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

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Conflict of interest

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

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Abstract:

Stressful conditions, like novel host environment, can stimulate mothers to produce offspring with phenotypes that better suit the conditions they are likely to experience (i.e. adaptive maternal effects). However, mothers might vary in their ability to adjust their offspring's phenotype in response to environmental cues. This could generate a maternal-by-environment interaction (M×E) that inflates estimates of genotype-by-environment effects (G×E). Our main aim in this study was to test for M×E with 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. Partitioning of offspring phenotypic variation indicated that maternal effects were very small for all the measured life-history traits, prohibiting a formal test for M×Es. There was also little evidence that the degree of maternal preference to oviposit on one host type predicted her offspring's relative performance on this host. Additive genetic variance for most traits was, however, relatively high on both hosts. While there was higher heritability in the novel host, there was no evidence for G×Es and most cross-host genetic correlations were highly 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 non-genetic

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

Introduction

Phytophagous insects are a valuable model for studying life-history evolution, especially in the context of trade-offs arising from adaptation to a preferred host (Agrawal *et al.*, 2010). Antagonistic pleiotropy is predicted to prevent populations of parasites or herbivores from becoming 'masters of all trades' and adapting perfectly to multiple hosts (Agrawal *et al.*, 2010). This prediction is based on the assumption that antagonistic pleiotropy leads to a trade-off in performance on different hosts (Joshi and Thompson, 1995). At the same time, phytophagous insects exhibit a variety of non-genetic maternal effects that can also influence life-history traits (Fox and Dingle, 1994; Fox *et al.*, 1997; Van Asch *et al.*, 2010; Cahenzli and Erhardt, 2013). Adaptive maternal effects that result in cross-generational plasticity are considered to be one way that individuals can perform well under new environmental conditions before selection acts to favour advantageous genetic variation (Fox *et al.*, 1997; Cahenzli *et al.*, 2015). Maternal effects can have far reaching consequences, including niche breadth expansion through shifts in phenology (Van Asch *et al.*, 2010), and even speciation when they facilitate host shifts (Forbes *et al.*, 2017).

Environmental challenges often lead mothers to alter investment in their offspring. This can either facilitate adaptation to new hosts (Fox *et al.*, 1997), or be detrimental to offspring (Magalhães *et al.*, 2011). Maternal

77 effects can moderate population dynamics (Benton, St Clair, & Plaistow,
78 2008), and sometimes even alter the likelihood of population extinction or
79 persistence (Bernardo, 1996). In addition, non-genetic maternal effects can
80 influence offspring in an environment-specific manner (Bernardo, 1996;
81 Fox *et al.*, 1997; Räsänen and Kruuk, 2007; Vega-Trejo *et al.*, 2018). It is
82 therefore no surprise that environment-specific maternal effects (M×E)
83 could falsely inflate estimates of a Genotype-by-Environment interaction
84 (G×E) (Vega-Trejo *et al.*, 2018). In the same way that maternal effects have
85 been shown to inflate estimates of genetic effects (Kruuk and Hadfield,
86 2007), M×E interactions may result in variation in the response of different
87 genotypes across environments being incorrectly treated as evidence for a
88 G×E interaction (Via and Lande, 1985; Saltz *et al.*, 2018). In such cases, a
89 genetic trade-off in the degree of adaptation to different hosts would be
90 artificially inflated.

91 In this study, we investigated the presence of maternal effects, as
92 well as the potential for an interaction between maternal effects and her
93 offspring's rearing environment on general offspring life-history traits, as
94 well as her daughters' egg laying preferences on different hosts in the seed
95 beetle, *Callosobruchus maculatus* (Coleoptera: Chrysomelidae).
96 *Callosobruchus maculatus* is a common pest to legume storages worldwide.
97 The larvae feed on multiple legume species (family Fabaceae) with varying

98 degrees of success (Gompert and Messina, 2016; Price *et al.*, 2017;
99 Messina *et al.*, 2018). Females lay individual eggs on host beans shortly
100 after copulation (Mitchell, 1975). Host choice is crucial as the larvae cannot
101 move between individual beans. Incorrect decisions on where a female
102 chooses to lay her eggs inevitably lead to lower quality or even non-viable
103 offspring (Mitchell, 1975; Messina and Fry, 2003; Messina *et al.*, 2007).
104 Larvae hatch 4-5 days after oviposition and burrow into the bean to feed
105 on the endosperm. Depending on the temperature and host species, adults
106 typically emerge within 26-36 days of oviposition (Fox *et al.*, 2003;
107 Messina, 2004a). *Callosobruchus maculatus* shows profound sexual
108 dimorphism in life-history traits with males emerging earlier, being smaller
109 and living shorter than females (Guntrip *et al.*, 1997; Fox, Bush, *et al.*,
110 2004).

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

115 1) There would be strong maternal effects on offspring life history
116 traits (Fox, 1993a; Messina and Fry, 2003). This led us to predict that
117 offspring from a single female (maternal full-siblings) are more similar to

each other than to their half-siblings (shared sire, different mother) or to offspring from families sired by other males than expected based solely on genetic relatedness.

2) Maternal effects are environment-specific (M×E). Specifically, we predicted there would be a negative correlation between full-sibling performance on the two host types, even after controlling for a negative genetic correlation due to antagonistic pleiotropy.

3) Novel host type would be challenging for offspring. Here, we predicted that 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 a shorter adult lifespan).

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

Methods

136 **Experiment overview.** We estimated genetic and maternal effects for
137 four life-history traits and host egg laying preference using a half-sib/full-
138 sib split brood design with two different host types - original vs. novel. We
139 used cowpea (*Vigna unguiculata*, Fabaceae) as the original and mung bean
140 (*V. radiata*) as the novel host species in our experiment. Cowpea and mung
141 are both suitable hosts for *C. maculatus* (Fox and Messina, 2018) but
142 populations kept on specific hosts for many generations show better
143 performance on their usual host beans compared to novel hosts (Messina,
144 2004a).

145

146 **Origin and maintenance of stock beetles.** Beetles used as the
147 parental generation for our experiment were obtained from a large stock
148 population originally sourced from the University of Western Australia
149 (Perth, Australia) in 2017 where they had been bred on cowpea for at least
150 90 generations. We maintained this stock in our lab at the Australian
151 National University on cowpea for another 9 generations before we began
152 our experiment. Our stock was maintained in four, regularly mixed (every 5
153 generations) populations of over 500 individuals, each kept on cowpea at
154 25-26 °C.

155

156 **Establishing the parental generation (P).** To obtain virgin males and
157 females for the parental generation (P), we exposed approximately 2000
158 un-infested cowpea beans to stock beetles for a period of 48 h. Each bean
159 was then placed in an individual Eppendorf tube (with a pinhole for airflow)
160 and had 5-8 eggs on its surface (a density which is usual for our stock).
161 Once isolated, we monitored these beans until adults began to emerge. We
162 collected virgin beetles each morning and used them in our experiment on
163 the same day. We knew that beetles were virgins as they were either the
164 only beetle to have emerged that day, or all beetles that had emerged
165 were of the same sex. Every evening, we discarded any beetles that had
166 emerged during that day. Using the parental beetles that emerged each
167 morning, we mated males and females according to a full-sib/half-sib
168 breeding design: each male was sequentially mated with four random
169 females over the day and the mating order was noted (similar to Fox *et al.*
170 (2003)). We aimed for a total of 89 families (sires) with 356 dams. Pairs
171 that did not copulate within 30 min were separated for half an hour before
172 being placed together for another mating attempt. Each female was
173 weighed prior to mating to the nearest 0.001 mg (Cubis Ultra-Micro
174 balance, Sartorius Lab Instruments GmbH., Goettingen, DEU). All matings
175 took place over six days ('day mated', range 1-6, see *Partitioning of*
176 *Phenotypic Variance*). There is therefore a positive correlation between

177 parental age (egg to adulthood) and 'day mated', but it is imperfect
178 because parents emerged from eggs initially laid over two days (i.e. 48
179 hours; see above). There is no correlation between 'day mated' and adult
180 parental age because all matings occurred on the day that the parents
181 emerged.

