



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

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Abstract

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

Introduction

Maternal effects modify phenotypes that undergo selection and are therefore a potentially important evolutionary force (Mousseau and Fox 1998; Räsänen and Kruuk 2007; Moore

et al. 2019). They may either facilitate adaptation to novel environments (Fox and Savalli 2000; Leftwich et al. 2019), or buffer against changing conditions through trans-generational phenotypic plasticity (Shama et al. 2014). Maternal effects have also been shown to have a range of other implications, such as moderating population dynamics (Plastow and Benton 2009), and increasing niche breadth (Van Asch et al. 2010). Maternal effects, which can arise due to both genetic and environmental variation among mothers, can be defined as 'the causal influence of the maternal genotype or phenotype on the offspring phenotype' (Wolf and Wade 2009). Genetic maternal effects might increase total heritability and facilitate evolution (Wilson et al. 2005; Räsänen and Kruuk 2007), as opposed to phenotypic (environmental) maternal effects. Irrespective of their genetic basis, maternal effects increase the degree of similarity between siblings and may thus bias estimates of direct genetic effects upward if ignored (Räsänen and Kruuk 2007; McAdam et al. 2014). This can lead to an over-estimation of the likely response to selection (McGlathlin and Galloway 2014).

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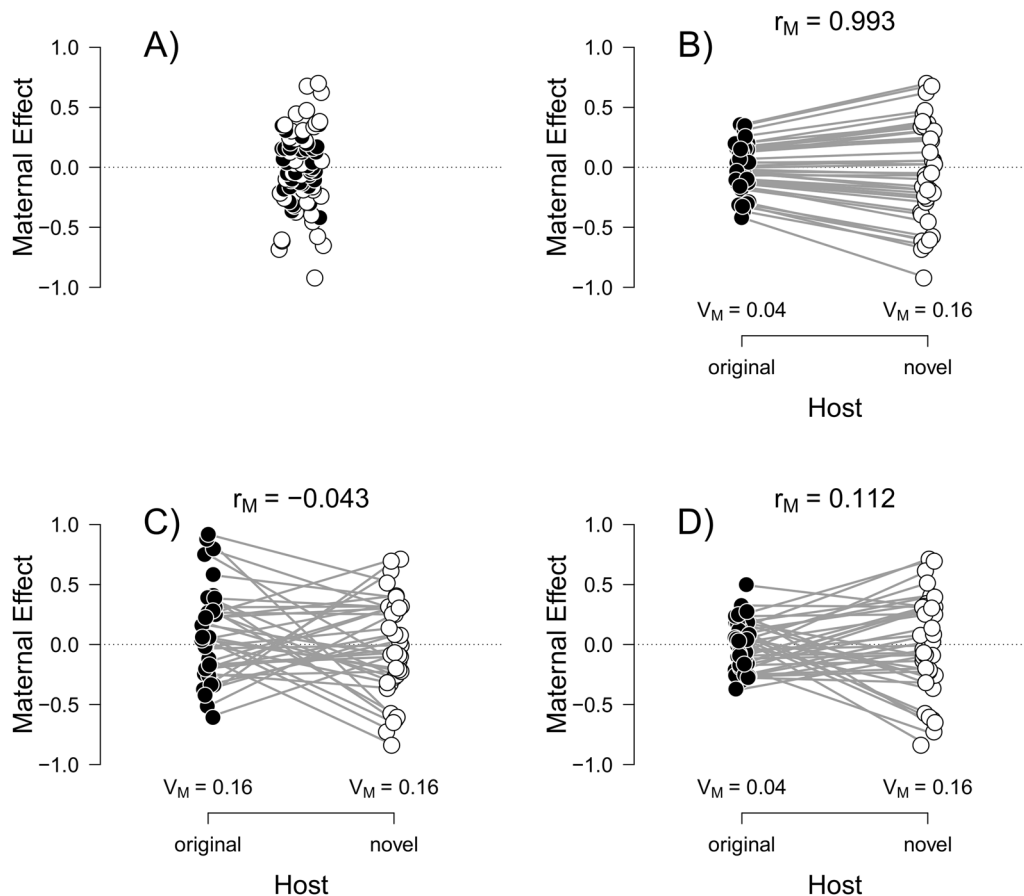


Fig. 1 Illustration of how maternal effects might differ between environments (host beans in our study). **A** Shows that ignoring the potential for environment-specific maternal effects, as indicated by the colour of points representing maternal effects in the original (black points) and the novel host (white points), could be misleading. **B** Represents a scenario where variance due to maternal effects (V_M) differs between the environments, i.e., the first type of Maternal-by-

Environment interaction ($M \times E$). **C** Illustrates the other type of $M \times E$ where the rank of maternal effects differs between the hosts. The evidence for the shift in ranking comes from the low cross-environmental correlation in maternal effects (r_M) despite the maternal effects variance (V_M) being comparable between the hosts. **D** represents a combination of (**B**) and (**C**).

