development duration, or body mass at emergence
256 (Zhang *et al.*, in preparation).

257 Once females had laid eggs on both host types, we collected up to 10
258 beans of each host type for each female. If a female had laid eggs on fewer
259 than 10 beans of a given type, we used them all. We ensured that each bean
260 had only one egg laid on it by scraping off surplus eggs with a scalpel. We
261 then weighed beans, to the nearest 0.001 mg, within 24 h of oviposition to
262 measure the resources available to the larvae. Beans with an egg were then
263 placed individually in Eppendorf tubes with perforated lids and incubated at
264 26 °C.

265 We started regular monitoring of F1 emergence on day 24 post-
266 oviposition. However, we missed the onset of emergence of 40 beetles on
267 mung (1.3% of all emerged offspring) by approximately 1 day as they
268 emerged sooner than expected. Uncertainty in the date of their emergence
269 could introduce noise into the estimates of larval development duration,
270 body mass at emergence and adult lifespan, so we removed these beetles
271 from the final dataset. Including these early emerging beetles did not
272 qualitatively change our results.

273

274 **Measurement of offspring (F1) traits.** We recorded the date of offspring
275 emergence from the bean, sex and body mass at emergence (to the nearest
276 0.001 mg), and then removed the bean from the tube. After weighing, the

beetle was returned to its tube and checked daily for survival. We also tested the host preference of two newly emerged female offspring per dam raised on each host type (total N = 4/dam). To do this we mated each daughter with a randomly selected male from the stock and then ran an egg laying preference trial identical to that described above for their mothers. We monitored survival until the death of all emerged offspring (day 79 post-oviposition). At that time, we also censused larval (egg-to-emergence) survival, assuming that larvae in beans from which a beetle had not yet emerged had died.

Sample sizes. Our target sample size was determined *a priori* based on Lynch and Walsh (1998). We created 89 families (89 sires with 356 dams) and aimed for 10 offspring per dam, per host type (i.e. 7 120 offspring). The final sample size (N = 3 431) is lower due to unsuccessful matings or too few eggs being laid. Despite not reaching our target sample size our final sample size is still higher than that in other similar studies of maternal effects (the studies in a meta-analysis by Moore *et al.* (2019), for example, have a mean sample size of 1 370, and a much lower median of 555). We analysed data for sons and daughters separately due to their large sexual dimorphism which invariably leads to strong interactions between sex and other effects.

297 We excluded offspring of dams that did not lay eggs during host preference
298 trials (285 individuals) and data from 13-24 daughters and 12-27 sons with
299 missing, or extreme values (>3 standard deviations (SD) from the mean),
300 with the exact number depending on the focal trait. We analysed four
301 offspring life-history traits: (egg-to-emergence) 'larval survival' (dead or
302 emerged; N = 3 146), 'duration of larval development' (number of days
303 between oviposition and offspring emergence; N = 1 420 daughters and 1
304 384 sons), 'body mass' (weight at emergence in mg; N = 1 431 daughters and
305 1 399 sons) and 'adult lifespan' (number of days between offspring
306 emergence and death; N = 1 425 daughters and 1 389 sons). In addition, we
307 measured the host egg laying preferences of 665 daughters. The analysed
308 offspring came from 82 sires and 245-249 dams for the life-history traits, and
309 239 dams for host preference analysis. The proportion of offspring reared
310 on the original host type was 52-57 % (see Supplementary Table S1). Prior to
311 any statistical analysis, but after all data had been collected, we registered
312 this project on the Open Science Forum webpage:
313 https://osf.io/ft7eq/?view_only=0bab0a33bb4246adb64c919601a72757
314 The final analytical approach we used was different, however, from the
315 original plan – partly due to feedback from reviewers. We explain our
316 changes in the *Annotated registration* section in the Supplementary
317 Information.

318

319 **Overview of data analysis approach.** Our main objective was to test for
320 maternal effects on the offspring traits (Prediction 1) and their potential
321 interaction with offspring rearing environment (Prediction 2). First, we built
322 a 'minimal model' containing only fixed effects directly attributable to the
323 experimental design. To test whether maternal effects are important, we
324 then created a set of candidate models with different random effects
325 structures (Table 1). We used the best-selected model for partitioning of
326 phenotypic variance (Table 2). Finally, we assess the effect of host type
327 (Prediction 3) and dam host egg laying preference (Prediction 4) on offspring
328 traits with a 'full' model containing additional fixed effects (Table 3).

329

330 **Model specification, model comparison and partitioning of phenotypic**
331 **variance.** We started data analysis with a minimal mixed-effects model that
332 contained, in the fixed-effects part, only variables ensuing from the
333 experimental design. These were 'host type' (original/novel), 'bean mass'
334 (standardized to zero mean and 1 SD variance, within each host type, to look
335 at the effect of size within each host type), 'dam mating order' (i.e. dam
336 position in a sire's mating sequence, integer 1 to 4), and 'day mated' (integer
337 1-6). We did not fit 'day mated' as a random effect because of the low

338 number of levels (Bolker *et al.*, 2009). We specified the random effects
339 structure using an animal model approach (Kruuk, 2004; Wilson *et al.*, 2010),
340 where variance-covariance estimates between relatives are computed from
341 a pedigree.

342 We fitted the models using Bayesian framework with package
343 MCMCglmm (ver. 2.29) (Hadfield, 2010) in R software (ver. 4.0.0; R Core
344 Team, 2020). The continuous response variables (duration of larval
345 development, body mass and adult lifespan) were fitted using Gaussian
346 family and identity link, while larval survival (dead or emerged) was fitted
347 using 'categorical' family (binomial distribution with logit link). Daughter
348 host preference was treated as a bivariate vector with the number of eggs
349 on the original host and the total number of eggs collected in the egg laying
350 preference trial using 'multinomial2' family (binomial distribution and log-
351 odds ratio link function) (Hadfield, 2010).