182

183 **Maternal host preference.** Once females had mated, we conducted
184 choice trials to determine their preferred host type for egg laying. We
185 considered females ready to lay eggs once the pair dismounted (Wilson
186 and Hill, 1989). For the host preference trials, we mixed cowpea (original
187 host) and mung beans (novel host) in covered Petri dish (ø 5.5 cm). We
188 used proportionally more mung than cowpea beans (8:4) because cowpea
189 beans have an approximately 1.6-times larger surface area (Paukku and
190 Kotiaho, 2008) and are 4-times heavier than mung beans (in our study the
191 average ± SD bean mass was 294±45 mg for cowpea, and 72±8 mg for
192 mung bean). Females were left to lay eggs for two hours, after which they
193 were removed and the number of eggs on each host bean type was
194 counted. Relative preference was calculated as the proportion of the eggs
195 that a female laid on the original host (cowpea). The values for relative
196 host preference therefore ranged between 0 and 1.

197

198 **Generation of offspring (F1).** Directly after the host preference trial,
199 we transferred individual dams to plastic containers (ø 4 cm, height 6 cm)
200 with 10-13 mung beans and left them to lay eggs for 14-18 h. We then
201 moved dams to new containers with 10-13 cowpea beans for 9-10 h. This
202 difference in laying time was required because initial trials showed that
203 more time was necessary for females to lay a sufficient number of eggs on
204 the novel host (mung beans), than on cowpea (the original host). Females
205 were presented with mung beans first to prevent them from laying all their
206 eggs on what we expected to be the preferred host type (cowpea)
207 (Messina and Slade, 1997). Maternal age and/or laying order effects are
208 unlikely to have influenced our results due to the short period of time we
209 allowed females to lay eggs (i.e. <24 h). Previous studies have shown no
210 effect of female age on offspring quality during the first 24 h of laying (Fox
211 and Dingle, 1994).

212 Once females had laid eggs on both host types, we collected up to 10
213 individual beans of each host type for each female. If a female had laid
214 eggs on fewer than 10 beans of a given type, we used them all. We ensured
215 that each bean had only one egg laid on it by haphazardly scraping off
216 surplus eggs with a scalpel. We weighed beans within 24 h after oviposition

217 to the nearest 0.001 mg to measure the resources available to the larvae.
218 Beans with an egg were then placed individually in Eppendorf tubes with
219 perforated lids and incubated at 26 °C.

220 We started regular monitoring of F1 emergence on day 24 post-
221 oviposition. However, we missed the onset of emergence of 40 beetles on
222 mung (1.2% of the total sample) by approximately 1 day as they emerged
223 sooner than expected. To be conservative, data from these early emerging
224 beetles was removed from the final dataset, because their emergence
225 could have been on that day or the day before. This uncertainty might not
226 only affect estimates of larval development duration, but also that of any
227 correlated traits such as body mass, as we did not provide adults with food.

228

229 **Measurement of offspring (F1) traits.** When an offspring emerged,
230 the date was recorded, and it was sexed and weighed (to the nearest 0.001
231 mg), and the bean was removed from the tube. After weighing, the beetle
232 was returned to its tube and checked daily for survival. We also tested the
233 host preference of two newly emerged female offspring per dam raised on
234 each host type (total N = 4/dam). To do this we mated each daughter with
235 a randomly selected male from the stock and then ran an egg laying
236 preference trial identical to that described above for their mothers. We

237 monitored survival until the death of all emerged offspring (day 79 post-
238 oviposition). At that time, we also censused larval (egg-to-emergence)
239 survival, assuming that larvae in beans from which a beetle had not yet
240 emerged had died.

241

242 **Sample sizes.** Our sample size was determined a priori based on
243 power analysis from Lynch and Walsh (1998) to create 89 families (89 sires
244 with 356 dams) and try to obtain 10 offspring per dam per host type (i.e. 7
245 120 offspring). The final sample size is lower due to unsuccessful matings
246 or too few eggs being laid. We analysed data for sons and daughters
247 separately due to their marked sexual dimorphism which invariably leads
248 to strong interactions between sex and other effects. We only included
249 offspring of dams that produced offspring reared on both host types, and
250 we removed offspring with extreme values (>3 standard deviations (SD)
251 from the mean). We collected data on four offspring life-history traits:
252 (egg-to-emergence) 'larval survival' (dead or emerged; N = 2 877),
253 'duration of larval development' (number of days between oviposition and
254 offspring emergence; N = 1 221 daughters and 1 189 sons), 'body mass'
255 (weight at emergence in mg; N = 1 228 daughters and 1 200 sons) and
256 'adult lifespan' (number of days between offspring emergence and death;

257 N = 1 226 daughters and 1 197 sons). In addition, we measured the host
258 egg laying preferences of 514 daughters. The slightly lower sample sizes
259 (<1%) for larval development or adult lifespan compared to body mass is
260 due to exclusion of response variable outliers and dams producing
261 offspring of certain sex on a single host type only. Prior to any statistical
262 analysis, but after all data has been collected, we registered this project on
263 the Open Science Forum webpage:
264 https://osf.io/ft7eq/?view_only=0bab0a33bb4246adb64c919601a72757
265 The final analytical approach we used was different, however, from the
266 original plan and we explain our changes in the Annotated registration
267 section in Supplementary Information.

268

269 **Partitioning of phenotypic variance.** To determine the strength of
270 maternal effects on offspring traits in *C. maculatus* (Prediction 1) and
271 whether maternal effects depend on the offspring rearing environment,
272 (i.e. the existence of a M×E interaction - Prediction 2), we built a 'minimal
273 model' containing only fixed effects directly attributable to the
274 experimental design. These were 'host type' (original/novel), 'bean mass'
275 (standardized within each host type to zero mean and 1 SD variance), 'dam
276 mating order' (i.e. dam position in sire's mating sequence, 1 to 4), and 'day

277 mated' (1-6). We did not fit 'day mated' as a random effect because it
278 resulted in overparametrized models that produced unstable and weak
279 variance estimates. As random effects, we used terms that reflected the
280 nested breeding design. We defined between-sire (family) variance as 'sire
281 ID', between-dam variance as 'dam ID' nested inside sire ID, and between-
282 individual variation as 'residual' variance.

