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

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

In this study, we investigated the presence of maternal effects, as well as the potential for an interaction between maternal effects and her offspring's rearing environment on general offspring life-history traits, as well as her daughters' egg laying preferences on different hosts in the seed beetle, *Callosobruchus maculatus* (Coleoptera: Chrysomelidae). *Callosobruchus maculatus* is a common pest to legume storages 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 individual eggs on host beans shortly after copulation (Mitchell, 1975). Host choice is crucial as the larvae cannot move between individual beans. Incorrect decisions on where a female chooses to lay her eggs inevitably lead to lower quality or even non-viable 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. Depending on the temperature and host species, adults typically emerge within 26-36 days of oviposition (Fox *et al.*, 2003; Messina, 2004a). *Callosobruchus maculatus* shows profound sexual dimorphism in life-history traits with males emerging earlier, being smaller and living shorter than females (Guntrip *et al.*, 1997; Fox, Bush, *et al.*, 2004).

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

1) There would be strong maternal effects on offspring life history traits (Fox, 1993a; Messina and Fry, 2003). This led us to predict that 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

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

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

Establishing the parental generation (P). To obtain virgin males and females for the parental generation (P), we exposed approximately 2000 un-infested cowpea beans to stock beetles for a period of 48 h. Each bean was then placed in an individual Eppendorf tube (with a pinhole for airflow) and had 5-8 eggs on its surface (a density which is usual for our stock). Once isolated, we monitored these beans until adults began to emerge. We collected virgin beetles each morning and used them in our experiment on the same day. We knew that beetles were virgins as they were either the only beetle to have emerged that day, or all beetles that had emerged were of the same sex. Every evening, we discarded any beetles that had emerged during that day. Using the parental beetles that emerged each morning, we mated males and females according to a full-sib/half-sib breeding design: each male was sequentially mated with four random females over the day and the mating order was noted (similar to Fox *et al.* (2003)). We aimed for a total of 89 families (sires) with 356 dams. Pairs that did not copulate within 30 min were separated for half an hour before being placed together for another mating attempt. Each female was weighed prior to mating to the nearest 0.001 mg (Cubis Ultra-Micro balance, Sartorius Lab Instruments GmbH., Goettingen, DEU). All matings took place over six days ('day mated', range 1-6, see *Partitioning of Phenotypic Variance*). There is therefore a positive correlation between parental age (egg to adulthood) and 'day mated', but it is imperfect because parents emerged from eggs initially laid over two days (i.e. 48 hours; see above). There is no correlation between 'day mated' and adult parental age because all matings occurred on the day that the parents emerged.

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

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

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

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

Measurement of offspring (F1) traits. When an offspring emerged, the date was recorded, and it was sexed and weighed (to the nearest 0.001 mg), and the bean was removed 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 sample size was determined a priori based on power analysis from Lynch and Walsh (1998) to create 89 families (89 sires with 356 dams) and try to obtain 10 offspring per dam per host type (i.e. 7 120 offspring). The final sample size is lower due to unsuccessful matings or too few eggs being laid. We analysed data for sons and daughters separately due to their marked sexual dimorphism which invariably leads to strong interactions between sex and other effects. We only included offspring of dams that produced offspring reared on both host types, and we removed offspring with extreme values (>3 standard deviations (SD) from the mean). We collected data on four offspring life-history traits: (egg-to-emergence) 'larval survival' (dead or emerged; N = 2 877), 'duration of larval development' (number of days between oviposition and offspring emergence; N = 1 221 daughters and 1 189 sons), 'body mass' (weight at emergence in mg; N = 1 228 daughters and 1 200 sons) and 'adult lifespan' (number of days between offspring emergence and death;

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

Partitioning of phenotypic variance. To determine the strength of maternal effects on offspring traits in *C. maculatus* (Prediction 1) and whether maternal effects depend on the offspring rearing environment, (i.e. the existence of a M×E interaction - Prediction 2), we built a 'minimal model' containing only fixed effects directly attributable to the experimental design. These were 'host type' (original/novel), 'bean mass' (standardized within each host type to zero mean and 1 SD variance), 'dam mating order' (i.e. dam position in sire's mating sequence, 1 to 4), and 'day mated' (1-6). We did not fit 'day mated' as a random effect because it resulted in overparametrized models that produced unstable and weak variance estimates. As random effects, we used terms that reflected the nested breeding design. We defined between-sire (family) variance as 'sire ID', between-dam variance as 'dam ID' nested inside sire ID, and between-individual variation as 'residual' variance.

