Environmental predictability favours adaptive behavioural plasticity and relaxes selection against deleterious alleles

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Abstract

Behavioural plasticity can play a key role in evolution by either facilitating or impeding genetic adaptation. The latter occurs when behaviours mitigate selection pressures that otherwise would target associated traits. Therefore, environments that facilitate the evolution of adaptive behavioural plasticity are predicted to relax natural selection overall, but experimental evidence for this prediction remains scarce. Here, we first demonstrate that adaptive behavioural plasticity in maternal care in the beetle *Callosobruchus maculatus* is dependent on reliable environmental cues that allow females to reduce larval competition via learning and informed oviposition choices. By comparing survival of larvae of low and high genetic quality in competition with the conspecific *C. phaseoli*, we show that predictable maternal environments relax selection on deleterious alleles in offspring. We further find that females of low genetic quality generally provide poorer care. However, in the predictable environment, the increased opportunity for learning reduced genetic differences in female care, further relaxing selection against deleterious alleles. We illustrate how the identified link between adaptive behavioural plasticity and the strength of natural selection can have important implications for the build-up of cryptic genetic loads and outcomes of interspecific competition across variable environments that differ in their predictability.

Introduction

Phenotypic plasticity plays a fundamental role in shaping organismal responses to changing environments (1–6). Plasticity can help organism to survive and reproduce despite initial adversities. This can allow populations to persist in novel environments and respond to selection, leading to increased genetic change over time (1,3,7–13). However, by mitigating selection pressures, phenotypic plasticity can also reduce the necessity for genetic adaptation (3,14,15). This forgiving nature of plasticity should relax purifying selection and lead to the build-up of genetic variance in quantitative traits that would be deleterious in the absence of plasticity (16–21). If this process continues over time, a population could become dependent on plasticity to survive, as without it, the built up load of conditionally deleterious alleles would become exposed to selection (18,19,22–24).

The evolution of adaptive plasticity is contingent on the organism's ability to change phenotype in accord with changes in the environment (17,25–28). This leads to the expectation that variable environments that provide reliable cues of future change should favour the evolution of adaptive plasticity, whereas unpredictable environments may hinder it when environmental fluctuations are too fast, and/or costs of plasticity are too high, to allow accurate phenotype-environment matching (17,27,29–31). Many behavioural phenotypes represent striking forms of plasticity, where a range of cognitive processes allows the organism to use and process information through experience and learning to fine-tune its strategies to fit the perceived environment (4,32,33). Indeed, adaptive behavioural plasticity in the form of learning has been argued to be a key determinant of evolution in fluctuating environments (3,4,17,34–36). Like for other forms of plasticity, however, learning requires reliable environmental cues to result in accurate behavioural adjustments (17,25,27,37–39). This central role of cue reliability suggests that populations inhabiting environments that differ in their predictability should exhibit systematic differences in learning and genetic load in associated traits. These dynamics are expected to have important consequences for both the levels of segregating genetic variation in natural populations (16,40–42) and for predicting responses to future environmental change (1,3,4,8,17,28,43–45).

Here, we investigated how environmental predictability impacts the rate of learning and the resulting strength of selection on deleterious genetic variation in the seed beetle *Callosobruchus maculatus* (**Fig. 1**). We studied behavioural plasticity in maternal care and females' ability to use information to assess future egg-laying opportunities and learn the spatial location of high-quality hosts. The immediate survival benefits of maternal care to offspring are obvious (46–48), but the flip-side of the coin is that by relaxing selection in offspring, maternal care should, at least theoretically, allow deleterious genetic variation to accumulate. Indeed, in burying beetles, populations that are deprived of parental care suffer immediate increases in juvenile mortality and inbreeding depression (49,50), but at the same time seem to more efficiently purge genetic variation in the long run (21,22,51).

Moreover, given that cognitive processes are costly and governed by many genes (17,52–56), it could be envisioned that the build-up of genetic load via relaxed selection in offspring also feeds back on parents' ability to learn and provide care. Genetic variation in parental care is well-known to impact the expression of genetic variation and selection on traits in offspring via indirect genetic effects (IGEs: the effect of genetic variation expressed in one individual on trait expression in interacting individuals (40–42,57–59)). Imagine that parents of high genetic quality provide better care for their young, who also have intrinsically higher survival due to their superior genetic quality. This positive covariance between parental and offspring breeding values increases genetic variance in offspring survival and is predicted to speed up responses to selection compared to a situation where IGEs are absent (40,57,58,60). Thus, if environmental predictability affects the amount of expressed covariance between adult and juvenile traits, it could have strong effects on evolutionary dynamics across variable environments (24,39,43,61,62).