Maternal effects are often environment sensitive (Rositter 1998; Galloway 2005; Räsänen and Kruuk 2007; McAdam et al. 2014). It is unclear, however, whether challenging or favourable conditions will result in stronger maternal effects (Charmantier and Garant 2005; Rowiński and Rogell 2017). A harsher environment is typically assumed to increase variation among offspring from different mothers (Charmantier and Garant 2005; Räsänen and Kruuk 2007). This may, for example, stem from differences in the maternal ability to provision offspring (Parichy and Kaplan 1992). On the other hand, thermal stress or high population densities can reduce offspring differences attributable to the effect of different mothers (Plaistow and Benton 2009; Shama et al. 2014). This environment-dependent variation in maternal effects represents a form of Maternal-by-Environment interaction, $M \times E$ (Fig. 1B). Another form of $M \times E$ occurs, irrespective of change in variance across environments, if individual mothers differ in how they affect their offspring in an environment-specific

manner (Fig. 1C). For example, how levels of carotenoids in great tit females will affect the fate and relative performance of their individual offspring depends on brood size (Berthouly et al. 2008). Higher maternal levels of carotenoids have a negative influence in control nests, but a positive one in nests with increased brood size. This interaction would cause cross-over of the maternal effect reaction norms because of the change in rank of maternal siblings between the two environments (Fig. 1C). In general, a quantitative genetic analysis of potential $M \times E$ can help us to identify the mechanisms that increase similarity between siblings within the same environment beyond genetic relatedness. That analysis would be especially useful if such mechanisms themselves are undescribed, or their role is not fully understood. Many cases probably involve a mixture of changes in ranking and variances (as in Fig. 1D), but a change in relative phenotype of offspring (i.e., shift in the rank) due to maternal effects is less often accounted for. In general, ignoring significant levels of $M \times E$ might bias

estimates of additive genetic effects in a host-specific way and inflate $G \times E$ as shown by Vega-Trejo et al. (2018). This could partially explain the inconsistency in $G \times E$ estimation across different studies (Saltz et al. 2018).

Phytophagous insects are a valuable model group to study life-history evolution, especially when we are interested in trade-offs arising from specialization to a preferred host (Via and Lande 1985; Agrawal 2000). At the same time, phytophagous insects exhibit a variety of maternal effects that influence key life-history traits (Fox and Dingle 1994; Rossiter 1996; Fox and Czesak 2000; Van Asch et al. 2010), including host-specific maternal effects (Fox et al. 1997; Cahenzli and Erhardt 2013). In the current study, we tested for the presence of maternal effects, and the potential for an interaction between maternal effects and offspring rearing host environment, on general offspring life-history traits, as well as daughters' egg-laying preferences for different host types in the seed beetle, *Callosobruchus maculatus* (Coleoptera: Chrysomelidae). This beetle is a common pest of stored legumes worldwide. The larvae feed on multiple legume species (family Fabaceae) with varying degrees of success (Gompert and Messina 2016; Price et al. 2017; Messina et al. 2018). Females lay eggs on host beans shortly after copulation (Mitchell 1975). Host choice is crucial as larvae cannot move between beans. Incorrect decisions about where a female chooses to lay her eggs inevitably lead to lower quality, or even dead, offspring (Mitchell 1975; Messina and Fry 2003; Messina et al. 2007). Larvae hatch 4–5 days after oviposition and burrow into the bean to feed on the endosperm. A single seed commonly harbours multiple larvae. The variable level of larval competition within seeds results in different sized adult beetles, which affects their condition, female reproductive performance and egg size (Fox and Savalli 1998). Depending on the temperature and host species, adults typically emerge within 26–36 days of oviposition (Fox et al. 2003; Messina 2004a). *C. maculatus* shows large sexual dimorphism in life-history traits with males emerging earlier, being smaller, and having a shorter lifespan than females (Guntrip et al. 1997; Fox et al. 2004; Iglesias-Carrasco et al. 2020).

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) and novel (mung bean). We hypothesized that:

- (1) There are strong maternal effects on offspring life-history traits (Fox 1993; Messina and Fry 2003). This led us to predict that a considerable component of offspring phenotypic variation, beyond that due to additive genetic effects, would be due to offspring having different mothers.
- (2) Maternal effects are environment-specific ($M \times E$). Specifically, we predicted that the maternal effects variance would differ between offspring host environments (Fig. 1B), and/or that the rank of offspring from the same mother will change between the two host types decreasing the cross-environmental maternal correlation (Fig. 1C, D).
- (3) Novel host type will be more challenging for offspring. Hence, offspring developing in the novel host would suffer reduced performance compared to those developing in the original host type (i.e., lower larval survival, longer larval development, lower body mass at emergence, and shorter adult lifespan).
- (4) Maternal host preference will predict offspring performance. We predicted that offspring would perform better on the host type preferred by their mother when she laid her eggs.

Methods

Experiment overview

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

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 (*Vigna unguiculata*, Fabaceae) 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 this 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 ~2000 un-infested cowpea beans to

stock beetles for a period of 48 h. Each bean, which had 5–8 eggs on its surface (a density which is usual for our stock), was then placed in an individual Eppendorf tube (with a pinhole for airflow). 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 extra beetles that had emerged during that day to aid in the collection of virgins the following day. Using the 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). 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 (to the nearest 0.001 mg) prior to mating (Cubis Ultra-Micro balance, Sartorius Lab Instruments GmbH., Goettingen, Germany). All matings took place over 6 days ('day mated', range 1–6, see *Model comparison and partitioning of phenotypic variance*). There is therefore a positive correlation between parental developmental duration (egg to adulthood) and 'day mated', but it is imperfect because parents emerged from eggs initially laid over 2 days (i.e. 48 h; 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

We used mung bean (*V. radiata*) as the novel host type. We define the host as novel in that it was 'unlikely to have been experienced by the study population within an evolutionary timescale' (Rowiński and Rogell 2017), approximately 100 generations in our case (see also Kawecki 1995). Cowpea and mung are both suitable hosts for *C. maculatus* (Messina 2004a; Fox and Messina 2018), but populations kept on a specific host for multiple generations usually show better performance on their usual host than a novel host (Messina 2004a).