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

Daughter host preference data was fitted differently, because we wanted to account for variation in the total number of eggs laid and not just fit the preference ratio (values 0-1) as a response. We again used a bivariate model, with the number of eggs on cowpea in the first column of the response, and the total number of eggs laid in the second column. To estimate variance components separately for offspring from each host type, we specified interactions with random effects: that is between host type and sire (HOST:sire ID); between host type and dam (HOST:dam ID); and between host type and the residual term.

Based on the outputs from the minimal models for each trait, we then performed the phenotypic variance partitioning and calculated the maternal-effects proportion (m^2) and the cross-environmental maternal-effects correlation (M×E) (r_M), narrow-sense heritability (h^2), evolvability (CV_A) and the cross-environmental correlation for additive genetic effects (G×E) (r_G). We used maternal effects proportion, $m^2 = V_M/V_{total} = (V_{dam}-V_{sire})/(V_{sire}+V_{dam}+V_{residual})$, to quantify the importance of maternal effects (Messina & Fry, 2003). The correlation between maternal effects for the two host types (M×E) was $r_M = COV_{M\ original\text{-}novel}/\surd(V_{M\ original})*\surd(V_{M\ novel})$, where $COV_{M\ original\text{-}novel} = COV_{dam\ original\text{-}novel} - COV_{sire\ original\text{-}novel}$. We calculated heritability as $h^2 = V_A/V_{total} = 4*V_{sire}/(V_{sire}+V_{dam}+V_{residual})$ (Lynch and Walsh, 1998), assuming dominance and epistatic effects were negligible. Evolvability was defined by Houle (1992) as $CV_A = \surd V_A/\mu = \surd(4*V_{sire})/\mu$, where μ is the mean of a trait (Garcia-Gonzalez *et al.*, 2012). Evolvability standardizes additive genetic variance over the trait mean and is therefore useful to compare the potential evolutionary response among traits, unlike heritability which is conditional on the amount of residual phenotypic variation (Hansen et al., 2011). The correlation between additive genetic effects on the two host types (G×E) was $r_G = COV_{sire\ original\text{-}novel}/\sqrt{(V_{sire\ original})}*\sqrt{(V_{sire\ novel})}$.

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

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

To fit the MCMC models, we used locally uninformative inverse-Wishart priors for the random-effects variance (G) with expected variance-covariance matrix at limit 'V' = 1 on the diagonal (i.e. two values – one per each host), and the degree of freedom 'nu' = 1.002. We also added parameter-expanded priors 'α mu' = 0 and 'α V' = 1 000 on diagonal to increase mixing and effective sample size (Hadfield, 2010). Priors for residual variance (R) were set as V = 1 on diagonal and nu = 1.002. In the analysis of survival, the residual variance had to be fixed to 1, so that the binomial mixed-effects model could be estimated (Hadfield, 2010). For fixed effects, we retained default priors with variance = 0 and mean = 10^{10}. To generate posterior distributions from the minimal model, we ran 120 000 iterations with burn-in of 20 000 and thinning interval of 100, so that we obtained an effective sample size of 1 000. In the full model, we increased number of iterations to 240 000, burn-in 40 000 and thinning interval to 200 for the Gaussian traits. For daughter host preference, the setup was 550 000 iterations with burn-in of 50 000 and 500 for the thinning interval. For model of larval survival, we increased the iterations to 1 200 000 with a burn-in of 200 000 and thinning interval of 1 000 as we were aiming for an autocorrelation <0.1 at the lag corresponding to the thinning interval (Wilson et al., 2010). Model convergence was assessed by visual examination of the traces using function ‘plot(mcmc.model)’. Estimates of heritability in larval survival and daughter host egg laying preference on the observed data scale were computed from the latent scale variance estimates using the package ‘QGglmm’ (de Villemereuil *et al.*, 2016). We always interpreted the outcome of the complete model (without simplification) and assessed the importance of individual model 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.