Female seed beetles provide care for their offspring by preferentially placing eggs on uninfested host seeds, a behaviour that can be finetuned by experience (63–66). First, we gave females the opportunity to choose between uninfested and infested hosts in a spatially complex environment that either provided reliable or unreliable information on infestation rates of future hosts. We show that learning is faster, and care behaviour more accurate, in females receiving reliable information about future hosts, providing evidence that adaptive behavioural plasticity is facilitated by environmental predictability. Second, we find that viability selection in offspring is significantly reduced by faster rates of female learning and improved maternal care in the predictable environment. Third, by comparing the accuracy of maternal care behaviour in mothers of different genetic quality, we find that improved learning in the predictable environment also reduces selection on deleterious alleles in adults. Together, this renders substantially weakened IGEs between maternal care and offspring survival in the predictable environment. Finally, we adopt an existing theoretical model and parametrize it with our experimental data to illustrate potential population-level consequences of the evolutionary feedback between adaptive behavioural plasticity, the strength of natural selection, and the accumulation of conditionally deleterious genetic variation. The results imply that populations evolving exclusively in predictable environments may build up cryptic genetic loads to such extent that they would be unable to colonize unpredictable environments with resident competitor species.

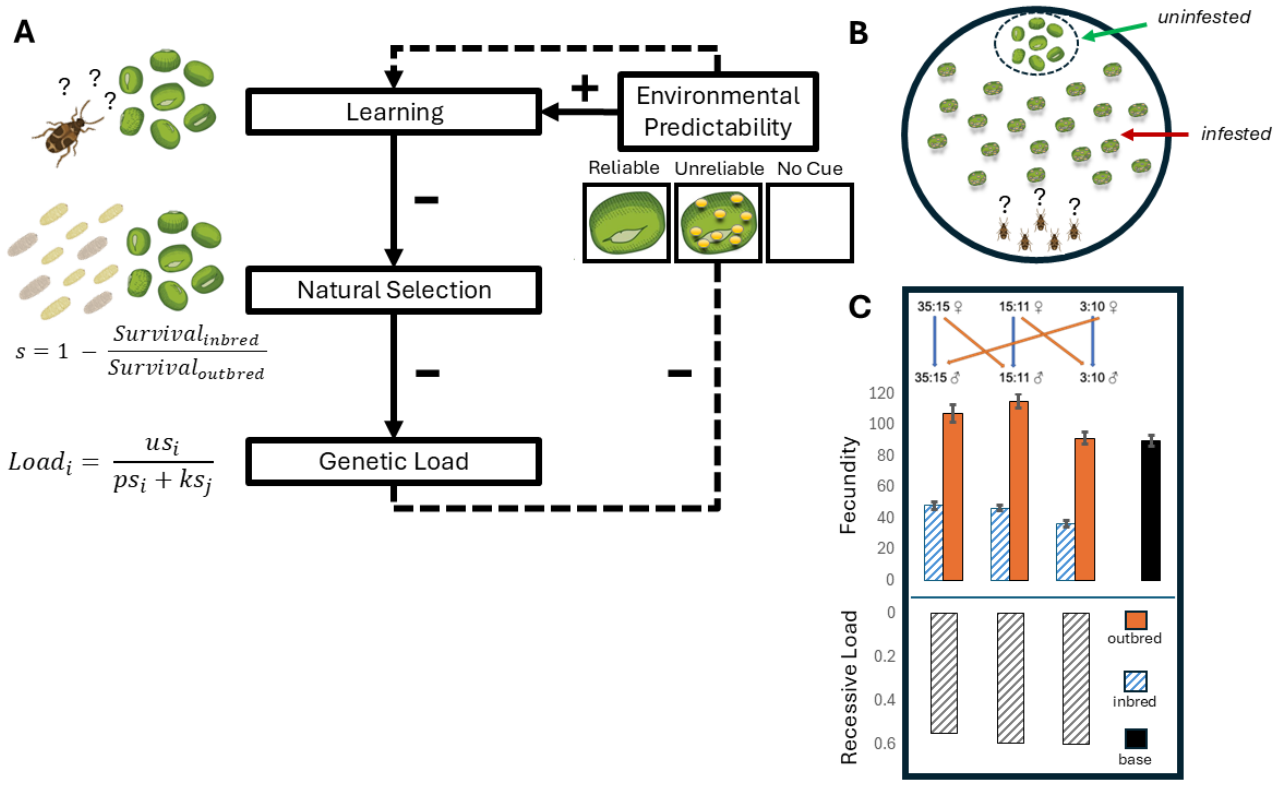

Figure 1: Study design.
A) Path diagram showing hypothesized relationships between environmental predictability, learning, natural selection, and genetic load. Environmental predictability is expected to favour adaptive behavioural plasticity in form of learning. Behavioural plasticity can mitigate genetic differences in trait expression and relax the strength of natural selection, thereby increasing the build-up of deleterious genetic variation over time (i.e. genetic load). The build-up of genetic load could in turn compromise adaptive behavioural plasticity that necessitates cognitive learning (broken arrow). However, the degree to which genetic load impairs learning could also depend on the available environmental cues used in the learning response. To test these hypotheses, we assessed how environmental predictability affected learning of maternal care, and how this in turn affected selection in larval offspring. **B)** Female *C. maculatus* were challenged to find and discriminate among hosts seeds in a repeated spatial learning task. The seeds were either uninfested or infested with eggs of the competitor *C. phaseoli.* We manipulated environmental predictability by giving females three different treatment cues before they performed the task; a reliable cue giving accurate information about the presence of uninfested hosts, an unreliable cue giving false information about the level of infestation of future hosts, and no cue at all. We measured the fitness consequence of maternal care behaviour and learning in each treatment by combining data on female oviposition choice with estimates of larval survival of *C. maculatus* under different levels of competition with *C. phaseoli*. **C)** Three highly inbred strains (blue stripes) were used and compared to themselves when outcrossed (orange) (base stock population; black). Fecundity estimates per line are given as mean ± 2se. The inbred strains show a recessive genetic load amounting to a reduction in fecundity of 55-60% relative to when outcrossed (grey striped bars). The comparison between the three strains in inbred and outbred state was used to assess the relative strength of viability selection in larvae (*s*) and the effect of recessive genetic load on female learning and maternal care, across the three treatments. Based on these estimates, we predicted the genetic load at mutation-selection balance in a meta-population experiencing the predictable, *i*, and unpredictable environment, *j*, at fraction *p* and *k* as a function of the deleterious mutation rate, *u*, and the strength of selection, *s*. See main text for further details.