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 cowpeas (original host) and mung beans (novel host) in a covered Petri dish (ø 5.5 cm). We used proportionally more mung than cowpea beans (8:4) to roughly equalize the available surface area of each bean type (similar to 10:5 used by Messina and Slade 1997). 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 \pm SD bean mass was 294 ± 45 mg for cowpea, and 72 ± 8 mg for mung bean). Females were left to lay eggs for 2 h, after which they were removed and the number of eggs on each bean was counted. Relative preference was calculated as the proportion of the eggs that a female laid on the original host type (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 differences between mung and cowpea-reared offspring 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 (hence laying order) on offspring quality during the first days of laying after emergence (Wasserman and Asami 1985; Fox 1993; Fox and Dingle 1994; Iglesias-Carrasco et al. 2018). Further in a separate experiment looking at oviposition preferences and offspring traits over the same time frame, one of the authors (ZZ) found that the order in which host beans are presented does not have any observable effect on offspring survival, development duration, or body mass at emergence (Supplementary File 1).

Once females had laid eggs on both host types, we collected up to 10 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 scraping off surplus eggs with a scalpel. We then weighed beans, to the nearest 0.001 mg, within 24 h of oviposition 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 (1.3% of all emerged offspring) by approximately 1 day as they emerged sooner than expected. Uncertainty in the date of their emergence could introduce noise into the estimates of larval development duration, body mass at emergence and adult lifespan,

Table 1 Model comparison to estimate the best random effects structure for minimal animal MCMC models.

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

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

so we removed these beetles from the final dataset. Including these early emerging beetles did not qualitatively change our results.

Measurement of offspring (F1) traits

We recorded the date of offspring emergence from the bean, sex and body mass at emergence (to the nearest 0.001 mg), and then removed the bean from the tube. After weighing, the beetle was returned to its tube and checked daily for survival. We also tested the host preference of two newly emerged female offspring per dam raised on each host type (total $N = 4$ /dam). To do this we mated each daughter with a randomly selected male from the stock and then ran an egg-laying preference trial identical to that described above for their mothers. We monitored survival until the death of all emerged offspring (day 79 post-oviposition). At that time, we also censused larval (egg-to-emergence) survival, assuming that larvae in beans from which a beetle had not yet emerged had died.

Sample sizes

Our target sample size was determined a priori based on Lynch and Walsh (1998). We created 89 families (89 sires with 356 dams) and aimed for 10 offspring per dam, per host type (i.e., 7 120 offspring). The final sample size

($N = 3\,431$) is lower due to unsuccessful matings or too few eggs being laid. Despite not reaching our target sample size, our final sample size (82 sires and 239–249 dams depending on offspring trait) is at the upper-end typical for laboratory quantitative genetic studies (e.g., see meta-analysis by Rowiński and Rogell 2017). We analyzed data for sons and daughters separately due to their large sexual dimorphism which invariably leads to strong interactions between sex and other effects. We excluded offspring of dams that did not lay eggs during host preference trials (285 individuals) and data from 13–24 daughters and 12–27 sons with missing or extreme values (>3 standard deviations (SD) from the mean), with the exact number depending on the focal trait. We analyzed four offspring life-history traits: (egg-to-emergence) 'larval survival' (dead or emerged; $N = 3146$), 'duration of larval development' (number of days between oviposition and offspring emergence; $N = 1420$ daughters and 1384 sons), 'body mass' (weight at emergence in mg; $N = 1431$ daughters and 1399 sons) and 'adult lifespan' (number of days between offspring emergence and death; $N = 1425$ daughters and 1389 sons). In addition, we measured the host egg-laying preferences of 665 daughters. The analyzed offspring came from 82 sires and 245–249 dams for the life-history traits, and 239 dams for host preference analysis. The proportion of offspring reared on the original host type was 52–57% (see Supplementary Table S1). Prior to any statistical analysis, but after

Table 2 Phenotypic variance partitioning based on the best model from the model comparison.