352 To test for the best random effects structure, we performed model
353 comparison on a set of 7 candidate models (Table 1) for each trait using the
354 Deviance Information Criterion (DIC) (Spiegelhalter *et al.*, 2002). DIC is a
355 Bayesian alternative to Akaike Information Criterion (AIC) that takes into
356 account the fit of the model but penalizes for model complexity, with lower
357 DIC values indicating a better model (Hadfield, 2010; Wilson *et al.*, 2010).

358 Model comparison with DIC should be performed cautiously for non-
359 Gaussian response variables (Hadfield, 2010; Wilson *et al.*, 2010), so we did
360 not conduct model selection for larval survival or host preference.

361 The simplest model 'G' included only additive genetic effects specified
362 by the random effect of 'animal'. We then also included dam identity to
363 estimate maternal effects in addition to additive genetic effects ('G+M'
364 model). These two models do not, however, take into account possible host-
365 specific differences in respective variance components (this is shown in
366 Figure 1A). We thus formulated more realistic models that estimated the
367 variance component (including residual variance) separately for each host
368 type (as in Figure 1B). These were specified through random-effect
369 interactions (Hadfield, 2010) with host type 'idh(HOST):animal' for 'G_{sep}', or
370 with 'idh(HOST):dam' for 'M_{sep}' models (Table 1). This is similar to fitting two
371 separate host-specific models. To account for potential change in the
372 ranking of additive genetic or maternal effects (Figure 1C), we fitted models
373 that also estimated cross-environmental covariance ('G_{cov}' or 'M_{cov}'). When
374 specifying variance-covariance matrix of the random-effect interaction we
375 used 'unstructured' form, e.g. 'us(HOST):animal' (Hadfield, 2010). As a
376 result, we not only obtained separate variance estimates for each host type,
377 but also the corresponding covariance to compute the cross-environmental
378 correlations (Figure 1D) – the proxies for Genotype-by-Environment (G×E),

379 or Maternal-by-Environment (M×E) interactions (Lynch and Walsh, 1998). In
380 the models estimating separate variances per host type, we always specified
381 host-specific residual variance (as 'rcov=~idh(HOST):units') (Hadfield, 2010).

382 We then performed phenotypic variance partitioning based on the
383 outputs of the best-selected minimal model for each trait. We calculated the
384 maternal-effects proportion (m^2), narrow-sense heritability (h^2), evolvability
385 (coefficient of additive genetic variation, CV_A) and the cross-environmental
386 correlation for additive genetic (r_G – potential G×E interaction) and for
387 maternal effects (r_M – potential M×E interaction). We used maternal effects
388 proportion, $m^2 = \frac{V_M}{V_P} = \frac{V_{dam}}{(V_{animal} + V_{dam} + V_{residual})}$, to quantify the
389 importance of maternal effects (as in e.g. Messina and Fry (2003); Vega-
390 Trejo *et al.* (2018); Moore *et al.* (2019)). The V_M contains both genetic and
391 non-genetic maternal effects, and potentially also genetic dominance, as we
392 did not separate them with our experimental design. We calculated
393 heritability as $h^2 = \frac{V_A}{V_P} = \frac{V_{animal}}{(V_{animal} + V_{dam} + V_{residual})}$ (Lynch and Walsh, 1998),
394 assuming epistatic effects were negligible. Evolvability was defined by
395 (Houle, 1992) as $CV_A = \frac{\sqrt{V_A}}{\mu} = \frac{\sqrt{V_{animal}}}{\mu}$, where μ is the mean of a trait.
396 Evolvability standardizes additive genetic variance over the trait mean and
397 is therefore useful to compare the potential evolutionary response among
398 traits, unlike heritability which is conditional on the amount of residual

399 phenotypic variation (Hansen *et al.*, 2011). The correlation between additive
400 genetic effects on the two host types (G×E interaction) was $r_G =$
401 $\frac{COV_{animal\,(original-nov\quad)}}{\sqrt{V_{animal\,(original)}V_{animal\,(novel)}}}$. The same formula was used for maternal
402 effects correlation between the two hosts (potential M×E interaction) using
403 the dam-related covariance across the two host types. Estimates of V_A, V_P
404 and h^2 for larval survival and host preference were back-transformed to the
405 original data scale using the function 'QGparams' (from QGglmm package,
406 ver.0.7.4; de Villemereuil *et al.* (2016)).

407

408 **Testing for host effect and dam host egg laying preference on offspring**
409 **phenotype.** To determine the effect of novel host type on offspring
410 performance (Prediction 3) and to test whether offspring performed better
411 on the host type that was preferred by their mother (Prediction 4), we built
412 a 'full model'. The full mixed-effects model always included all the terms
413 outlined above for the minimal model with the random effects from the
414 best-selected minimal model (Table 1). We then included 'dam host
415 preference' (i.e. the relative preference ratio: 0-1 values) and the interaction
416 between preference and host type 'HOST:dam host preference' to test if the
417 effect of the strength of the preference for the original host on offspring
418 traits differs depending on the host type. We also included interactions

419 between host type and bean mass 'HOST:bean mass', as well as host type
420 and day mated 'HOST:day mated' as fixed effects to test for potential host-
421 specific effects.