283 We fitted a bivariate model for each life-history trait to allow the
284 components of offspring phenotypic variance to differ between the two
285 host types. It means that for each random factor we estimated two values
286 for variance in each model: one for offspring on cowpeas and the other for
287 offspring on mung beans. The bivariate model then allowed us to estimate
288 the covariance between offspring traits on the two host types. The
289 response variables for the bivariate model, therefore, consisted of two sub-
290 traits created from the single column of trait values. The first column (sub-
291 trait) contained trait values recorded for offspring raised on cowpea with
292 the values for those raised on mung bean left blank. The other column
293 contained values from offspring raised on mung bean and rows for cowpea
294 offspring were left blank.

295 Daughter host preference data was fitted differently, because we
296 wanted to account for variation in the total number of eggs laid and not

297 just fit the preference ratio (values 0-1) as a response. We again used a
298 bivariate model, with the number of eggs on cowpea in the first column of
299 the response, and the total number of eggs laid in the second column. To
300 estimate variance components separately for offspring from each host
301 type, we specified interactions with random effects: that is between host
302 type and sire (HOST:sire ID); between host type and dam (HOST:dam ID);
303 and between host type and the residual term.

304 Based on the outputs from the minimal models for each trait, we
305 then performed the phenotypic variance partitioning and calculated the
306 maternal-effects proportion (m^2) and the cross-environmental maternal-
307 effects correlation (M×E) (r_M), narrow-sense heritability (h^2), evolvability
308 (CV_A) and the cross-environmental correlation for additive genetic effects
309 (G×E) (r_G). We used maternal effects proportion, $m^2 = V_M/V_{total} = (V_{dam}-$
310 $V_{sire})/(V_{sire}+V_{dam}+V_{residual})$, to quantify the importance of maternal effects
311 (Messina & Fry, 2003). The correlation between maternal effects for the
312 two host types (M×E) was $r_M = COV_{M\ original\text{-}novel}/\sqrt{(V_{M\ original})}*\sqrt{(V_{M\ novel})}$,
313 where $COV_{M\ original\text{-}novel} = COV_{dam\ original\text{-}novel} - COV_{sire\ original\text{-}novel}$. We calculated
314 heritability as $h^2 = V_A/V_{total} = 4*V_{sire}/(V_{sire}+V_{dam}+V_{residual})$ (Lynch and Walsh,
315 1998), assuming dominance and epistatic effects were negligible.
316 Evolvability was defined by Houle (1992) as $CV_A = \sqrt{V_A}/\mu = \sqrt{(4*V_{sire})}/\mu$,
317 where μ is the mean of a trait (Garcia-Gonzalez *et al.*, 2012). Evolvability

318 standardizes additive genetic variance over the trait mean and is therefore
319 useful to compare the potential evolutionary response among traits, unlike
320 heritability which is conditional on the amount of residual phenotypic
321 variation (Hansen et al., 2011). The correlation between additive genetic
322 effects on the two host types (G×E) was $r_G = COV_{sire\ original\text{-}novel}/\sqrt{(V_{sire\ original})}*\sqrt{(V_{sire\ novel})}$.
323

324

325 **Testing for host effect and dam host egg laying preference on**
326 **offspring phenotype.** To determine the effect of novel host type on
327 offspring (Prediction 3) and to test whether offspring performed better on
328 the host type that was preferred by their mother (Prediction 4), we built a
329 'full model'. The full model always included all the terms outlined above for
330 the minimal model, as well as, 'dam host preference' (i.e. the relative
331 preference ratio: 0-1 values). We included the interaction between host
332 preference and host type 'HOST:dam host preference' to test if the effect
333 of the strength of the preference for the original host on offspring traits
334 differs depending on the host type. We also included interactions between
335 host type and bean mass 'HOST:bean mass', as well as host type and day
336 mated 'HOST:day mated' as fixed effects to test for potential host-specific
337 influences.

338

339 **Model fitting.** We fitted the models using the package MCMCglmm
340 (ver. 2.28) (Hadfield, 2010) in R software (ver. 3.5.3). The continuous
341 response variables - duration of larval development, body mass and adult
342 lifespan; were fitted using Gaussian family and identity link, while larval
343 survival (binomial distribution) was fitted as a categorical variable (with
344 implicit logit link). All continuous variables, including the response, were
345 standardized to zero mean and variance in units of SD (standardised y = (y-
346 μ)/SD). Note that standardisation allows for direct among-trait comparison
347 by transforming response variable to SD scale (Matsumura *et al.*, 2012).
348 Daughter host preference was tested as bivariate vector with the number
349 of eggs on original host and total number of eggs using a binomial
350 distribution (specified as 'multinomial2' in the MCMCglmm) (Hadfield,
351 2010).

352 To fit the MCMC models, we used locally uninformative inverse-
353 Wishart priors for the random-effects variance (G) with expected variance-
354 covariance matrix at limit 'V' = 1 on the diagonal (i.e. two values – one per
355 each host), and the degree of freedom 'nu' = 1.002. We also added
356 parameter-expanded priors 'α mu' = 0 and 'α V' = 1 000 on diagonal to
357 increase mixing and effective sample size (Hadfield, 2010). Priors for

358 residual variance (R) were set as V = 1 on diagonal and nu = 1.002. In the
359 analysis of survival, the residual variance had to be fixed to 1, so that the
360 binomial mixed-effects model could be estimated (Hadfield, 2010). For
361 fixed effects, we retained default priors with variance = 0 and mean = 10^{10}.
362 To generate posterior distributions from the minimal model, we ran 120
363 000 iterations with burn-in of 20 000 and thinning interval of 100, so that
364 we obtained an effective sample size of 1 000. In the full model, we
365 increased number of iterations to 240 000, burn-in 40 000 and thinning
366 interval to 200 for the Gaussian traits. For daughter host preference, the
367 setup was 550 000 iterations with burn-in of 50 000 and 500 for the
368 thinning interval. For model of larval survival, we increased the iterations
369 to 1 200 000 with a burn-in of 200 000 and thinning interval of 1 000 as we
370 were aiming for an autocorrelation <0.1 at the lag corresponding to the
371 thinning interval (Wilson et al., 2010). Model convergence was assessed by
372 visual examination of the traces using function 'plot(mcmc.model)'.
373 Estimates of heritability in larval survival and daughter host egg laying
374 preference on the observed data scale were computed from the latent
375 scale variance estimates using the package 'QGglmm' (de Villemereuil *et*
376 *al.*, 2016). We always interpreted the outcome of the complete model
377 (without simplification) and assessed the importance of individual model
378 terms based on their credible intervals (CrI).

Results

Prediction 1 and 2 – testing for maternal effects and M×E interaction. We observed very weak maternal effects for all the measured traits. Posterior estimates of variation due to maternal effects ($V_M = V_{dam} - V_{sire}$) ranged between -0.271-0.437 in the minimal models (Table 1). Note that negative values for variance are not meaningful, so the real maternal effects were close to zero. As a consequence, posterior estimates of maternal effects proportion (m^2) credible intervals did not exclude zero (Table 2). Given the low maternal effects whose estimates were even negative in some cases, it was not possible to calculate cross-environmental correlation of maternal effects (r_M), and to test for M×E interactions. Although we extracted the cross-environmental maternal effects covariance, to calculate r_M we also needed the product of the square-root of maternal effects variances (V_M) from the two host types as the denominator. A square-root is, however, not defined for negative values on real number scale.

Table 1. Variance-covariance structure and fixed-effects estimates based

on the minimal models.