Host type	Par.	Development duration		Body mass		Adult lifespan	
		Daughters (N = 1 420)	Sons (N = 1 384)	Daughters (N = 1 431)	Sons (N = 1399)	Daughters (N = 1425)	Sons (N = 1389)
Original	V_A	0.430 (0.105,0.678)	0.448 (0.208,0.876)	0.215 (0.147,0.317)	0.070 (0.034,0.114)	19.981 (11.423,26.851)	9.694 (5.578,14.841)
	V_p	1.768 (1.578,1.948)	2.167 (1.979,2.409)	0.501 (0.446,0.555)	0.310 (0.282,0.343)	39.267 (35.595,45.099)	28.298 (24.908,31.138)
	h^2	0.229 (0.084,0.387)	0.210 (0.082,0.374)	0.447 (0.327,0.615)	0.225 (0.122,0.358)	0.459 (0.301,0.624)	0.333 (0.218,0.505)
	CV_A	0.020 (0.012,0.027)	0.021 (0.014,0.030)	0.084 (0.066,0.097)	0.075 (0.058,0.100)	0.195 (0.148,0.226)	0.184 (0.146,0.234)
	V_A	0.349 (0.213,0.622)	0.527 (0.355,0.892)	0.250 (0.176,0.319)	0.103 (0.068,0.148)	16.664 (10.973,27.715)	16.304 (11.261,24.817)
Novel	V_p	0.956 (0.853,1.083)	1.154 (1.028,1.339)	0.374 (0.340,0.426)	0.211 (0.186,0.236)	37.645 (33.595,43.241)	26.675 (23.763,31.265)
	h^2	0.365 (0.241,0.606)	0.495 (0.348,0.708)	0.649 (0.501,0.786)	0.513 (0.355,0.669)	0.507 (0.334,0.684)	0.627 (0.480,0.854)
	CV_A	0.020 (0.016,0.026)	0.026 (0.020,0.031)	0.077 (0.065,0.087)	0.082 (0.067,0.099)	0.168 (0.131,0.204)	0.208 (0.176,0.260)
	r_G	0.706 (0.277,0.981)	0.147 (-0.279,0.533)	0.901 (0.670,0.995)	0.996 (0.750,1.000)	0.790 (0.615,0.982)	0.967 (0.777,0.999)

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

all data had 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—partly due to feedback from reviewers. We explain our changes in the *Annotated registration* section (Supplementary File 2).

Overview of data analysis approach

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

Model specification, model comparison and partitioning of phenotypic variance

We started data analysis with a minimal mixed-effects model that contained, in the fixed-effect part, only variables ensuing from the experimental design. These were ‘host type’ (original/novel), ‘bean mass’ (standardized to zero mean and 1 SD variance, within each host type, to look at the effect of size within each host type), ‘dam mating order’ (i.e., dam position in a sire’s mating sequence, integer 1 to 4), and ‘day mated’ (integer 1–6). We did not fit ‘day mated’ as a random effect because of the low number of levels (Bolker et al. 2009). We specified the random effects structure using an animal model approach (Kruuk 2004; Kruuk and Hadfield 2007; Wilson et al. 2010), where variance-covariance estimates between relatives are computed from a pedigree.

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

Table 3 The effect of host type, other experimental variables and dam host preference on three offspring life-history traits (fixed-effects estimates from the full animal models).

Term	Development duration [days]		Body mass [mg]		Adult lifespan [days]	
	Daughters (N = 1420)	Sons (N = 1384)	Daughters (N = 1431)	Sons (N = 1399)	Daughters (N = 1425)	Sons (N = 1389)
	Intercept (original HOST)	31.899 (31.713, 32.103)	31.442 (31.187, 31.607)	5.784 (5.660, 5.904)	3.466 (3.414, 3.593)	23.62 (22.432, 24.739)
Novel HOST effect	-1.285 (-1.388, -1.115)	-1.148 (-1.296, -0.935)	0.728 (0.650, 0.792)	0.349 (0.303, 0.408)	3.338 (2.595, 3.975)	2.355 (1.792, 2.885)
Bean mass (original)	0.145 (0.035, 0.229)	0.105 (-0.017, 0.189)	-0.083 (-0.130, -0.032)	-0.039 (-0.089, -0.011)	-0.499 (-0.930, -0.111)	-0.365 (-0.742, -0.038)
Dam mating order	0.060 (-0.002, 0.136)	0.054 (-0.013, 0.134)	0.007 (-0.037, 0.052)	0.006 (-0.017, 0.047)	-0.306 (-0.766, 0.069)	0.210 (-0.116, 0.587)
Day mated (original)	0.326 (0.206, 0.454)	0.122 (0.028, 0.291)	0.058 (-0.006, 0.149)	0.074 (0.037, 0.139)	0.443 (-0.113, 1.273)	0.797 (0.199, 1.262)
Dam preference for cowpea (original)	-0.073 (-0.180, 0.031)	-0.025 (-0.174, 0.068)	0.086 (0.027, 0.144)	0.000 (-0.042, 0.046)	0.219 (-0.366, 0.733)	0.128 (-0.267, 0.572)
Interaction: bean mass (novel)	-0.092 (-0.196, 0.032)	0.031 (-0.131, 0.138)	0.047 (-0.022, 0.102)	0.040 (-0.011, 0.091)	0.456 (-0.052, 1.124)	-0.060 (-0.463, 0.560)
Interaction: day mated (novel)	-0.017 (-0.141, 0.142)	0.112 (-0.026, 0.326)	-0.057 (-0.127, 0.020)	-0.018 (-0.072, 0.035)	-0.625 (-1.272, 0.117)	-0.360 (-0.910, 0.237)
Interaction: dam preference (novel)	0.051 (-0.056, 0.206)	0.051 (-0.084, 0.228)	-0.081 (-0.146, -0.015)	0.008 (-0.038, 0.063)	-0.369 (-0.916, 0.402)	-0.109 (-0.590, 0.470)

The intercept always corresponds to the trait average on the original host type and the 'novel HOST effect' is the effect of the novel host type (i.e., difference between the two means). The same applies to interaction terms, where the interaction gives the estimate for the difference between the effect on the novel and the original host type. Credible intervals (in brackets) that do not overlap zero are highlighted in bold. The estimates and their credible intervals come from posterior distribution of sex-specific animal MCMC models.