422

423 **Model fitting.** To fit the MCMC models, we used non-informative priors for
424 the random-effects variance (G) with expected variance-covariance matrix
425 at limit 'V' = 1, and the degree of freedom 'nu' = 0.002 for each random term
426 (with nu = 1.002 in models with the random effects estimated separately per
427 host type) (Wilson *et al.*, 2010). To further improve mixing and effective
428 sample size, we specified parameter-expanded priors as 'α mu' = 0 and 'α V'
429 = 1 000 (Hadfield, 2010). Priors for residual variance (R) were set as V = 1 and
430 nu = 0.002 (nu = 1.002 when residual variance was estimated separately for
431 each host type). In the analysis of survival, the residual variance had to be
432 fixed to 1, so that the binomial mixed-effects model could be estimated
433 (Hadfield, 2010). For fixed effects (B), we retained default priors with mean
434 = 0 and variance = 10^{10}. To generate posterior distributions from the minimal
435 and full models, we ran 360 000 iterations with burn-in of 60 000 and
436 thinning interval of 300, so that we obtained an effective sample size of 1
437 000 for each estimated model term. For larval survival, we increased the
438 iterations to 5 500 000 with a burn-in of 500 000 and thinning interval of

439 5000 as we were aiming for an autocorrelation <0.1 at the lag corresponding
440 to the thinning interval (Wilson *et al.*, 2010). Model convergence was
441 evaluated by visual examination of the traces using function
442 'plot(mcmc.model)'. We assessed the importance of individual model terms
443 based on their credible intervals (CrI).

444

445

446 ## Results

447 **Prediction 1 and 2 – testing for maternal effects and M×E interaction.** The
448 model comparison suggests very weak maternal effects for all the measured
449 traits. The models incorporating maternal effects performed poorly (Table
450 1), and the best model contained only additive genetic effects estimated for
451 each host type and the cross-environmental covariance (the 'G_{cov}' model).
452 This shows that either additive genetic variance, residual variance or both
453 differed between host types and that the cross-environmental genetic
454 covariance differed from zero. Estimate of the cross-environmental
455 covariance has to be examined directly to see whether the correlation differs
456 from +1 indicating a potential Genotype-by-Environment interaction (see
457 below).

Table 1. Model comparison.

458

459 **Components of phenotypic variance related to additive genetic effects -**
460 **heritability, evolvability and G×E.** We observed higher heritability for
461 offspring life-history traits in the novel host type (h^2 = 0.365-0.649), than on
462 the original host (h^2 = 0.210-0.459) (Table 2). However, the additive genetic
463 variance was substantially higher in the novel host only for adult lifespan of
464 sons. For the other traits, we recorded a similar magnitude of additive
465 genetic variance in the two hosts, but higher residual phenotypic variance in
466 the original host type, thereby reducing trait heritability (Table 2). The
467 presence of similar levels of additive genetic variance in both hosts is also
468 apparent in the estimates of evolvability (variance due to additive genetic
469 effects standardised over trait means) which were comparable for the two
470 host types (Table 2). When comparing evolvability among traits (across sexes
471 and host types) we found that it was highest for adult lifespan (CV_A = 16.8-
472 20.8 %, Table 2). For the non-Gaussian traits (larval survival and host egg
473 laying preference), estimates of additive genetic variance and heritability
474 obtained from the G_{cov} model were very low (h^2 = 0.001-0.060, Table 4A)
475 when compared to the Gaussian life-history traits.

476 We recorded highly positive correlations between offspring
477 performance on the two host types for additive genetic effects (r_G) (Table 2).
478 The only exception was for the development duration of sons, which
479 exhibited only a weak genetic correlation between hosts (Table 2). The
480 credible interval (-0.279, 0.533) suggests a Genotype-by-Environment
481 interaction (G×E).

Table 2. Phenotypic variance partitioning.

482

483 **Predictions 3 and 4 – testing for host type suitability and host preference-**
484 **performance.** Unexpectedly, given our predictions, offspring generally
485 performed better on the novel host (mung) than on the original host
486 (cowpea) (Table 3; Supplementary Table S1). We recorded very high larval
487 survival overall, however, so that survival on mung beans was only
488 marginally better than on cowpea (Table 4B). We did not find a positive
489 relationship between the strength of the dam host preference for egg laying
490 and the performance of their offspring on either host type. The one
491 exception was for daughter body mass: daughters of dams that more
492 strongly preferred the cowpea emerged heavier when raised on cowpea, but
493 not when raised on mung beans (Table 3). Daughters reared on the original
494 cowpea host also exhibited a higher egg laying preference for cowpeas than

495 those reared on mung beans. Raw average host preference ratio of
496 daughters reared on cowpea was 0.681 versus 0.517 for those from mung
497 (where 1 is a strict preference for cowpeas). The host preference ratio of
498 their mothers (reared on cowpea) was 0.724.

Table 3. Fixed-effects estimates from the full models.

499

500 **Effect of experimental variables on offspring traits - bean size, mating date**
501 **and mating order.** Host-specific relative bean size (zero-centered per host
502 type) and mating date were important predictors of offspring traits. For both
503 host types, offspring that developed in larger beans had a poorer outcome:
504 increased development duration in daughters, as well as reduced body mass
505 and lower adult lifespan in both sexes. The effects of mating day on offspring
506 performance were, however, mixed (Table 3). Offspring of later mated
507 families took longer to develop, but sons emerged at a larger size and lived
508 longer. Daughters from later mated families also showed a modest decrease
509 in the preference for the original host type (Table 4B). Finally, if a dam was
510 later in the sire's mating sequence this marginally extended the
511 development duration of her daughters.