Methods

Study species

Callosobruchus maculatus is a capital breeding bruchid beetle and a cosmopolitan pest of leguminous crops common in the tropical and subtropical regions. It is facultatively aphagous, i.e. adults do not require food or water to reproduce at high rates (67,68). Adults typically die 7-14 days after emergence in the absence of food and water in standard laboratory conditions of 29°C and 50%RH (69). Both sexes can start reproducing on the day of adult eclosion and females lay 70-90% of their eggs during the first few days of their life (67). The juvenile phase is completed in 3-4 weeks, and egg-to adult-survival rate on preferred hosts *Vigna unguiculata* (black eyed bean) and *V. radiata* (mung bean) is typically around 90% in standard laboratory conditions (70–72). Female host plant search and discrimination is complex. *C. maculatus* has a wide repertoire of fabaceus host plants (73) but females have a clear host hierarchy and preference, and they discriminate between high and low quality species (74,75). Females also heavily discriminate against egg-laden seeds and actively avoid competition with other egg-laying females (63,65), as high larval density limits survival and size at maturity, and thus comes at substantial fitness costs (75–77). *C. maculatus* utilizes both natural habitats where host plant patches used for both egg laying and adult nectar feeding are widely distributed, as well as grain storages where adult food is absent but egg laying substrate is abundant and population density is higher (73,75,76). Thus, selection on spatial cognition and chemosensory cues is likely always strong in natural populations but may take different forms, which is predicted to maintain genetic variation in the cognitive traits under study, as seen for other characters related to these alternative environments (78).

Inbred lines

The three genetic lines used in the experiments were derived from a population isolated from *Vigna unguiculata* (black-eyed bean) seed pods collected at a small-scale agricultural field close to Lomé, Togo (06°10'N 01°13'E) in October and November, 2010 (79). Virgin males and females hatching out of beans were paired randomly and each pair founded an isofemale line that was expanded to a population size of approximately 200 adults over the first two generations. In total, 41 lines were established. These lines have previously been shown to harbor abundant genetic variation for life-history traits and fitness correlates (80). The three inbred genetic lines were created by successive full-sib matings of the 41 lines, resulting in loss of inbred lines and at the end, following more than 30 generations of full-sib mating, the three most productive lines were kept and used for the experiments described below. Thus, these lines represent extremely inbred lines that are next to completely homozygous. Therefore, the comparisons of these lines in inbred and outcrossed state do not correspond to the effect of natural levels of inbreeding. The near complete homozygosity prevents further evolution during the experiments and limits within-line variation due to segregation. These lines should therefore be seen as a powerful tool to inspect the fitness consequences of

genome-wide homozygosity and estimate the strength of selection across genomic sites harboring deleterious alleles.