To test for the best random effects structure, we performed model comparison on a set of seven candidate models (Table 1) for each trait using the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002). DIC is a Bayesian alternative to Akaike Information Criterion that takes into account the fit of the model but penalizes for model complexity, with lower DIC values indicating a better model (Hadfield 2010; Wilson et al. 2010). Model comparison with DIC should be performed cautiously for non-Gaussian response variables (Hadfield 2010; Wilson et al. 2010), so we did not conduct model selection for larval survival or host preference.

The simplest model 'G' included only additive genetic effects specified by the random effect of 'animal'. We then also included dam identity to estimate maternal effects in addition to additive genetic effects ('G + M' model). These two models do not, however, take into account possible host-specific differences in respective variance components (this is shown in Fig. 1A). We thus formulated more realistic models that estimated the variance component (including residual variance) separately for each host type (as in Fig. 1B). These were specified through random-effect interactions (Hadfield 2010) with host type 'idh(HOST):animal' for 'G_{sep}', or with 'idh(HOST):dam' for 'M_{sep}' models (Table 1). This is similar to fitting two separate host-specific models. To account for potential change in the ranking of additive genetic or maternal effects (Fig. 1C), we fitted models that also estimated cross-environmental covariance ('G_{cov}' or 'M_{cov}'). When specifying variance-covariance matrix of the random-effect interaction we used 'unstructured' form, e.g., 'us(HOST):animal' (Hadfield 2010). As a result, we not only obtained separate variance estimates for each host type, but also the corresponding covariance to compute the cross-environmental correlations (Fig. 1D)—the proxies for Genotype-by-Environment (G × E), or Maternal-by-Environment (M × E) interactions (Lynch and Walsh 1998). In the models estimating separate variances per host type, we always specified host-specific residual variance (as 'rcov = ~idh(HOST):units') (Hadfield 2010).

We then performed phenotypic variance partitioning based on the outputs of the best-selected minimal model for each trait. We calculated the maternal-effect proportion (m^2), narrow-sense heritability (h^2), evolvability (coefficient of additive genetic variation, CV_A) and the cross-environmental correlation for additive genetic (r_G – potential G × E interaction) and for maternal effects (r_M – potential M × E interaction). We used maternal effects proportion, $m^2 = \frac{V_M}{V_P} = \frac{V_{\text{dam}}}{(V_{\text{animal}} + V_{\text{dam}} + V_{\text{residual}})}$, to quantify the importance of maternal effects (as in e.g. Messina and Fry (2003); Vega-Trejo et al. (2018); Moore et al.

(2019)). The V_M contains both genetic and non-genetic maternal effects, and potentially also genetic dominance, as we did not separate them with our experimental design. We calculated heritability as $h^2 = \frac{V_A}{V_P} = \frac{V_{\text{animal}}}{(V_{\text{animal}} + V_{\text{dam}} + V_{\text{residual}})}$ (Lynch and Walsh 1998), assuming epistatic effects were negligible. Evolvability was defined by (Houle 1992) as $CV_A = \frac{\sqrt{V_A}}{\mu} = \frac{\sqrt{V_{\text{animal}}}}{\mu}$, where μ is the mean of a trait. 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 ($G \times E$ interaction) was $r_G = \frac{COV_{\text{animal (original-novel)}}}{\sqrt{V_{\text{animal (original)}} V_{\text{animal (novel)}}}}$. The same formula was used for maternal effects correlation between the two hosts (potential $M \times E$ interaction) using the dam-related covariance across the two host types. Estimates of V_A , V_P and h^2 for larval survival and host preference were back-transformed to the original data scale using the function ‘QGparams’ (from QGglmm package, ver.0.7.4; de Villemereuil et al. (2016)).

Testing for host effect and dam host egg-laying preference on offspring phenotype

To determine the effect of novel host type on offspring performance (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 mixed-effects model always included all the terms outlined above for the minimal model with the random effects from the best-selected minimal model (Table 1). We then included ‘dam host preference’ (i.e., the relative preference ratio: 0–1 values) and the interaction between 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 effects.

Model fitting

To fit the MCMC models, we used non-informative priors for the random-effect variance (G) with expected variance–covariance matrix at limit ‘ $V = 1$ ’, and the degree of freedom ‘ $\nu = 0.002$ ’ for each random term (with $\nu = 1.002$ in models with the random effects estimated separately per host type) (Wilson et al. 2010). To further improve mixing and effective sample size, we specified parameter-expanded priors as ‘ $\alpha \mu = 0$ ’ and ‘ $\alpha V = 1000$ ’

(Hadfield 2010). Priors for residual variance (R) were set as $V = 1$ and $\nu = 0.002$ ($\nu = 1.002$ when residual variance was estimated separately for each host type). We have run a sensitivity analysis and different values of ν (up to $\nu = 3$) had a negligible effect on the estimated parameters. 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 (B), we retained default priors with mean = 0 and variance = 10^{10} . To generate posterior distributions from the minimal and full models, we ran 360,000 iterations with burn-in of 60,000 and thinning interval of 300, so that we obtained an effective sample size of 1000 for each estimated model term. For larval survival, we increased the iterations to 5,500,000 with a burn-in of 500,000 and thinning interval of 5000 as we were aiming for an autocorrelation between -0.1 and $+0.1$ at the lag corresponding to the thinning interval (Wilson et al. 2010). Model convergence was evaluated by visual examination of the traces using function ‘plot(mcmc.model)’. We assessed the importance of individual model terms based on their credible intervals (CrI).