Table 4. Phenotypic variance partitioning and full model inference for the non-Gaussian traits.

512

513

514 ## Discussion

515 **Summary.** Our main aim was to test for environment-specific maternal
516 effects on offspring life-history traits and their correlation, that is, Maternal-
517 by-Environment interactions (M×E). We used a full-sib/half-sib split brood
518 design with seed beetles (*C. maculatus)* reared on two types of host: original
519 – cowpea; and novel – mung bean. Maternal effects, however, proved to be
520 negligible for all of the measured traits, on both host types. Instead, we
521 found that additive genetic variance played an important role in determining
522 phenotypic variation. Contrary to our predictions, offspring reared on the
523 novel host type performed better for all the measured traits. Daughters
524 whose mothers preferred to lay eggs on the original host were heavier on
525 this host than those of mothers that preferred the novel host type. There
526 was, however, no equivalent effect of host preference on body mass in the
527 novel host. Below we discuss our findings in more detail.

528

529 **Weak maternal effects.** We used an original and a novel host type to
530 examine whether mothers affect their offspring's phenotype in a host-

specific way. Previous studies have shown that environmental stress can either increase or decrease the magnitude of maternal effects (Charmantier and Garant, 2005; Rowiński and Rogell, 2017). Maternal effects variation is sometimes not evident in resource rich conditions as differences among mothers are reduced compared to a poor environment where differences are exacerbated (e.g. Parichy and Kaplan (1992)). If both host types in our study are resource rich (especially when few eggs are laid per bean) this could explain the negligible maternal effects that we see here. Previous quantitative genetic studies employing a similar approach to ours have reported significant maternal effects in *C. maculatus*. This has been, however, in other hosts (adzuki (*Vigna angularis*) in Fox (1993)) or when testing the effect of bean removal after beetle emergence on adult traits (Messina and Fry, 2003). The host species we used are both thought to be highly favourable to *C. maculatus* (Messina, 2004a; Fox and Messina, 2018) (discussed further below). This, in addition to the fact we prevented larval competition with our experimental design, may have substantially reduced the role of maternal effects in the current experiment.

Heritability was higher in the novel host type, but evolutionary potential was similar in both hosts. Heritability of fitness-related traits is traditionally assumed to be low, as additive genetic variation is expected to be depleted

552 by natural selection (Mousseau and Roff, 1987; Hill, 2010). Egg size, body
553 size, fecundity or lifespan were nevertheless previously shown to have
554 intermediate to high heritability in *C. maculatus* (h^2 from 0.27 to 0.74) (Fox,
555 1993; Messina, 1993; Fox *et al.*, 2003; Fox and Messina, 2018). Here, we
556 recorded considerable heritability in all life-history traits (except larval
557 survival), with the highest values occurring for daughter body mass and son
558 adult lifespan (both $h^2 > 0.65$). Heritability was notably higher in the novel
559 host environment (mung bean), with the one exception of adult lifespan of
560 daughters. Holloway *et al.* (1990) proposed that a novel environment should
561 yield higher additive genetic variance due to new genes being expressed
562 thereby uncovering cryptic genetic variation (Hoffmann and Merilä, 1999).
563 Indeed, Messina and Fry (2003) found that *C. maculatus* exhibited increased
564 additive genetic variance for longevity under a novel environment (absence
565 of host beans after emergence). Our results indicate, however, that it was
566 lower residual variance in the novel host (mung bean), rather than increased
567 additive genetic variation, that was responsible for higher heritability in the
568 novel environment. Residual phenotypic variation may entail non-additive
569 genetic, environmental variance and developmental noise (Rowiński and
570 Rogell, 2017) and the influence of at least some of these factors apparently
571 declined in the novel host type. More elaborated breeding design would be
572 required (see e.g. Tucić and Šešlija (2007), or Bilde *et al.* (2008)), however,

573 to examine their respective effects in *C. maculatus*. Interpretation of
574 heritability as the proportion of additive genetic versus total variance can
575 therefore become problematic (Hansen *et al.,* 2011) and evolvability offers
576 a more conclusive comparison of evolutionary potential (Houle, 1992;
577 Hansen *et al.*, 2011). Similar values of trait evolvability indicated that the
578 traits measured in our study possess similar evolutionary potential in the
579 two host types.

580 Genetic trade-offs are thought to prevent populations of parasites or
581 herbivores from becoming 'masters of all trades' and performing well on
582 multiple hosts (Joshi and Thompson, 1995; Agrawal *et al.*, 2010). In
583 phytophagous insects, performance trade-offs on different hosts are,
584 however, rarely reported (Ueno *et al.*, 2003; Scheirs *et al.*, 2005; Messina
585 and Durham, 2015). This includes studies of *C. maculatus* where offspring
586 from the same family usually perform similarly across hosts without
587 exhibiting a G×E interaction (Fox, 1993; Guntrip and Sibly, 1998; Messina,
588 2004a). We also found strong positive cross-environmental genetic
589 correlations indicating parallel reaction norms for offspring from different
590 families when reared on the two host types. Only the development duration
591 of sons showed a low genetic correlation between the two host types
592 indicating that it could evolve differently on cowpea and mung (Via and
593 Lande, 1985). It is, however, important to bear in mind that breeding design

594 studies cannot definitively conclude there are no genetic trade-offs in
595 adaptation to different hosts because they lack mechanistic explanation.
596 This can be obtained through analysis of long-term selected lines (Agrawal
597 *et al.*, 2010) or data on the potential genes involved (Gompert and Messina,
598 2016).