To provide an estimate of the inbreeding load in the used lines, we estimated the fecundity (number of hatched eggs produced over the first week of reproduction) in females that were either produced by within- (inbred) or between- (outbred) line-crosses. Outcrossing between the three lines was performed in a round-robin fashion following a particular schedule (**Fig. 1C**) and should hide the fitness effects of segregating recessive deleterious alleles, given that these are relatively rare and unlikely to be shared among the three lines. To ensure that bad sperm from inbred males played no part in the fecundity estimates, all females were mated with males from the outbred Lome stock population. We assayed 15 females from each of the six crosses (three inbred and three outbred). For comparison we also scored the fecundity of 15 females from the Lome stock population. Each female was placed into a 35mm petri dish filled with mung beans. These petri dishes were placed in a climate cabinet set at standard conditions and the females were left to lay for the next 7 days after which females were removed. After another 7 days beans were removed, and the number of hatched eggs were counted. This showed that inbreeding has led to a decrease in female fecundity of 55-60% relative to the outbred state (**Fig. 1C,** Supplementary 1).

The Competitor

To estimate the fitness effects of variation in maternal care of *C. maculatus*, we let females choose between uninfested mung beans and mung beans infested with larvae of the closely related competitor, *C. phaseoli*, which has strongly overlapping geographical distribution and host plant preference with *C. maculatus* (81–83). The two species also have similar life-histories (84), although the lab stock of *C. phaseoli* has a 20-30% smaller body size than *C. maculatus* (85). The relative success during interspecific competition inside host seeds could be quantified by counts of relative adult offspring numbers emerging from beans as the species differ in colour patterning. To estimate how variation in maternal care affects offspring fitness, all experiments were performed using mung beans, which is a preferred host of both species but small enough to typically allow for only one or two adults to emerge (**Fig. 1A**).

Learning and maternal care in predictable and unpredictable environments

To decide on the spatial and temporal context in which to assess the ability of *C. maculatus* females to learn the location of host seeds and discriminate their quality, we performed several pilot experiments informed by previous findings showing that females improve their host choice throughout repeated learning trials (66). Based on the previous findings and our pilot data, we constructed arenas from 150 mm diameter petri dishes with the bottom covered in paper to improve traction for females exploring their spatial surroundings. Each arena consisted of a ‘starting zone’ at

one side of the petri dish, where the females were later to be released. Within the petri dish 35 mung beans, each infested with 2-4 *C. phaseoli* eggs, were spread out in the area outside of the starting zone. Approximately 35 uninfested mung beans were placed into a small 35mm petri dish so that its bottom was covered by a single layer of beans. This petri dish was then inverted into the arena in a designated area opposite to the starting zone after which the dish was removed leaving just the beans (**Fig. 1B**).

Virgin females from the three lines were collected upon adult emergence from mung beans that had been individually isolated in 24-welled chambers. These adult emergences were staggered to allow a constant supply of individuals over a period of a few weeks, so when used in trials females were always between 2 and 4 days old. Virgin females were placed *en masse* in 90mm petri dishes on warming plates set to 30°C. Newly emerged males from the same inbred line were also placed in the petri dish and mating pursued. Mating couples were removed from the petri dish and once mating was over, the female was moved to a small 35mm petri dish and left there for at least 24 hours without beans (29°C and 12:12LD).