Results

Prediction 1 and 2—testing for maternal effects and $M \times E$ interaction

The model comparison suggests very weak maternal effects for all the measured traits. The models incorporating maternal effects performed poorly (Table 1), and the best model contained only additive genetic effects estimated for each host type and the cross-environmental covariance (the ‘ G_{cov} ’ model). This shows that either additive genetic variance, residual variance or both differed between host types and that the cross-environmental genetic covariance differed from zero. An estimate of the cross-environmental covariance has to be examined directly to see whether the correlation differs from $+1$ indicating a potential Genotype-by-Environment interaction (see below).

Components of phenotypic variance related to additive genetic effects—heritability, evolvability and $G \times E$

We observed higher heritability for offspring life-history traits in the novel host type ($h^2 = 0.365\text{--}0.649$), than on the original host ($h^2 = 0.210\text{--}0.459$) (Table 2). However, the additive genetic variance was substantially higher in the novel host only for adult lifespan of sons. For the other traits, we recorded a similar magnitude of additive genetic variance in the two hosts, but higher residual phenotypic variance in the original host type, thereby reducing trait

Table 4 Phenotypic variance partitioning (A) and full model inference (B) based on G_{cov} model for the non-Gaussian traits—larval survival and host egg-laying preference.

A)			
Host type	Par.	Larval survival Juveniles ($N = 3\ 146$)	Host preference Daughters ($N = 665$)
original	V_A	0.006	<0.001
	V_P	0.094	0.671
	h^2	0.060	0.001
	CV_A	0.084	0.033
novel	V_A	0.003	0.001
	V_P	0.065	0.522
	h^2	0.040	0.003
	CV_A	0.055	0.071
	r_G	0.286 ^a (−0.469,0.985) ^a	−0.046 ^a (−0.905,0.948) ^a
B)			
Term		Larval survival juveniles ($N = 3\ 146$)	Host preference daughters ($N = 665$)
Intercept (original HOST)		2.868 (2.341,3.441)	−0.409 (−0.528,−0.338)
novel HOST effect		0.512 (−0.094,1.447)	−0.247 (−0.324,−0.180)
bean mass (original)		−0.161 (−0.353,0.050)	0.010 (−0.046,0.049)
dam mating order		−0.021 (−0.206,0.124)	−0.001 (−0.027,0.047)
day mated (original)		0.095 (−0.153,0.350)	−0.053 (−0.094,0.004)
dam preference for cowpea (original)		−0.042 (−0.258,0.183)	0.014 (−0.041,0.057)
Interaction: bean mass (novel)		−0.035 (−0.376,0.221)	0.017 (−0.075,0.076)
Interaction: day mated (novel)		−0.122 (−0.501,0.240)	−0.016 (−0.066,0.083)
Interaction: dam preference (novel)		0.242 (−0.106,0.549)	−0.037 (−0.096,0.049)

The estimates for the variance parameters (A) are back-transformed to the original data scale. The effect of host type, the additional experimental variables and dam host preference (B) for larval survival is on logit scale and for host preference on the log scale. Credible intervals (in brackets) that do not overlap zero are highlighted in bold. The intercept always corresponds to the trait average on the original host type and the ‘novel HOST effect’ is the effect of the novel host type (i.e., difference between the two means). The same applies to interaction terms, where the interaction gives the estimate for the difference between the effect on the novel and the original host type. The estimates and their credible intervals come from posterior distribution of animal MCMC models.

^aThese estimates are on the transformed (latent) scale.

heritability (Table 2). The presence of similar levels of additive genetic variance in both hosts is also apparent in the estimates of evolvability (variance due to additive genetic effects standardized over trait means) which were comparable for the two host types (Table 2). When comparing evolvability among traits (across sexes and host types) we found that it was highest for adult lifespan ($CV_A = 16.8\text{--}20.8\%$, Table 2). For the non-Gaussian traits (larval survival and host egg-laying preference), estimates of additive genetic variance and heritability obtained from the G_{cov} model were very low ($h^2 = 0.001\text{--}0.060$, Table 4A) when compared to the Gaussian life-history traits.

We recorded highly positive correlations between offspring performance on the two host types for additive genetic effects (r_G) (Table 2). The only exception was for the development duration of sons, which exhibited only a weak genetic correlation between hosts (Table 2). The credible interval (−0.279, 0.533) suggests a Genotype-by-Environment interaction ($G \times E$). For completeness, we present the outcome of minimal models with saturated random-effect structure ($G_{\text{cov}} + M_{\text{cov}}$) in Supplementary Table S2.