397

398 **Components of phenotypic variance related to additive genetic**
399 **effects - heritability, evolvability and G×E.** We observed higher heritability
400 for 3 offspring life-history traits in the novel host, but evolvability was
401 similar for the two host types. We found medium to high heritability on the
402 novel host (h^2 = 0.471-0.621) for development duration of sons, body mass
403 of daughters and adult lifespan of both sexes (Table 2). The adult lifespan
404 of daughters also had medium heritability in offspring from the original
405 host type (h^2 = 0.367), but the credible interval was wide and came close to
406 including zero (Table 2). Despite a trend for higher heritability on the novel
407 host type, the estimates of evolvability (variance due to additive genetic
408 effects standardised over trait mean) were rather similar for the two host
409 types. Comparing evolvability among traits across sexes and host types, it
410 was highest for body mass at emergence (CV_A = 8.4-12.6 %, Table 2).

411 We recorded highly positive correlations of additive genetic effects
412 (r_G) for offspring performance on the two host types (Table 2). The only
413 exceptions were for the larval survival and development duration of sons,
414 which exhibited negative genetic correlation but with wide credible
415 intervals overlapping zero (Table 2). The within-family larval survival and

416 development duration of sons on the novel host did not correspond to that
417 on the original host, potentially suggesting a Genotype-by-Environment
418 interaction (G×E).

Table 2. Phenotypic variance partitioning.

419

420 **Predictions 3 and 4 – testing for host type suitability and host**
421 **preference-performance.** Unexpectedly, given our predictions, offspring
422 generally performed better on the novel host (mung) than on the original
423 host (cowpea) (Table 1, 3; see Supplementary Table 1 for the list of average
424 trait estimates for both host types). We did not find a positive relationship
425 between the strength of the dam host egg laying preference and the
426 performance of their offspring on either host type. The one exception was
427 for daughter body mass: the daughters of dams that more strongly
428 preferred the cowpea host emerged heavier when raised on cowpea,
429 whereas we observed no such effect for daughters raised on mung beans
430 (Table 3). Daughters reared on the original cowpea host also exhibited a
431 higher egg laying preference for cowpeas than those reared on mung
432 beans (raw average host preference ratio of 0.677 versus 0.516; where 1 is
433 a strict preference for cowpeas).

434

Effect of experimental variables on offspring traits - bean size, mating order and mating date. Host-type specific relative bean size (zero-centered per host type) and mating date were important predictors of offspring traits. For both host types, offspring that developed in larger beans had a poorer outcome: increased development duration for both sexes, reduced body mass in daughters and lower adult lifespan in sons. The effects of mating day were, however, mixed (Table 3). Daughters of later mated families took longer to develop, but sons emerged at a larger size, and both sexes subsequently lived longer. Daughters from later mated families also showed a stronger egg laying preference for the novel host type.

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

Discussion

Summary. Our main aim was to test for environment-specific maternal effects on offspring life-history traits, that is Maternal-by-Environment interactions (M×E). We used a full-sib/half-sib split brood design with seed beetles (*C. maculatus)* reared on two types of host: original – cowpea; and novel – mung bean. Maternal effects proved to be

454 negligible on both host types, making it meaningless to estimate maternal
455 effect correlations across the two hosts and thereby test for M×E
456 interactions. Instead, we found that additive genetic variance played an
457 important role, particularly in the novel environment. Contrary to our
458 predictions, developing on the novel host type did not lower offspring
459 performance for any of the measured traits. On the original host type,
460 daughters whose mothers preferred to lay eggs on this host were heavier
461 than those of mothers that preferred the novel host type. Daughters
462 reared on the original host also preferred to lay eggs on this host, while
463 those from the novel host did not exhibit a preference. Below we discuss
464 our findings in more detail.

465

466 **Missing maternal effects.** We were unable to formally test for a
467 difference in the relative importance of maternal effects in different
468 environments, because maternal effects were very weak in both host
469 types. Intriguingly, previous studies on *C. maculatus* have reported strong
470 maternal effects on male development duration (Fox, 1993a), female
471 fecundity, adult body mass and lifespan (Messina and Fry, 2003). However,
472 these non-genetic maternal effects in experimental studies with *C.*
473 *maculatus* mostly seem to stem from variation in maternal age (Fox and
474 Dingle, 1994; Fox *et al.*, 2003; Lind *et al.*, 2015). Older *C. maculatus* females

475 have previously been shown to produce offspring with lower egg-to-adult
476 survival, longer larval development (Fox *et al.*, 2003; Lind *et al.*, 2015) and a
477 shorter lifespan (Lind *et al.*, 2015). In our study, neither male nor female
478 adult parental age varied as we collected parental beetles and mated them
479 on the day of emergence. While mating day, which is imperfectly
480 correlated with lifetime age (i.e. zygote to emergence), had notable effects
481 on several offspring life-history traits and daughters' host egg laying
482 preference, removing it from the model did not increase estimates of
483 maternal effect proportions (Supplementary Table 2). This suggests that
484 mating day acts like a 'block' factor that accounts for experimental
485 variation that affected the entire family sired by a given sire (and not to
486 lifetime age *per se*) due to stochastic daily fluctuations of unknown origin.
487 Non-genetic maternal effects due to variation in age were therefore
488 eliminated by mating dams of the same age to the single sire in each
489 family.

490

491 **Heritability of some life-history traits was higher in the novel**
492 **environment, but evolvability was similar between hosts and the genetic**
493 **correlations between hosts were highly positive.** Heritability of fitness-
494 related traits is traditionally assumed to be low as additive genetic
495 variation is expected to be depleted by natural selection (Mousseau and

496 Roff, 1987; Teplitsky *et al.*, 2009). Here, we recorded considerably higher
497 heritability for a number of life-history traits in the novel host environment
498 (mung beans), especially son's development duration, daughter's body
499 mass and adult lifespan. Higher heritability can be the result of higher
500 additive genetic variance, reduced residual variance, or both, because it is
501 defined by a ratio. The traits with non-zero heritability in our current study
502 showed increased additive genetic variance rather than reduced residual
503 variance in the novel environment. This suggests there was larger standing
504 genetic variation for these traits in the novel environment. However,
505 similar values of trait evolvability, the additive genetic variance
506 standardised over trait mean, indicated that the traits are likely to respond
507 at a similar rate to selection on both host types. We also found strong
508 positive genetic correlations indicating parallel reaction norms for offspring
509 from different families when reared on the two host types. It is important
510 to bear in mind, however, that quantitative genetic studies are ultimately
511 inconclusive about whether or not there is genetic trade-off in adaptation
512 to different hosts (Gompert and Messina, 2016) and any results based on
513 inspection of genetic correlation should be viewed with caution.

514

515 **The novel host type appeared to be better for offspring.** Offspring
516 life-history traits differed between the two host types in an unexpected

517 way with offspring performing better on the novel host type. While
518 offspring survival was almost 90 % on cowpeas (the original host), it was
519 even higher on the novel host (mung bean), exceeding 90 %. There was no
520 obvious cost as the duration of larval development was shorter on mung
521 beans, and the beetles that emerged were larger and lived longer as adults.
522 It is not straightforward, however, to tell which host species is generally
523 better for *C. maculatus*, because it depends on other factors such as the
524 level of competition (Messina, 2004a; Fox and Messina, 2018),
525 temperature (Stillwell *et al.*, 2007) and the population's evolutionary
526 history (Messina, 2004a).