Based on a previous study (66), we decided to assay females in groups of five, as this stimulates locomotor activity. A trial started by dividing fifteen mated females equally between three 35mm petri dishes (hereafter known as a 'holding dishes'). Arenas with their associated holding dishes were placed on a single heating plate set to keep the temperature at about 30°C. Females spent five minutes in their holding dish, and approximately 1 minute before being placed in the arena, an environmental cue treatment was added to the holding dish. To one holding dish, 5 non-infested seeds were added (reliable cue), to another holding dish 5 highly infested seeds with over 10 eggs on them were added (unreliable cue), and the final holding dish was left empty (no cue) (**Fig. 1A**). After the final minute with the environmental cue, the females were removed from their holding dish and placed in the starting zone of the arena and left for 10 minutes during which their location (on uninfested beans or not) was recorded every 30 seconds. At the end of the 10 minutes, the females were placed back into their holding dish for five minutes and the procedure to introduce the environmental cues was repeated. During this time, the uninfested beans in the arena were also replaced by new beans. The five females in each of the three environmental cue treatments were exposed to the arena five times (from hereon: "runs"). Previous studies have shown that females of *C. maculatus* adjust their expectations and egg-laying behaviour based on the quality of previously encountered host seeds (63,65,66). We therefore predicted that the environment with the reliable cue would make females perform more accurate host choices as these females had gotten correct information about the presence of uninfested seeds (later found at the other end of the arena). From hereon, we refer to this treatment as the "predictable environment". For the no cue and unreliable cue environments, we expected females to take longer to find the uninfested seeds. For females receiving no cue, we predicted that these females would be less stimulated to start their search for

hosts, as they yet had received any information about the presence of hosts, and that they might regard the hosts with competitor eggs acceptable in the absence of other obvious alternatives. For females receiving the unreliable cue, we predicted that these females would spend more time inspecting the infested seeds found in the arena and also would be more willing to lay eggs on them, as these seeds are of comparatively good quality relative to the seeds that the females had been exposed to in the holding dish before each run. From hereon we refer to these two treatments as the "unpredictable environments".

The first 12 trials were conducted with two environmental treatments simultaneously (6 with reliable versus unreliable cue, and 6 with reliable versus no cue). Once the observer was used to the protocol, we included all three environmental treatments simultaneously, to run an additional 24 trials. The observations were conducted without blinding the observer (LC) due to practical limitations. However, to assess the potential for observer-bias, we later repeated the behavioral assays with a blind observer (TM), conducting another 12 trials using the Lome base population. This showed that all three experiments (2-treatment, 3-treatment and 3-treatment blinded trials) produced qualitatively the same result (summarized in Supplementary 1). We therefore combined all data for the final analysis presented in the main text, based on 66,000 observations of behavior from 660 females in total.

Learning was quantified as the improvement between runs (from 1 to 5) in the rate that females found the patch with uninfested seeds. Thus, to evaluate the effect of environmental predictability on learning, we first analyzed the number of females found on uninfested beans in each arena as a binomial response (maximum value of all five females and minimum value of 0 females) using mixed effects generalized linear models using the lme4 package (86) for R (87). We included fixed effects of time (10 minutes within each run) and run (1-5) crossed with treatment (reliable/unreliable/no cue). Time and run were both added as continuous variables fitted with a second-degree polynomial to account for non-linearities in their effect on the response. Additionally, we included female age and the line ID as additional fixed effects. We included the trial ID as a random effect crossed with treatment. We note that we did not analyze line ID as a random term crossed with treatment, although strictly this could be seen as a relevant level of replication in our experiment, especially in latter analyses comparing the lines in inbred and outbred state (see further below). However, fitting line as a crossed random term with only three levels proved difficult as the mixed models had problems converging. We therefore instead estimated the consistency of the responses in the three lines with reference to treatment and inbreeding status. This showed that the three lines behaved qualitatively the same, and we report a summary of all results from line comparisons in Supplementary 1.

We also quantified differences in learning between the three environments by comparing the number of eggs laid on infested and uninfested seeds from the two non-blinded experiments for a total of

480 females scored in fives over 96 trials. One model was run with a binomial response variable to inspect the fraction of eggs laid on the two types of seeds at the end of each trial. This model included environmental cue and line ID as fixed effects. The second model analyzed the number of eggs laid on the uninfested (high-quality) hosts during each of the five consecutive runs of each trial as a Poisson distributed response variable. This model included environmental cue, run, and their interactions as fixed effects, and trial as a random term. Note that eggs on infested seeds were only counted after the end of each trial and not every run within trials.