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 3; Supplementary Table S1). We recorded very high larval survival overall, however, so that survival on mung beans was only marginally better than on cowpea (Table 4B). We did not find a positive relationship between the strength of the dam host preference for egg laying and the performance of their offspring on either host type. The one exception was for daughter body mass: daughters of dams that more strongly preferred the cowpea emerged heavier when raised on cowpea, but not when 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 daughters reared on cowpea was 0.681 versus 0.517 for those from mung (where 1 is a strict preference for cowpeas). The host preference ratio of their mothers (reared on cowpea) was 0.724.

Effect of experimental variables on offspring traits—bean size, mating date and mating order

Host-specific relative bean size (zero-centred 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 in daughters, as well as reduced body mass and lower

adult lifespan in both sexes. The effects of mating day on offspring performance were, however, mixed (Table 3). Offspring of later mated families took longer to develop, but sons emerged at a larger size and lived longer. Daughters from later mated families also showed a modest decrease in the preference for the original host type (Table 4B). Finally, if a dam was later in the sire's mating sequence this marginally extended the development duration of her daughters.

Discussion

Summary

Our main aim was to test for environment-specific maternal effects on offspring life-history traits and their correlation, that is, Maternal-by-Environment interactions ($M \times E$). 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. However, maternal effects proved to be negligible for all of the measured traits, on both host types. Instead, we found that additive genetic variance played an important role in determining phenotypic variation. Contrary to our predictions, offspring reared on the novel host type performed better for all the measured traits. Daughters whose mothers preferred to lay eggs on the original host were heavier on this host than those of mothers that preferred the novel host type. There was, however, no equivalent effect of host preference on body mass in the novel host. Below we discuss our findings in more detail.

Weak maternal effects

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

to the fact that we prevented larval competition with our experimental design, may have substantially reduced the role of maternal effects in the current experiment.

Heritability was higher in the novel host type, but evolutionary potential was similar in both hosts

Heritability of fitness-related traits is traditionally assumed to be low, as additive genetic variation is expected to be depleted by natural selection (Mousseau and Roff 1987; Hill 2010). Egg size, body size, fecundity or lifespan were nevertheless previously shown to have intermediate to high heritability in *C. maculatus* (h^2 from 0.27 to 0.74) (Fox 1993; Messina 1993; Fox et al. 2003; Fox and Messina 2018). Here, we recorded considerable heritability in all life-history traits (except larval survival), with the highest values occurring for daughter body mass and son adult lifespan (both $h^2 > 0.65$). Heritability was notably higher in the novel host environment (mung bean), with the one exception of adult lifespan of daughters. Holloway et al. (1990) proposed that a novel environment should yield higher additive genetic variance due to new genes being expressed thereby uncovering cryptic genetic variation (Hoffmann and Merilä 1999). Indeed, *C. maculatus* exhibits increased additive genetic variance for longevity in a novel environment (absence of host beans after emergence) (Messina and Fry 2003). Our results indicate, however, that it was lower residual variance in the novel host (mung bean), rather than increased additive genetic variation, that was responsible for higher heritability in the novel environment. Residual phenotypic variation may entail non-additive genetic, environmental variance and developmental noise (Rowiński and Rogell 2017) and the influence of at least some of these factors apparently declined in the novel host type (Houle 1992). To examine their respective effects in *C. maculatus*, more elaborate breeding design would be required (see e.g. Tucić and Šešlija (2007), or Bilde et al. (2008)). Interpretation of heritability as the proportion of additive genetic versus total variance can therefore become problematic (Hansen et al. 2011) and evolvability offers a more conclusive comparison of evolutionary potential (Houle 1992; Hansen et al. 2011). Similar values of trait evolvability indicated that the traits measured in our study possess similar evolutionary potential in the two host types.

Genetic trade-offs are thought to prevent populations of parasites or herbivores from becoming 'masters of all trades' and performing well on multiple hosts (Joshi and Thompson 1995; Agrawal et al. 2010). In phytophagous insects, performance trade-offs on different hosts are, however, rarely reported (Ueno et al. 2003; Scheirs et al. 2005; Messina and Durham 2015). This includes studies of *C. maculatus* where offspring from the same family usually perform similarly across hosts without exhibiting a $G \times E$

interaction (Fox 1993; Guntrip and Sibly 1998; Messina 2004a). We also found strong positive cross-environmental genetic correlations indicating parallel reaction norms for offspring from different families when reared on the two host types. Only the development duration of sons showed a low genetic correlation between the two host types indicating that it could evolve differently on cowpea and mung (Via and Lande 1985). It is, however, important to bear in mind that breeding design studies cannot definitively conclude there are no genetic trade-offs in adaptation to different hosts because they lack mechanistic explanation. This can be more readily obtained through analysis of long-term selected lines (Agrawal et al. 2010) or data on the potential genes involved (Gompert and Messina 2016).