527 In the present study, we eliminated any effect of larval competition
528 by rearing one larva per bean. We therefore reduced the fitness advantage
529 that cowpeas provide due to their larger size when there is larval
530 competition (Fox and Savalli, 1998; Messina, 2004a; Fox and Messina,
531 2018). In our experiment, the original host type was cowpeas. Although
532 adult lifespan on mung beans can be longer than that on cowpea (Fox,
533 Bush, *et al.*, 2004), cowpea strains are overall more viable than those from
534 mung beans (Messina, 2004a). Currently, we still lack a good explanation
535 for the observed positive effect of a novel host type on the measured life-
536 history traits, but we offer some speculative suggestions.

537 First, the seemingly higher performance of *C. maculatus* on the novel
538 host type could be caused by female avoidance of this host. We only
539 analysed data from offspring of dams that laid eggs on both hosts. Our
540 interpretation of the data would change, if the offspring of dams that only
541 lay eggs on cowpea are of inferior quality. In total about 10 % of dams (36
542 in total) produced offspring on one host only, and of these 21 dams
543 showed strict cowpea preference in the host egg-laying preference trials.
544 There is therefore a possibility that the dams producing lower quality
545 offspring avoided mung as a host. Unfortunately, including the data on
546 offspring from the excluded dams will not resolve the issue, because we do
547 not know how their offspring would perform on mung beans.

548 Second, we note that the lower performance of offspring on cowpea
549 might have been because, following the preference trial, females were
550 provided with mung beans to lay eggs, and only after that with cowpea.
551 Eggs laid late in the laying sequence have previously been shown to be of
552 lower quality in some insects (Rossiter, 1996). The lifetime fecundity of *C.*
553 *maculatus* is 60-80 eggs and depends on female body size, and mate and
554 host availability (Mitchell, 1975; Wilson and Hill, 1989; Messina and Fry,
555 2003). The dams in our experiment laid around 30 eggs per 24 h and were
556 therefore probably still far from nearing the end of egg laying in our
557 experiment. In addition, past studies suggest there is no negative effect of

558 maternal age on offspring performance on the first day of female
559 reproductive life (Fox and Dingle, 1994). We therefore suggest that the
560 sequence of host type presentation for egg laying is very unlikely to explain
561 poorer offspring performance on cowpeas.

562

563 **Host preference of *C. maculatus* was only weakly related to**
564 **offspring performance on each host species.** We tested two relationships
565 with regard to female host egg laying preference – whether dam host
566 preference correlated with offspring performance on each host, and if
567 rearing host type affected a daughter's host preference. Host egg laying
568 preference often predicts offspring performance on that host in
569 phytophagous insects (Gripenberg *et al.*, 2010). However, despite the
570 critical role of oviposition choice in *C. maculatus*, for all the traits we
571 measured, the strength of the dam preference for cowpea only correlated
572 with daughter body mass. Specifically, dams that more strongly preferred
573 cowpea produced heavier daughters on cowpea but not on mung.

574 Previous studies show that strains of *C. maculatus* maintained for >
575 40 generations on mung bean or cowpea exhibit a strong preference for
576 their recent host type (Messina, 2004b). (Fox, Stillwell, *et al.*, 2004) used
577 different host strains to demonstrate that there is no immediate effect of

578 the current host type (i.e. switching a strain to another host for 1
579 generation) on the host preference. Variation in host preference in *C.*
580 *maculatus* is mainly due to additive genetic effects, but is also influenced
581 by dominance and epistasis (Fox, 1993b; Fox, Stillwell, *et al.*, 2004).
582 However, we found that while daughters reared on cowpea preferred
583 cowpea over a novel host (mung bean), those reared on mung beans
584 showed no preference for either host type. This suggests that there might
585 be a G×E interaction affecting host egg laying preferences and more
586 generations would be necessary to see whether the host preference
587 evolves after the host switch (as in Fox, Stillwell, *et al.* (2004) or Messina
588 (2004b)).

589

590 **Conclusion.** Maternal effects were low for all measured traits in our study
591 for offspring reared on either a novel or familiar host. We therefore did not
592 test for Maternal-by-Environment interactions. A next step in the
593 exploration of the role of M×E interaction on estimates of genetic variation
594 and G×E interactions in *C. maculatus* would be to run tests using a less
595 favourable novel host as the species we used are both of high quality to *C.*
596 *maculatus* (Gompert *et al.*, 2015). By creating more challenging conditions
597 for offspring, maternal effects might emerge as an important factor
598 affecting variation in offspring performance (Fox *et al.*, 1997; Räsänen and

Kruuk, 2007). Despite being unable to test for an interaction between maternal effects and environment (M×E), we still provided a way to formally test for it. Studies partitioning phenotypic variation across environments should not only account for variation in performance of different genotypes between environments (G×E), which is a common practice, but also control for potential M×E.

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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 are stored at OSF (link: https://osf.io/ft7eq/?view_only=0bab0a33bb4246adb64c919601a72757) and FigShare (link: https://figshare.com/s/7878e68e31590dce594d).

Supplementary Information

Supplementary information is available at *bioRxiv* website along the manuscript file.

References

Agrawal AA, Conner JK, Rasmann S (2010). Tradeoffs and negative correlations in evolutionary ecology. In: *Evolution since Darwin: the first 150 years*, Sinauer, pp 243–268.

Van Asch M, Julkunen-Tiito R, Visser ME (2010). Maternal effects in an insect herbivore as a mechanism to adapt to host plant phenology.

638 *Funct Ecol* **24**: 1103–1109.

639 Bernardo J (1996). Maternal effects in animal ecology. *Am Zool* **36**: 83–105.

640 Cahenzli F, Erhardt A (2013). Transgenerational acclimatization in an
641 herbivore-host plant relationship. *Proc R Soc B Biol Sci* **280**.

642 Cahenzli F, Wenk BA, Erhardt A, Rosenheim JA (2015). Female butterflies
643 adapt and allocate their progeny to the host-plant quality of their own
644 larval experience. *Ecology* **96**: 1966–1973.

645 Forbes AA, Devine SN, Hippee AC, Tvedte ES, Ward AKG, Widmayer HA, *et*
646 *al.* (2017). Revisiting the particular role of host shifts in initiating insect
647 speciation. *Evolution (N Y)* **71**: 1126–1137.

648 Fox CW (1993a). Maternal and genetic influences on egg size and larval
649 performance in a seed beetle. *Heredity* **73**: 509–517.

650 Fox CW (1993b). A quantitative genetic analysis of oviposition preference
651 and larval performance on two hosts in the bruchid beetle,
652 *Callosobruchus maculatus*. *Evolution* **47**: 166–175.

653 Fox CW, Bush ML, Roff DA, Wallin WG (2004). Evolutionary genetics of
654 lifespan and mortality rates in two populations of the seed beetle,
655 *Callosobruchus maculatus*. *Heredity* **92**: 170–181.

656 Fox CW, Bush ML, Wallin WG (2003). Maternal age affects offspring

657 lifespan of the seed beetle. *Funct Ecol* **17**: 811–820.

658 Fox CW, Dingle H (1994). Dietary mediation of maternal age effects on
659 offspring performance in a seed beetle (Coleoptera: Bruchidae). *Funct*
660 *Ecol* **8**: 600–606.