Maternal care and the strength of selection on recessive deleterious alleles

To estimate the fitness consequences of variation in maternal care, ultimately leading to either correctly placed eggs onto seeds without competitors, or misplaced eggs onto seeds with many competitors, we tracked survival of *C. maculatus* larvae competing with *C. phaseoli*. To estimate the strength of selection on recessive deleterious alleles at different levels of competition, we compared survival of inbred and outbred *C. maculatus* larvae. We achieved this by mating parents either within (inbred) or between (outbred) lines (**Fig .1C**), reasoning that survival differences between inbred and outbred larvae should reflect natural selection against recessive deleterious alleles revealed by homozygosity in inbred individuals (88). The experiment was carried out in two temporal blocks. Two females (mated either within or between lines), were placed in a 35mm petri dish with mung beans. The seeds were either uninfested or infested with a known number (1, 2, 3 or 4) of *C. phaseoli* eggs that had been laid on the seeds a week earlier (as in the behavioural trials). After 72 hours, the females were removed from the petri dishes and the beans were taken out and checked for eggs. If new eggs were found, they were counted, and beans were placed individually into 24-welled chambers. These chambers were placed into climate cabinets set at standard conditions and were later checked to see how many adults that had emerged of each species.

The data consisted of three replicates (each of two females) per line, inbreeding status, and competition level (0-4 *C. phaseoli* eggs), for a total of 60 female duos, laying 8323 eggs on 2450 mung beans. We analysed the survival of *C. maculatus* as a binomially distributed response, with inbreeding status (inbred/outbred), the number of competitor eggs, and their interaction as fixed effects. The ID of the female duo was added as a random effect. Note that we chose to sum the eggs of both *C. maculatus* and *C. phaseoli* as a measure of competition intensity, as mung beans had 1-3 *C. maculatus* egg laid on them, with one egg being most common and three eggs rare. Additionally, seven seeds had more than three *C. maculatus* eggs on them. We chose to discard these seeds from the analysis since these were unevenly distributed with six of seven seeds from outbred females. A summary of the distribution of eggs laid by both species is presented in Supplementary 7.

To predict the strength of selection, we refitted the mixed effect model within a Bayesian framework using the MCMCglmm package (89) for R. Based on the posterior estimates of model coefficients transformed from log-odds back to original scale, we calculated the strength of selection (with 95% credible intervals) for different levels of competition, *c*, as : $\Delta\omega_c = 1 - \frac{v_{c,I}}{(v_{c,O})}$, where v_I and v_O is viability of inbred and outbred offspring, respectively. For all Bayesian analyses in this study, we ran models for 100,000 iterations, preceded by 50,000 burn-in iterations, and stored every 100th iteration, resulting in 1000 uncorrelated posterior estimates of model coefficients. We used flat and weak priors for the random effects.

Learning and maternal care by mothers of different genetic quality

Using the same set-up as for the original behavioural assays, we quantified the effect of inbreeding load on females' ability to use the environmental cues and adjust their maternal care behaviour. For this we compared inbred and outbred females resulting from within- and between line crosses of the three inbred strains. To minimize the risk that inbred males' sperm would negatively affect female fecundity and their motivation for host search, all females were mated with outbred males from the Lome stock population. The data consisted of 18 trials. In each trial, the three cue treatments were included. Nine trials were run with inbred females and nine with outbred females (i.e. three replicates of five females per line and inbreeding status). This resulted in a total of 27,000 behavioural observations from 270 females. The data was analysed by the same model fitting procedure as for the first experimental data, analysing behavioural responses and the fraction and total number of eggs laid on infested and uninfested seeds, with the addition of adding inbreeding status (inbred/outbred) as a fully crossed fixed effect.

Genetic load in predictable and unpredictable environments

To quantify the fitness cost associated with the revealed recessive deleterious alleles in each of the three environments of our experiment, we refitted the mixed models on juvenile survival (see Fig. 4) and female behavioural plasticity (see Fig. 6) in inbred and outbred individuals using a Bayesian framework, which allowed us to calculate the predicted strength of selection against recessive deleterious alleles based on model posterior distributions. Fitness (ω) of inbred and outbred genotypes could thus be calculated by weighting the number of eggs laid on infested and uninfested seeds by the predictions for larval survival at no competition (uninfested seeds) and three competitors (the mean number of *C. phaseoli* eggs on infested seeds in the behavioural experiments). The genome-wide strength of selection against deleterious alleles in environment *j* was then calculated as: $s_j = 1 - \omega_{i,j} / \omega_{o,j}$. Using the estimates of *s* for each environment we then predicted the long-term fitness consequences and genetic load at mutation-selection balance in our predictable and unpredictable environments using a previously published model by Kawecki et al. (1997) (23). Details are described in Supplementary 6.