Offspring performed better on the novel host type

We treated mung bean as a novel host type. This was despite mung bean regularly being used to rear other strains of *C. maculatus* (e.g. the Southern India strain (Fox et al. 2004)), and regarded with cowpea as a favourable host species for *C. maculatus* (Fox and Messina 2018). Our stock population was kept on cowpea for at least 100 generations. In addition, cowpea strains are overall more viable than those from mung bean (Messina 2004a) and the cowpea is generally considered to be the ancestral host for *C. maculatus* (Kébé et al. 2017). Due to these reasons, and the fact that a previous study showed that long-term maintenance on a specific host yields decreased viability on other hosts (Messina 2004a), we predicted a lower suitability of the novel host type (mung bean). Our finding that offspring performed better on the novel host type (mung bean) was therefore unexpected. While offspring survival was almost 90% on cowpea, it was even higher on the novel host (93 % on mung bean). There was no obvious cost to the offspring of rearing in the novel host, as the duration of larval development was shorter on mung bean. However, beetles that emerged from mung beans were larger and lived longer as adults than those that emerged from cowpeas. It is not straightforward to tell which of the two host species is generally better for *C. maculatus*, because it depends on other factors such as the level of competition (Messina 2004a; Paukku and Kotiaho 2008; Fox and Messina 2018), temperature (Stillwell et al. 2007) and the population's evolutionary history (Messina 2004a). In the present study, we eliminated the effects of larval competition by rearing one larva per bean. We therefore removed the fitness advantage that cowpea may provide due to its larger size when there is larval competition (Fox and Savalli 1998). Surprisingly, relative bean size within a given host type also negatively affected body mass and lifespan as well as extending the developmental duration of daughters.

We cannot reject the hypothesis that the host effect recorded in our experiment was confounded by egg-laying

order, as eggs were laid first on mung bean (see “Methods” for the experimental justification). The lower performance of offspring on cowpea might have been because, following the preference trial, females were first provided with mung beans to lay eggs, and only after that with cowpeas. There are, however, several reasons to think that an effect of laying order in our experiment is unlikely. The lifetime fecundity of *C. maculatus* is 60–80 eggs (Mitchell 1975; Credland and Wright 1989; Wilson and Hill 1989; Messina and Fry 2003). The dams in our experiment laid around 30 eggs per 24 h and probably still possessed more than half of their lifetime fecundity after they had finished laying in our experiment. Crucially, past studies suggest there is no negative effect of maternal age on offspring performance on the first day of egg laying (i.e., the relevant time period in our study) (Wasserman and Asami 1985; Fox 1993; Fox and Dingle 1994; Iglesias-Carrasco et al. 2018). See also Supplementary File 1 for an additional experiment confirming there is no significant effect of egg laying order on offspring performance in our population of *C. maculatus*. We therefore think that the sequence of host types available for egg laying is unlikely to explain the poorer offspring performance on cowpea. If present, the potential laying order effect would be tied with dam-related variance. In addition, our results on negligible maternal effects suggest that the phenotypic variance partitioning analysis was not biased by any variance stemming from laying order effects (through maternal effects).

Host preference of *C. maculatus* increased daughter body mass and rearing host affected host preference

An egg-laying preference for a particular host often predicts offspring performance on that host in phytophagous insects (Gripenberg et al. 2010). However, despite the critical role of oviposition choice for larval success in *C. maculatus*, of the five offspring traits we measured, the strength of dam preference for cowpea only correlated with daughter body mass. Dams that showed a stronger preference for cowpea produced heavier-than-average daughters on cowpea, but not when laying on mung. This contributes to mother fitness through higher daughter reproductive potential in cowpea as body size is a good proximate measure for fecundity in *C. maculatus* (Messina and Fry 2003). In mung bean, however, daughters' body mass was not affected by their mothers' host preference and the preference–performance relationship thus only holds for daughter body mass in cowpea. The weak overall relationship between mother's host preference for one host type and the performance of her offspring on that host suggests that *C. maculatus* females might aim to maximize their own fitness and not that of individual offspring (i.e. they prioritize offspring number over offspring

quality), perhaps through saving searching time for the best host (Wood et al. 2018).

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 et al. (2004) used different host strains to demonstrate that switching a strain to another host for just a single generation has no effect on host preference. We found that while daughters reared on cowpea preferred cowpea over the novel host (mung bean), those reared on mung beans showed no preference for either host type. This suggests that there might be a $G \times E$ interaction affecting host egg-laying preferences, but tracking of more generations is necessary to test whether the host preference evolves after the host switch (as in Fox 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 a familiar host. A next step in the exploration of whether $M \times E$ interactions affect estimates of genetic variation, and of $G \times E$ interactions specifically, would be to conduct experiments using less favourable novel hosts of *C. maculatus*, for example, adzuki bean (Fox 1993) or lentil (Gompert and Messina 2016). The host species we used are both considered to be of high quality (Fox and Messina 2018). By creating more challenging conditions for offspring, maternal effects might emerge as an important host-specific factor that affects variation in offspring performance (Fox et al. 1997; Räsänen and Kruuk 2007). Despite the fact that maternal effects were negligible in our study, we still argue that it is important to test for $M \times E$ interactions. $M \times E$ effects have the potential to bias measurements of $G \times E$ and the lack of research on $M \times E$ interaction is an obstacle towards understanding their role in adaptive processes.

Data availability

Data with accompanying R code are stored at OSF (link: https://osf.io/ft7eq/?view_only=0bab0a33bb4246adb64c9196701a72757) and FigShare repository (link: <https://figshare.com/s/7878e68e31590dce594d>).

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

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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