599

600 **Offspring performed better on the novel host type.** We treated mung bean
601 as a novel host type. This was despite mung bean regularly being used to
602 rear other strains of *C. maculatus* (e.g. the Southern India strain (Fox, Bush,
603 *et al.*, 2004)), and regarded with cowpea as a favourable host species for *C.*
604 *maculatus* (Fox and Messina, 2018). Our stock population was kept on
605 cowpea for at least 100 generations. In addition, cowpea strains are overall
606 more viable than those from mung bean (Messina, 2004a) and the cowpea
607 is generally considered to be the ancestral host for *C. maculatus* (Kébé *et al.*,
608 2017). Due to these reasons and the fact that a previous study showed that
609 long-term maintenance on a specific host yields decreased viability on other
610 hosts (Messina, 2004a), we predicted a lower suitability of the novel host
611 type (mung bean). Our finding that offspring performed better on the novel
612 host type (mung bean) was therefore unexpected. While offspring survival
613 was almost 90 % on cowpea, it was even higher on the novel host (93 % on
614 mung bean). There was no obvious cost to the offspring of rearing in the

615 novel host, as the duration of larval development was shorter on mung bean.
616 However, beetles that emerged from mung beans were larger and lived
617 longer as adults than those that emerged from cowpeas. It is not
618 straightforward, however, to tell which of the two host species is generally
619 better for *C. maculatus*, because it depends on other factors such as the level
620 of competition (Messina, 2004a; Paukku and Kotiaho, 2008; Fox and
621 Messina, 2018), temperature (Stillwell *et al.*, 2007) and the population's
622 evolutionary history (Messina, 2004a). In the present study, we eliminated
623 effects of larval competition by rearing one larva per bean. We therefore
624 removed the fitness advantage that cowpea may provide due to its larger
625 size when there is larval competition (Fox and Savalli, 1998). Surprisingly,
626 relative bean size within a given host type also negatively affected body mass
627 and lifespan as well as extending the developmental duration of daughters.

628 We cannot reject the hypothesis that the host effect recorded in our
629 experiment was confounded by egg laying order, as eggs were laid first on
630 mung bean (see Methods for the experimental justification). The lower
631 performance of offspring on cowpea might have been because, following
632 the preference trial, females were first provided with mung beans to lay
633 eggs, and only after that with cowpeas. There are, however, several reasons
634 to think that an effect of laying order in our experiment is unlikely. The
635 lifetime fecundity of *C. maculatus* is 60-80 eggs (Mitchell, 1975; Credland

636 and Wright, 1989; Wilson and Hill, 1989; Messina and Fry, 2003). The dams
637 in our experiment laid around 30 eggs per 24 h and probably still possessed
638 more than half of their lifetime fecundity after they had finishing laying in
639 our experiment. Crucially, past studies suggest there is no negative effect of
640 maternal age on offspring performance on the first day of egg laying (i.e. the
641 relevant time period in our study) (Wasserman and Asami, 1985; Fox, 1993;
642 Fox and Dingle, 1994; Iglesias-Carrasco *et al.*, 2018; Zhang *et al.*, in
643 preparation). We therefore think that the sequence of host types available
644 for egg laying is unlikely to explain the poorer offspring performance on
645 cowpea.

646

647 **Host preference of *C. maculatus* increased daughter body mass and rearing**
648 **host affected host preference.** An egg laying preference for a particular host
649 often predicts offspring performance on that host in phytophagous insects
650 (Gripenberg *et al.*, 2010). However, despite the critical role of oviposition
651 choice for larval success in *C. maculatus*, of the five offspring traits we
652 measured, the strength of dam preference for cowpea only correlated with
653 daughter body mass. Dams that showed a stronger preference for cowpea
654 produced heavier-than-average daughters on cowpea, but not when laying
655 on mung. This contributes to mother fitness through higher daughter
656 reproductive potential in cowpea as body size is a good proximate measure

657 for fecundity in *C. maculatus* (Messina and Fry, 2003). In mung bean,
658 however, daughters' body mass was not affected by their mothers' host
659 preference and the preference-performance relationship thus only holds for
660 daughter body mass in cowpea. The weak overall relationship between
661 mother's host preference for one host type and the performance of her
662 offspring on that host suggests that *C. maculatus* females might aim to
663 maximize their own fitness and not that of individual offspring (i.e. they
664 prioritise offspring number over offspring quality), perhaps through saving
665 searching time for the best host (Wood *et al.*, 2018).

666 Previous studies show that strains of *C. maculatus* maintained for > 40
667 generations on mung bean or cowpea exhibit a strong preference for their
668 recent host type (Messina, 2004b). Fox, Stillwell, *et al.* (2004) used different
669 host strains to demonstrate that switching a strain to another host for just a
670 single generation has no effect on host preference. We found that while
671 daughters reared on cowpea preferred cowpea over the novel host (mung
672 bean), those reared on mung beans showed no preference for either host
673 type. This suggests that there might be a G×E interaction affecting host egg
674 laying preferences, but tracking of more generations is necessary to test
675 whether the host preference evolves after the host switch (as in Fox,
676 Stillwell, *et al.* (2004), or Messina (2004b)).