661 Fox CW, Messina FJ (2018). Evolution of larval competitiveness and
662 associated life-history traits in response to host shifts in a seed beetle.
663 *J Evol Biol* **31**: 302–313.

664 Fox CW, Savalli UM (1998). Inheritance of environmental variation in body
665 size: Superparasitism of seeds affects progeny and grandprogeny body
666 size via a nongenetic maternal effect. *Evolution* **52**: 172.

667 Fox CW, Stillwell RC, Amarillo-Suárez AR, Czesak ME, Messina FJ (2004).
668 Genetic architecture of population differences in oviposition
669 behaviour of the seed beetle Callosobruchus maculatus. *J Evol Biol* **17**:
670 1141–1151.

671 Fox CW, Thakar MS, Mousseau TA (1997). Egg size plasticity in a seed
672 beetle: an adaptive maternal effect. *Am Nat* **149**: 149–163.

673 Garcia-Gonzalez F, Simmons LW, Tomkins JL, Kotiaho JS, Evans JP (2012).
674 Comparing evolvabilities: Common errors surrounding the calculation
675 and use of coefficients of additive genetic variation. *Evolution* **66**:
676 2341–2349.

677 Gompert Z, Jahner JP, Scholl CF, Wilson JS, Lucas LK, Soria-Carrasco V, *et al.*
678 (2015). The evolution of novel host use is unlikely to be constrained by
679 trade-offs or a lack of genetic variation. *Mol Ecol* **24**: 2777–2793.

680 Gompert Z, Messina FJ (2016). Genomic evidence that resource-based
681 trade-offs limit host-range expansion in a seed beetle. *Evolution* **70**:
682 1249–1264.

683 Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010). A meta-analysis of
684 preference-performance relationships in phytophagous insects. *Ecol*
685 *Lett* **13**: 383–393.

686 Guntrip J, Sibly RM, Holloway GJ (1997). The effect of novel environment
687 and sex on the additive genetic variation and covariation in and
688 between emergence body weight and development period in the
689 cowpea weevil, *Callosobruchus maculatus* (Coleoptera, Bruchidae).
690 *Heredity* **78**: 158–165.

691 Hadfield JD (2010). MCMC methods for multi-response generalized linear
692 mixed models: The MCMCglmm R package. *J Stat Softw* **33**.

693 Houle D (1992). Comparing evolvability and variability of quantitative traits.
694 *Genetics* **130**: 195–204.

695 Joshi A, Thompson JN (1995). Trade-offs and the evolution of host
696 specialization. *Evol Ecol* **9**: 82–92.

697 Kruuk LEB, Hadfield JD (2007). How to separate genetic and environmental
698 causes of similarity between relatives. *J Evol Biol* **20**: 1890–1903.

699 Lind MI, Berg EC, Alavioon G, Maklakov AA (2015). Evolution of differential
700 maternal age effects on male and female offspring development and
701 longevity. *Funct Ecol* **29**: 104–110.

702 Lynch M, Walsh B (1998). *Genetics and Analysis of Quantitative Traits*.
703 Sinauer, pp. 980.

704 Magalhães S, Blanchet E, Egas M, Olivieri I (2011). Environmental effects on
705 the detection of adaptation. *J Evol Biol* **24**: 2653–2662.

706 Matsumura S, Arlinghaus R, Dieckmann U (2012). Standardizing selection
707 strengths to study selection in the wild: A critical comparison and
708 suggestions for the future. *Bioscience* **62**: 1039–1054.

709 Messina FJ (2004a). Predictable modification of body size and competitive
710 ability. *Evolution* **58**: 2788–2797.

711 Messina FJ (2004b). How labile are the egg-laying preferences of seed
712 beetles? *Ecol Entomol* **29**: 318–326.

713 Messina FJ, Fry JD (2003). Environment-dependent reversal of a life history
714 trade-off in the seed beetle *Callosobruchus maculatus*. *J Evol Biol* **16**:
715 501–509.

716 Messina FJ, Lish AM, Gompert Z (2018). Variable responses to novel hosts
717 by populations of the seed beetle *Callosobruchus maculatus*
718 (Coleoptera: Chrysomelidae: Bruchinae). *Environ Entomol* **47**: 1194–
719 1202.

720 Messina FJ, Morrey JL, Mendenhall M (2007). Why do host-deprived seed
721 beetles 'dump' their eggs? *Physiol Entomol* **32**: 259–267.

722 Messina FJ, Slade AF (1997). Inheritance of host-plant choice in the seed
723 beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Ann*
724 *Entomol Soc Am* **90**: 848–855.

725 Mitchell R (1975). The evolution of oviposition tactics in the bean weevil,
726 *Callosobruchus maculatus* (F.). *Ecology* **56**: 696–702.

727 Mousseau TA, Roff DA (1987). Natural selection and the heritability of
728 fitness components. *Heredity* **59**: 181–197.

729 Paukku S, Kotiaho JS (2008). Female oviposition decisions and their impact
730 on progeny life-history traits. *J Insect Behav* **21**: 505–520.

731 Price TN, Leonard A, Lancaster LT (2017). Warp-speed adaptation to novel
732 hosts after 300 generations of enforced dietary specialisation in the
733 seed beetle *Callosobruchus maculatus* (Coleoptera: Chrysomelidae:
734 Bruchinae). *Eur J Entomol* **114**: 257–266.

735 Räsänen K, Kruuk LEB (2007). Maternal effects and evolution at ecological

736 time-scales. *Funct Ecol* **21**: 408–421.

737 Rossiter M (1996). Incidence and consequences of inherited environmental
738 effects. *Annu Rev Ecol Syst* **27**: 451–476.

739 Saltz JB, Bell AM, Flint J, Gomulkiewicz R, Hughes KA, Keagy J (2018). Why
740 does the magnitude of genotype-by-environment interaction vary?
741 *Ecol Evol* **8**: 6342–6353.

742 Stillwell RC, Wallin WG, Hitchcock LJ, Fox CW (2007). Phenotypic plasticity
743 in a complex world: Interactive effects of food and temperature on
744 fitness components of a seed beetle. *Oecologia* **153**: 309–321.

745 Teplitsky C, Mills JA, Yarrall JW, Merilä J (2009). Heritability of fitness
746 components in a wild bird population. *Evolution* **63**: 716–726.

747 Vega-Trejo R, Head ML, Jennions MD, Kruuk LEB (2018). Maternal-by-
748 environment but not genotype-by-environment interactions in a fish
749 without parental care. *Heredity* **120**: 154–167.

750 Via S, Lande R (1985). Genotype-environment interaction and the evolution
751 of phenotypic plasticity. *Evolution* **39**: 505–522.

752 de Villemereuil P, Schielzeth H, Nakagawa S, Morrissey MB (2016). General
753 methods for evolutionary quantitative genetic inference from
754 generalized mixed models. *Genetics* **204**: 1281–1294.

Wilson K, Hill L (1989). Factors affecting egg maturation in the bean weevil *Callosobruchus maculatus*. *Physiol Entomol* **14**: 115–126.

Tables

Table 1. Variance-covariance structure and main effects estimates based on the minimal models. Phenotypic variance decomposition based on these estimates is presented in Table 2. (A) gives model summary for larval survival and life history in male offspring (sons); (B) is for life history of female offspring (daughters) and their host preference. Estimates whose credible interval does not overlap zero are emphasised in bold. Note that residual variance for both host types in the binomial model of larval survival was set to 1 by default. The host type effect needs to be added to the intercept (value for original host type) to obtain an estimate for the effect in the novel host type.