To further explore potential consequences of the build-up of genetic load for the outcome of interspecific competition, we analysed how the survival of the competitor, *C. phaseoli*, depended on the density of eggs and the inbreeding status of *C. maculatus* (the later as a surrogate measure of genetic load) in the experiment on larval survival (Fig. 4). We also estimated the competitive outcome between the two species by comparing the relative numbers of adults emerging from coinhabited beans. Both models thus fitted survival as a binomial response as a function of the number of *C. phaseoli* and *C. maculatus* eggs, with the latter variable crossed with inbreeding status of *C. maculatus*. The ID of the female duo that laid the *C. maculatus* eggs was added as a random effect in both models. To assess the predicted outcome of interspecific competition depending on the genetic load of *C. maculatus*, we also calculated interspecific competition coefficients between the species, separately for inbred and outbred *C. maculatus*, based on how each species' larval survival was affected by competing eggs of its own and the other species. We approximated each species' carrying capacity for a single mung bean based on the survival data (Supplementary 7; K ≈ 2 for both species). Based on these approximations, we calculated interspecific competition isoclines and mapped them on the model predictions of relative survival of the two species (Fig. 7E).

Results

Learning and maternal care in predictable and unpredictable environments

We first explored whether environmental predictability affected females' ability to learn and express maternal care. Within each of the five runs of a trial, females explored the arena, resulting in more females finding the patch with uninfested seeds as time progressed (χ^2_2 = 4851.9, p < 0.001, Fig. 2). There were clear signs of learning during the trials, signified by a general increase in the proportion of females finding the uninfested beans between the five consecutive runs (χ^2_2 = 5818.0, p < 0.001, Fig. 2). There was evidence for increased learning in the predictable environment compared to the two unpredictable environments providing an unreliable cue or no cue (Fig. 2). This was evident as an effect of environment on the proportion of females finding the uninfested seeds (χ^2_2 = 108.8, p < 0.001) and as a difference between environments in how this proportion increased between runs (Environment:Run interaction: χ^2_4 = 72.9, p < 0.001, Fig. 2). Because females in the predictable environment found the uninfested seeds faster compared to females in the two unpredictable environments, there was also a stronger saturation in the proportion of females found on the uninfested seeds with time in the predictable environment (Environment:Run:Time interaction: χ^2_4 = 116.7, p < 0.001, Fig. 2). Summary of results in Supplementary Table 2.

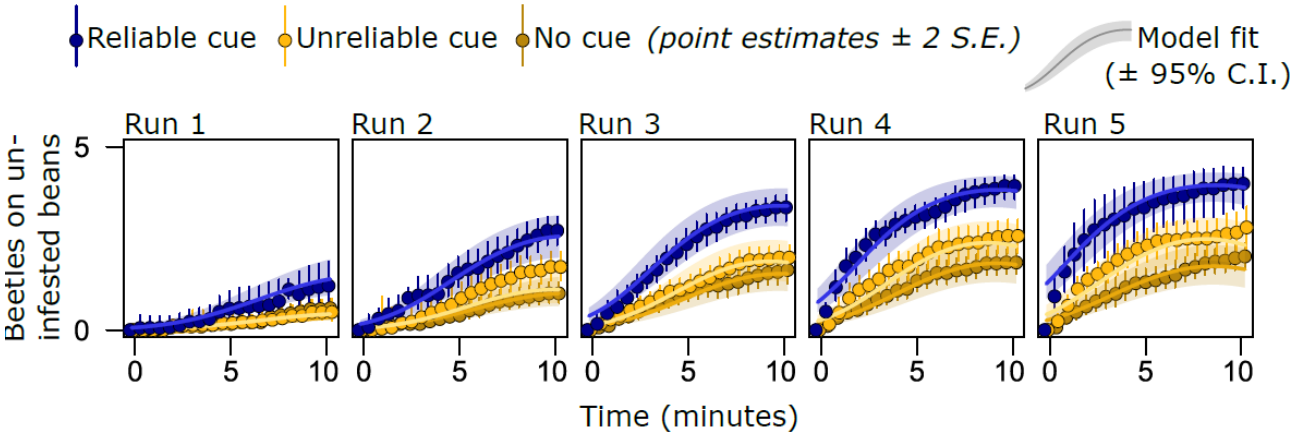

Figure 2: The effect of environmental predictability on female host search
With time, more females located the patch with uninfested host seeds both within and between runs. The improvement over runs demonstrates learning during the experiment. The rate of learning was highest in females exposed to the reliable cue (blue) compared to those exposed to the unreliable cue (yellow) or no cue (brown).