677

678 **Conclusion.** Maternal effects were low for all measured traits in our study
679 for offspring reared on either a novel or a familiar host. A next step in the
680 exploration of whether M×E interactions affect estimates of genetic
681 variation, and of G×E interactions specifically, would be to conduct
682 experiments using less favourable novel hosts of *C. maculatus*, for example
683 adzuki bean (Fox, 1993) or lentil (Gompert and Messina, 2016). The host
684 species we used are both considered to be of high quality (Fox and Messina,
685 2018). By creating more challenging conditions for offspring, maternal
686 effects might emerge as an important host-specific factor that affects
687 variation in offspring performance (Fox *et al.*, 1997; Räsänen and Kruuk,
688 2007). Despite the fact that maternal effects were negligible in our study,
689 we still argue that it is important testing for M×E interactions. The M×E
690 effects have potential to bias measurements of G×E and the lack of research
691 on M×E interaction is an obstacle towards understanding their role in
692 adaptive processes.

693

694

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Author contribution

MV, PJCC, MLH and MDJ conceived and designed the study; MV, PJCC and MIC collected data; MV analysed the data and drafted the manuscript; and PJCC, MIC, MLH and MDJ revised it. All authors approved the final version of the manuscript.

Conflict of interest

We declare that we do not have any conflict of interest.

Data archiving

Data with accompanying R code will be made available after manuscript acceptance.

717 ## Supplementary Information

718 Table S1 and Annotated Registration.

719

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938 **TABLES**

939 **Table 1.** Model comparison to estimate the best random effects structure for minimal animal MCMC models. The table shows the difference
940 between Deviance Information Criterion (DIC) for each candidate model and the model with the lowest DIC (denoted as '-'). Model 'G' contained
941 additive genetic variance only. The model with 'M' included also maternal effects variance. Models where variance was estimated separately
942 '$_{sep}$' for each host type are 'G_{sep}' or 'M_{sep}'. Models 'G_{cov}' (or 'M_{cov}') estimated covariance '$_{cov}$' between the two host types in addition to the host-
943 specific variance. When the host-specific interaction was fitted as a random effect (models '$_{sep}$' and '$_{cov}$'), we also estimate residual variance
944 separately for each host type. Further details on model fitting are in the Methods. Please note that the low DIC for model 'G_{cov}' means that the
945 genetic covariance between the host types is different from zero. It is, however, inconclusive about Genotype-by-Environment interaction as
946 the covariance can still be highly positive (i.e. the rank order of genotypes does not change). So we also examined the cross-environmental
947 genetic correlation (r_G) estimates from the model given in Table 2. DIC is not reliable for model comparison in non-Gaussian traits (Hadfield,
948 2010; Wilson *et al.*, 2010) and we thus did not perform model selection for larval survival and host egg laying preference of daughters and used
949 model G_{cov} for inference.

950

951

Model	Random effects	Development duration		Body mass		Adult lifespan	
		daughters	sons	daughters	sons	daughters	sons
G	animal	137.6	225.4	82	78.8	70.4	125.6
G+M	animal + dam	151.8	233.3	136.3	115.9	79.4	153.2
G_{sep}	idh(HOST):animal	10.4	-	18.1	46.3	15.6	72.8
G_{cov}	us(HOST):animal	-	0.4	-	-	-	-
G_{sep}+M_{sep}	idh(HOST):animal + idh(HOST):dam	42.5	29.6	97.5	108.9	39.2	133.1
G_{cov}+M_{sep}	us(HOST):animal + idh(HOST):dam	23.7	33.5	31.3	22.1	16.3	17.6
G_{cov}+M_{cov}	us(HOST):animal + us(HOST):dam	30.1	31.3	53.3	63.6	17.2	34.6

Table 2. Phenotypic variance partitioning based on the best model from the model comparison. We used model 'G_{cov}' for all the traits (Table 1) as it estimates cross-environmental genetic covariance and models with DIC difference <2 are usually considered equally supported. We estimated host-specific additive genetic effects (V_A), proportion of additive genetic variance in total phenotypic variance (V_P) - heritability (h^2), additive genetic variance standardized over trait mean - evolvability (CV_A), and cross-environmental genetic correlation (r_G). The estimates and their credible intervals (in brackets) come from posterior distribution of sex-specific animal MCMC models.

		Development duration		**Body mass**		**Adult lifespan**	
Host type	**Par.**	daughters (N = 1 420)	sons (N = 1 384)	daughters (N = 1 431)	sons (N = 1 399)	daughters (N = 1 425)	sons (N = 1 389)
original	V_A	0.430 (0.105,0.678)	0.448 (0.208,0.876)	0.215 (0.147,0.317)	0.070 (0.034,0.114)	19.981 (11.423,26.851)	9.694 (5.578,14.841)
	V_P	1.768 (1.578,1.948)	2.167 (1.979,2.409)	0.501 (0.446,0.555)	0.310 (0.282,0.343)	39.267 (35.595,45.099)	28.298 (24.908,31.138)
	h^2	0.229 (0.084,0.387)	0.210 (0.082,0.374)	0.447 (0.327,0.615)	0.225 (0.122,0.358)	0.459 (0.301,0.624)	0.333 (0.218,0.505)
	CV_A	0.020 (0.012,0.027)	0.021 (0.014,0.030)	0.084 (0.066,0.097)	0.075 (0.058,0.100)	0.195 (0.148,0.226)	0.184 (0.146,0.234)
novel	V_A	0.349 (0.213,0.622)	0.527 (0.355,0.892)	0.250 (0.176,0.319)	0.103 (0.068,0.148)	16.664 (10.973,27.715)	16.304 (11.261,24.817)
	V_P	0.956 (0.853,1.083)	1.154 (1.028,1.339)	0.374 (0.340,0.426)	0.211 (0.186,0.236)	37.645 (33.595,43.241)	26.675 (23.763,31.265)
	h^2	0.365 (0.241,0.606)	0.495 (0.348,0.708)	0.649 (0.501,0.786)	0.513 (0.355,0.669)	0.507 (0.334,0.684)	0.627 (0.480,0.854)
	CV_A	0.020 (0.016,0.026)	0.026 (0.020,0.031)	0.077 (0.065,0.087)	0.082 (0.067,0.099)	0.168 (0.131,0.204)	0.208 (0.176,0.260)
	r_G	0.706 (0.277,0.981)	0.147 (-0.279,0.533)	0.901 (0.670,0.995)	0.996 (0.750,1.000)	0.790 (0.615,0.982)	0.967 (0.777,0.999)