Table 2. Phenotypic variance partitioning. Estimates of maternal effects proportion (m^2), heritability (h^2), cross-environmental correlations (r_M and r_G) and evolvability (CV_A) in sons (A) and daughters (B). Heritability and evolvability estimates for larval survival and daughter host preference (asterisk) were recalculated to the observed data scale using the package

774 'QGglmm' (de Villemereuil *et al.*, 2016). Bold emphasis is put on the
775 estimates with credible intervals not overlapping zero.

776

777 **Table 3.** Fixed-effects estimates from the full models. (A) gives larval
778 survival and life-history traits in male offspring (sons); (B) is for life history
779 of female offspring and their host preference. Bold emphasis is put on
780 estimates with credible intervals not overlapping zero. The host type effect
781 needs to be added to the intercept (value for original host type) to obtain
782 an estimate for the effect in the novel host type. The same applies to the
783 host-specific interactions.

Table 1. Variance-covariance structure and fixed-effects estimates based on the minimal models.

(A)

	Trait	Larval survival		Duration of larval development		Adult body mass		Adult lifespan	
	Sex (Sample size)	juveniles (N = 2877)		sons (N = 1189)		sons (N = 1200)		sons (N = 1195)	
	Parameter	Estimate	CrI	Estimate	CrI	Estimate	CrI	Estimate	CrI
Variance-covariance	V_{sire} orig	0.002	(0.000,0.361)	0.001	(0.000,0.101)	0.001	(0.000,0.103)	0.053	(0.000,0.120)
	V_{dam} orig	0.403	(0.000,0.946)	0.107	(0.000,0.207)	**0.129**	(0.044,0.221)	**0.110**	(0.037,0.205)
	V_{res} orig	1	-	**0.941**	(0.857,1.136)	**0.855**	(0.754,0.968)	**0.736**	(0.687,0.886)
	V_{sire} novel	0.004	(0.000,1.083)	**0.081**	(0.008,0.131)	0.001	(0.000,0.110)	**0.107**	(0.022,0.226)
	V_{dam} novel	0.005	(0.000,0.654)	**0.057**	(0.004,0.127)	**0.138**	(0.075,0.238)	**0.138**	(0.051,0.258)
	V_{res} novel	1	-	**0.420**	(0.367,0.482)	**0.500**	(0.438,0.575)	**0.642**	(0.570,0.741)
	COV_{sire} orig-novel	0.000	(-0.179,0.266)	-0.002	(-0.040,0.032)	0.000	(-0.008,0.083)	0.047	(-0.002,0.130)
	COV_{dam} orig-novel	-0.001	(-0.140,0.425)	0.017	(-0.025,0.073)	**0.096**	(0.043,0.181)	**0.090**	(0.035,0.178)
Main effects	Intercept (orig HOST)	**2.567**	(2.203,3.083)	**0.302**	(0.160,0.476)	**-0.449**	(-0.602,-0.228)	**-0.351**	(-0.543,-0.17)
	novel HOST	**0.502**	(0.133,0.945)	**-0.814**	(-0.920,-0.659)	**0.665**	(0.556,0.785)	**0.496**	(0.355,0.594)
	bean mass	**-0.193**	(-0.303,-0.013)	**0.086**	(0.026,0.121)	-0.022	(-0.078,0.019)	**-0.080**	(-0.127,-0.022)
	mating order	0.026	(-0.186,0.139)	0.042	(-0.015,0.102)	0.041	(-0.033,0.112)	0.051	(-0.012,0.133)
	day mated	0.088	(-0.091,0.282)	**0.167**	(0.097,0.240)	**0.119**	(0.062,0.219)	**0.110**	(0.010,0.193)

(B)

	Trait	Host preference		Duration of larval development		Adult body mass		Adult lifespan	
	Sex (sample size)	daughters (N = 514)		daughters (N = 1221)		daughters (N = 1228)		daughters (N = 1224)	
	Parameter	Estimate	CrI	Estimate	CrI	Estimate	CrI	Estimate	CrI
Variance-covariance	V_{sire} orig	0.000	(0.000,0.006)	0.001	(0.000,0.082)	0.001	(0.000,0.122)	**0.082**	(0.012,0.186)
	V_{dam} orig	0.000	(0.000,0.005)	**0.092**	(0.016,0.197)	**0.133**	(0.077,0.275)	**0.104**	(0.038,0.229)
	V_{res} orig	**0.034**	(0.023,0.048)	**0.799**	(0.713,0.931)	**0.674**	(0.596,0.782)	**0.721**	(0.656,0.865)
	V_{sire} novel	0.000	(0.000,0.008)	0.018	(0.000,0.075)	**0.088**	(0.004,0.162)	**0.116**	(0.047,0.233)
	V_{dam} novel	0.000	(0.000,0.006)	**0.078**	(0.025,0.143)	**0.117**	(0.070,0.229)	**0.093**	(0.011,0.166)
	V_{res} novel	**0.033**	(0.024,0.055)	**0.397**	(0.351,0.459)	**0.440**	(0.384,0.492)	**0.660**	(0.589,0.767)
	COV_{sire} orig-novel	0.000	(-0.002,0.003)	0.000	(-0.011,0.045)	0.035	(-0.004,0.110)	**0.077**	(0.015,0.160)
	COV_{dam} orig-novel	0.000	(-0.001,0.002)	0.037	(-0.004,0.093)	**0.146**	(0.069,0.205)	**0.064**	(0.012,0.142)
Main effects	Intercept (orig HOST)	**-0.426**	(-0.567,-0.329)	**0.428**	(0.306,0.614)	**-0.582**	(-0.757,-0.377)	**-0.215**	(-0.404,-0.043)
	novel HOST	**-0.254**	(-0.339,-0.172)	**-1.001**	(-1.104,-0.876)	**0.988**	(0.862,1.073)	**0.537**	(0.433,0.671)
	bean mass	0.007	(-0.036,0.049)	**0.083**	(0.036,0.121)	**-0.079**	(-0.119,-0.034)	-0.021	(-0.070,0.034)
	mating order	0.016	(-0.025,0.059)	0.020	(-0.012,0.101)	0.032	(-0.054,0.087)	-0.045	(-0.112,0.026)
	day mated	**-0.059**	(-0.099,-0.007)	**0.242**	(0.168,0.298)	0.088	(-0.004,0.176)	0.049	(-0.033,0.171)

Table 2. Phenotypic variance partitioning.