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

We recorded highly positive correlations of additive genetic effects (r_G) for offspring performance on the two host types (Table 2). The only exceptions were for the larval survival and development duration of sons, which exhibited negative genetic correlation but with wide credible intervals overlapping zero (Table 2). The within-family larval survival and development duration of sons on the novel host did not correspond to that on the original host, potentially suggesting a Genotype-by-Environment interaction (G×E).

Table 2. Phenotypic variance partitioning.

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

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

Missing maternal effects. We were unable to formally test for a difference in the relative importance of maternal effects in different environments, because maternal effects were very weak in both host types. Intriguingly, previous studies on *C. maculatus* have reported strong maternal effects on male development duration (Fox, 1993a), female fecundity, adult body mass and lifespan (Messina and Fry, 2003). However, these non-genetic maternal effects in experimental studies with *C. maculatus* mostly seem to stem from variation in maternal age (Fox and Dingle, 1994; Fox *et al.*, 2003; Lind *et al.*, 2015). Older *C. maculatus* females have previously been shown to produce offspring with lower egg-to-adult survival, longer larval development (Fox *et al.*, 2003; Lind *et al.*, 2015) and a shorter lifespan (Lind *et al.*, 2015). In our study, neither male nor female adult parental age varied as we collected parental beetles and mated them on the day of emergence. While mating day, which is imperfectly correlated with lifetime age (i.e. zygote to emergence), had notable effects on several offspring life-history traits and daughters' host egg laying preference, removing it from the model did not increase estimates of maternal effect proportions (Supplementary Table 2). This suggests that mating day acts like a 'block' factor that accounts for experimental variation that affected the entire family sired by a given sire (and not to lifetime age *per se*) due to stochastic daily fluctuations of unknown origin. Non-genetic maternal effects due to variation in age were therefore eliminated by mating dams of the same age to the single sire in each family.

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

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

The novel host type appeared to be better for offspring. Offspring life-history traits differed between the two host types in an unexpected way with offspring performing better on the novel host type. While offspring survival was almost 90 % on cowpeas (the original host), it was even higher on the novel host (mung bean), exceeding 90 %. There was no obvious cost as the duration of larval development was shorter on mung beans, and the beetles that emerged were larger and lived longer as adults. It is not straightforward, however, to tell which host species is generally better for *C. maculatus*, because it depends on other factors such as the level of competition (Messina, 2004a; Fox and Messina, 2018), temperature (Stillwell *et al.*, 2007) and the population's evolutionary history (Messina, 2004a).

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

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

Second, we note that the lower performance of offspring on cowpea might have been because, following the preference trial, females were provided with mung beans to lay eggs, and only after that with cowpea. Eggs laid late in the laying sequence have previously been shown to be of lower quality in some insects (Rossiter, 1996). The lifetime fecundity of *C. maculatus* is 60-80 eggs and depends on female body size, and mate and host availability (Mitchell, 1975; Wilson and Hill, 1989; Messina and Fry, 2003). The dams in our experiment laid around 30 eggs per 24 h and were therefore probably still far from nearing the end of egg laying in our experiment. In addition, past studies suggest there is no negative effect of maternal age on offspring performance on the first day of female reproductive life (Fox and Dingle, 1994). We therefore suggest that the sequence of host type presentation for egg laying is very unlikely to explain poorer offspring performance on cowpeas.

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

Previous studies show that strains of *C. maculatus* maintained for > 40 generations on mung bean or cowpea exhibit a strong preference for their recent host type (Messina, 2004b). (Fox, Stillwell, *et al.*, 2004) used different host strains to demonstrate that there is no immediate effect of the current host type (i.e. switching a strain to another host for 1 generation) on the host preference. Variation in host preference in *C. maculatus* is mainly due to additive genetic effects, but is also influenced by dominance and epistasis (Fox, 1993b; Fox, Stillwell, *et al.*, 2004). However, we found that while daughters reared on cowpea preferred cowpea over a novel host (mung bean), those reared on mung beans showed no preference for either host type. This suggests that there might be a G×E interaction affecting host egg laying preferences and more generations would be necessary to see whether the host preference evolves after the host switch (as in Fox, Stillwell, *et al.* (2004) or Messina (2004b)).

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

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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

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

Table 3. Fixed-effects estimates from the full models. (A) gives larval survival and life-history traits in male offspring (sons); (B) is for life history of female offspring and their host preference. Bold emphasis is put on estimates with credible intervals not overlapping zero. 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. The same applies to the 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)