Table 3. The effect of host type, other experimental variables and dam host preference on three offspring life-history traits (fixed-effects estimates from the full animal models). The intercept always corresponds to the trait average on the original host type and the 'novel HOST effect' is the effect of the novel host type (i.e. difference between the two means). The same applies to interaction terms, where the interaction gives the estimate for the difference between the effect on the novel and the original host type. We embolden any credible intervals (in brackets) that do not overlap zero. The estimates and their credible intervals come from posterior distribution of sex-specific animal MCMC models.

Term	Development duration [days]		Body mass [mg]		Adult lifespan [days]	
	daughters (N = 1 420)	sons (N = 1 384)	daughters (N = 1 431)	sons (N = 1 399)	daughters (N = 1 425)	sons (N = 1 389)
Intercept (original HOST)	31.899 (31.713,32.103)	31.442 (31.187,31.607)	5.784 (5.660,5.904)	3.466 (3.414,3.593)	23.62 (22.432,24.739)	16.298 (15.338,17.259)
novel HOST effect	**-1.285 (-1.388,-1.115)**	**-1.148 (-1.296,-0.935)**	**0.728 (0.650,0.792)**	**0.349 (0.303,0.408)**	**3.338 (2.595,3.975)**	**2.355 (1.792,2.885)**
bean mass (original)	**0.145 (0.035,0.229)**	0.105 (-0.017,0.189)	**-0.083 (-0.130,-0.032)**	**-0.039 (-0.089,-0.011)**	**-0.499 (-0.930,-0.111)**	**-0.365 (-0.742,-0.038)**
dam mating order	0.060 (-0.002,0.136)	0.054 (-0.013,0.134)	0.007 (-0.037,0.052)	0.006 (-0.017,0.047)	-0.306 (-0.766,0.069)	0.210 (-0.116,0.587)
day mated (original)	**0.326 (0.206,0.454)**	**0.122 (0.028,0.291)**	0.058 (-0.006,0.149)	**0.074 (0.037,0.139)**	0.443 (-0.113,1.273)	**0.797 (0.199,1.262)**
dam preference for cowpea (original)	-0.073 (-0.180,0.031)	-0.025 (-0.174,0.068)	**0.086 (0.027,0.144)**	0.000 (-0.042,0.046)	0.219 (-0.366,0.733)	0.128 (-0.267,0.572)
Interaction: bean mass (novel)	-0.092 (-0.196,0.032)	0.031 (-0.131,0.138)	0.047 (-0.022,0.102)	0.040 (-0.011,0.091)	0.456 (-0.052,1.124)	-0.060 (-0.463,0.560)
Interaction: day mated (novel)	-0.017 (-0.141,0.142)	0.112 (-0.026,0.326)	-0.057 (-0.127,0.020)	-0.018 (-0.072,0.035)	-0.625 (-1.272,0.117)	-0.360 (-0.910,0.237)
Interaction: dam preference (novel)	0.051 (-0.056,0.206)	0.051 (-0.084,0.228)	**-0.081 (-0.146,-0.015)**	0.008 (-0.038,0.063)	-0.369 (-0.916,0.402)	-0.109 (-0.590,0.470)

967 **Table 4.** Phenotypic variance partitioning (A) and full model inference (B) based on G_{cov}
968 model for the non-Gaussian traits – larval survival and host egg laying preference. The
969 estimates for the variance parameters (A) are back-transformed to original data scale. The
970 effect of host type, the additional experimental variables and dam host preference (B) for
971 larval survival is on logit scale and for host preference on log scale. We embolden any
972 credible intervals (in brackets) that do not overlap zero. The intercept always corresponds to
973 the trait average on the original host type and the 'novel HOST effect' is the effect of the
974 novel host type (i.e. difference between the two means). The same applies to interaction
975 terms, where the interaction gives the estimate for the difference between the effect on the
976 novel and the original host type. The estimates and their credible intervals come from
977 posterior distribution of animal MCMC models.

978 A)

Host type	**Par.**	**Larval survival**	**Host preference**
		juveniles (N = 3 146)	daughters (N = 665)
original	V_A	0.006	<0.001
	V_P	0.094	0.671
	h^2	0.060	0.001
	CV_A	0.084	0.033
novel	V_A	0.003	0.001
	V_P	0.065	0.522
	h^2	0.040	0.003
	CV_A	0.055	0.071
	r_G	0.286* (-0.469,0.985)*	-0.046* (-0.905,0.948)*