(A)

Trait	**Larval survival**			**Duration of larval development**		**Adult body mass**		**Adult lifespan**	
Sex	juveniles			sons		sons		sons	
Parameter	**Estimate**	**CrI**	**Estimate***	**Estimate**	**CrI**	**Estimate**	**CrI**	**Estimate**	**CrI**
V_M orig	0.437	(-0.237,0.970)	-	0.088	(-0.086,0.212)	0.110	(-0.046,0.214)	0.062	(-0.065,0.185)
m^2 orig	0.158	(-0.144,0.500)	-	0.079	(-0.070,0.191)	0.114	(-0.046,0.199)	0.064	(-0.065,0.193)
V_M novel	-0.271	(-1.161,0.549)	-	-0.016	(-0.097,0.115)	0.084	(-0.008,0.243)	0.043	(-0.143,0.228)
m^2 novel	-0.303	(-0.523,0.314)	-	0.002	(-0.180,0.193)	0.203	(-0.008,0.326)	0.046	(-0.160,0.236)
r_M	-	-	-	-	-	-	-	-	-
h^2 orig	0.006	(0.000,0.862)	0.029	0.001	(0.000,0.364)	0.002	(0.000,0.394)	0.215	(0.000,0.484)
h^2 novel	1.431	(0.000,1.962)	0.095	**0.472**	(0.116,0.938)	0.004	(0.000,0.593)	**0.471**	(0.072,0.922)
r_G	-0.499	(-0.961,0.850)	-	-0.228	(-0.935,0.607)	0.977	(-0.458,0.999)	**0.989**	(0.468,0.999)
CV_A orig	-	-	-	0.008	(0.000,0.020)	**0.087**	(0.001,0.183)	**0.027**	(0.008,0.044)
CV_A novel	-	-	-	**0.019**	(0.009,0.025)	**0.126**	(0.003,0.171)	**0.036**	(0.016,0.050)

(B)

Trait	**Host preference**			**Duration of larval development**		**Adult body mass**		**Adult lifespan**	
Sex	daughters			daughters		daughters		daughters	
Parameter	**Estimate**	**CrI**	**Estimate***	**Estimate**	**CrI**	**Estimate**	**CrI**	**Estimate**	**CrI**
V_M orig	0.000	(-0.005,0.007)	-	0.090	(-0.042,0.200)	0.095	(-0.012,0.281)	0.030	(-0.120,0.199)
m^2 orig	0.000	(-0.140,0.169)	-	0.087	(-0.046,0.207)	0.142	(-0.014,0.292)	0.031	(-0.118,0.201)
V_M novel	0.000	(-0.009,0.006)	-	0.037	(-0.031,0.138)	0.079	(-0.071,0.209)	-0.090	(-0.193,0.102)
m^2 novel	0.001	(-0.161,0.159)	-	0.070	(-0.064,0.253)	0.081	(-0.121,0.289)	-0.119	(-0.214,0.093)
r_M	-	-	-	-	-	-	-	-	-
h^2 orig	0.004	(0.000,0.572)	0.004	0.002	(0.000,0.344)	0.003	(0.000,0.518)	**0.367**	(0.017,0.700)
h^2 novel	0.005	(0.000,0.644)	0.004	0.003	(0.000,0.550)	**0.482**	(0.068,0.947)	**0.621**	(0.247,0.980)
r_G	0.832	(-0.872,0.999)	-	0.727	(-0.727,0.999)	**0.937**	(0.004,0.999)	**0.876**	(0.394,0.999)
CV_A orig	-	-	-	0.008	(0.000,0.018)	**0.084**	(0.002,0.121)	**0.025**	(0.013,0.040)
CV_A novel	-	-	-	**0.012**	(0.002,0.019)	**0.091**	(0.044,0.134)	**0.032**	(0.018,0.038)

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

(A)

	Trait	Larval survival		Duration of larval development		Adult body mass		Adult lifespan	
	Sex (Sample size)	juveniles (N = 2877)		sons (N = 1189)		sons (N = 1200)		sons (N = 1197)	
	Parameter	Estimate	CrI	Estimate	CrI	Estimate	CrI	Estimate	CrI
Host	Intercept (orig HOST)	**2.542**	(2.259,3.114)	**0.261**	(0.145,0.474)	**-0.392**	(-0.602,-0.244)	**-0.405**	(-0.548,-0.182)
	novel HOST	**0.554**	(0.101,0.920)	**-0.810**	(-0.925,-0.646)	**0.653**	(0.570,0.783)	**0.483**	(0.351,0.580)
	bean mass (orig)	-0.177	(-0.327,0.045)	**0.094**	(0.007,0.170)	-0.060	(-0.146,0.009)	**-0.090**	(-0.160,-0.010)
	Interaction: bean mass (novel)	-0.102	(-0.376,0.197)	-0.026	(-0.111,0.089)	0.029	(-0.031,0.157)	0.063	(-0.083,0.122)
Dam properties	dam mating order	-0.012	(-0.178,0.153)	0.043	(-0.016,0.098)	0.046	(-0.035,0.111)	0.060	(-0.017,0.128)
	day mated	0.164	(-0.092,0.370)	0.097	(-0.005,0.200)	**0.131**	(0.044,0.248)	**0.126**	(0.012,0.220)
	Interaction: day mated (novel)	-0.198	(-0.513,0.212)	0.081	(-0.028,0.233)	-0.017	(-0.128,0.081)	-0.034	(-0.154,0.072)
	dam preference for cowpea (orig)	-0.043	(-0.219,0.216)	-0.031	(-0.136,0.057)	0.012	(-0.104,0.087)	0.006	(-0.099,0.082)
	Interaction: dam preference (novel)	0.105	(-0.179,0.463)	0.051	(-0.071,0.163)	0.045	(-0.069,0.137)	0.008	(-0.115,0.097)

(B)

	Trait	Host preference		Duration of larval development		Adult body mass		Adult lifespan	
	Sex (Sample size)	daughters (N = 514)		daughters (N = 1221)		daughters (N = 1228)		daughters (N = 1226)	
	Parameter	**Estimate**	**CrI**	**Estimate**	**CrI**	**Estimate**	**CrI**	**Estimate**	**CrI**
Host	Intercept (orig HOST)	**-0.457**	(-0.553,-0.337)	**0.412**	(0.277,0.600)	**-0.558**	(-0.737,-0.369)	**-0.188**	(-0.409,-0.042)
	novel HOST	**-0.228**	(-0.333,-0.166)	**-0.983**	(-1.094,-0.868)	**0.981**	(0.863,1.074)	**0.571**	(0.429,0.679)
	bean mass (orig)	-0.004	(-0.054,0.062)	**0.111**	(0.053,0.203)	**-0.125**	(-0.198,-0.055)	-0.073	(-0.143,0.002)
	Interaction: bean mass (novel)	0.013	(-0.074,0.088)	-0.044	(-0.167,0.024)	0.103	(-0.008,0.171)	0.047	(-0.018,0.176)
Dam properties	dam mating order	0.017	(-0.026,0.057)	0.036	(-0.017,0.102)	0.025	(-0.049,0.090)	-0.033	(-0.116,0.022)
	day mated	**-0.059**[#]	(-0.122,0.000)	**0.255**	(0.148,0.352)	**0.127**	(0.019,0.240)	0.126	(-0.001,0.220)
	Interaction: day mated (novel)	0.017	(-0.077,0.091)	-0.011	(-0.127,0.107)	-0.085	(-0.197,0.020)	-0.074	(-0.220,0.029)
	dam preference for cowpea (orig)	-0.001	(-0.051,0.064)	-0.029	(-0.125,0.048)	**0.103**	(0.012,0.203)	-0.014	(-0.110,0.078)
	Interaction: dam preference (novel)	-0.022	(-0.110,0.059)	0.029	(-0.062,0.143)	**-0.096**	(-0.196,-0.009)	-0.003	(-0.132,0.085)

[#] marginally important (upper limit of the Credible Interval = -0.0003839)