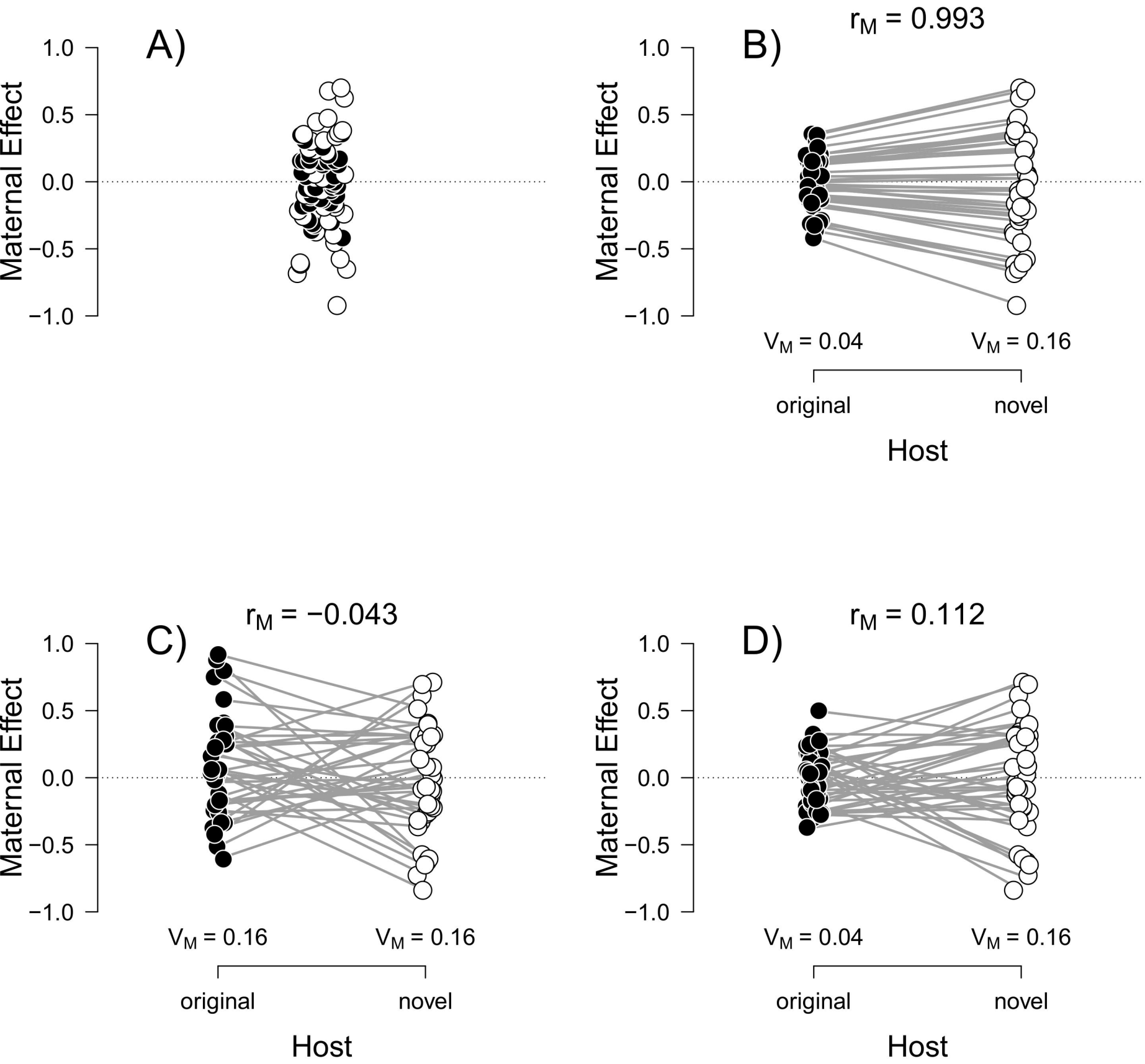
979 * these estimates are on the transformed (latent) scale
980

B)

Term	Larval survival	Host preference
	juveniles (N = 3 146)	daughters (N = 665)
Intercept (original HOST)	2.868 (2.341,3.441)	-0.409 (-0.528,-0.338)
novel HOST effect	0.512 (-0.094,1.447)	**-0.247 (-0.324,-0.180)**
bean mass (original)	-0.161 (-0.353,0.050)	0.010 (-0.046,0.049)
dam mating order	-0.021 (-0.206,0.124)	-0.001 (-0.027,0.047)
day mated (original)	0.095 (-0.153,0.350)	-0.053 (-0.094,0.004)
dam preference for cowpea (original)	-0.042 (-0.258,0.183)	0.014 (-0.041,0.057)
Interaction: bean mass (novel)	-0.035 (-0.376,0.221)	0.017 (-0.075,0.076)
Interaction: day mated (novel)	-0.122 (-0.501,0.240)	-0.016 (-0.066,0.083)
Interaction: dam preference (novel)	0.242 (-0.106,0.549)	-0.037 (-0.096,0.049)

984 ## Figure caption

985 **Figure 1.** Illustration of how maternal effects might differ between environments (host beans
986 in our study). Panel A) shows that ignoring the potential for environment-specific maternal
987 effects, as indicated by the colour of points representing maternal effects in the original (black
988 points) and the novel host (white points), could be misleading. Panel B) represents a scenario
989 where variance due to maternal effects (V_M) differs between the environments, i.e. the first
990 type of Maternal-by-Environment interaction (M×E). Panel C) illustrates the other type of M×E
991 where the rank of maternal effects differs between the hosts. The evidence for the shift in
992 ranking comes from the low cross-environmental correlation in maternal effects (r_M) despite
993 the maternal effects variance (V_M) being comparable between the hosts. Panel D) represents
994 a combination of B) and C).


A)
B)
C)
D)
r_M = 0.993
r_M = −0.043
r_M = 0.112
Maternal Effect
1.0
0.5
0.0
−0.5
−1.0
V_M = 0.04
V_M = 0.16
V_M = 0.16
V_M = 0.04
V_M = 0.16
original
novel
Host