Females in the predictable environment also laid a larger fraction of eggs (χ^2_2 = 204.3, p < 0.001, Fig. 3, Supplementary Table 3A), and more eggs in total (χ^2_2 = 224.4, p < 0.001, Fig. 3, Supplementary Table 3B), on uninfested seeds. Thus, environmental predictability, providing the opportunity for learning of maternal care, is likely to reduce competition in larval offspring.

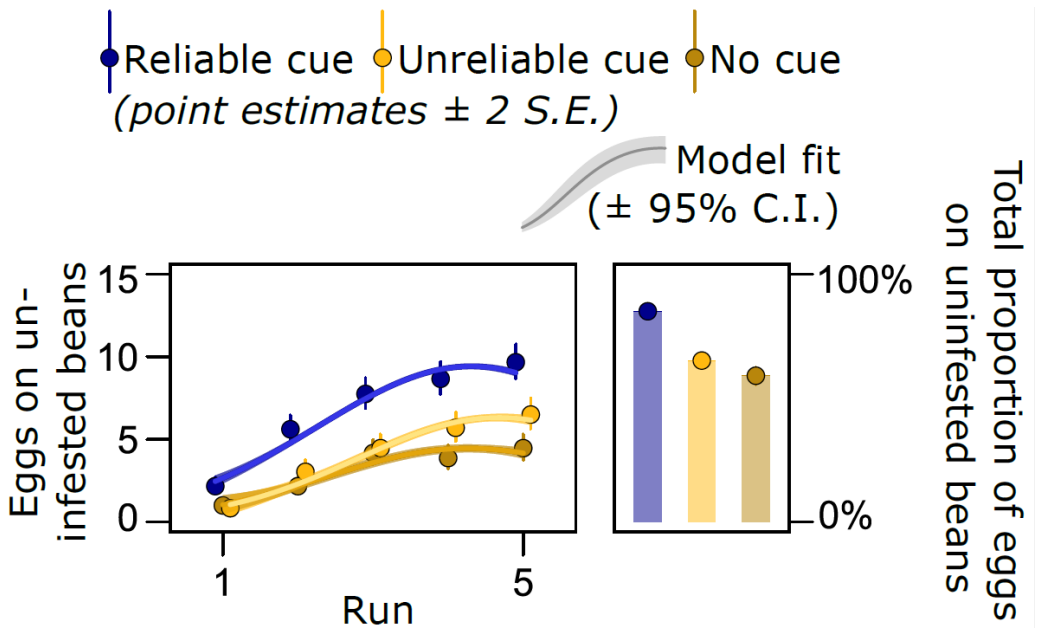

Figure 3: The effect of environmental predictability on female host choice
Females laid more eggs on uninfested hosts in later runs of the experiment, showing that they got better at locating the patch with uninfested seeds. The rate of improvement was highest in females exposed to the reliable cue (blue) compared to those exposed to the unreliable cue (yellow) or no cue (brown). This also resulted in females receiving the reliable cue placing a higher proportion of their eggs on uninfested seeds relative to females receiving the other treatments.

Maternal care and the strength of selection on recessive deleterious alleles

To estimate the fitness consequences of variation in maternal care, ultimately leading to either correctly placed eggs onto seeds without competitors, or misplaced eggs onto seeds with many competitors, we tracked survival of *C. maculatus* larvae competing with its close relative, *C. phaseoli*. As expected, the density of competitor eggs had a negative impact on egg-to-adult survival of *C. maculatus* (χ_1^2 = 52.6, p < 0.001, Fig 4). To estimate the strength of selection on recessive deleterious alleles expressed in offspring, we compared the effect of larval competition in inbred and outbred *C. maculatus larvae*. As expected, inbreeding reduced larval survival (χ_1^2 = 49.2, p < 0.001, Fig. 4). Moreover, inbred larvae suffered more from the effect of competition compared to outbred offspring (Inbreeding:Egg density interaction: χ_1^2 = 3.72, p = 0.035, Fig. 4, Supplementary Table 4), confirming that competition increases selection on genetic quality.

Interaction coefficients in logistic regression models represent deviations from multiplicative effects on odds ratios. However, the relevant currency in the eyes of natural selection is given by relative differences in survival among genotypes. Therefore, we estimated the strength of natural selection against recessive deleterious alleles by comparing the relative survival of outbred and inbred larvae at low density (no competition) and high density (six competitors – the maximum observed within our data range) based on estimates from a Bayesian mixed effect model, with the strength of selection at the level of competition, *c*, proportional to: $\Delta\omega_c = 1 - \frac{v_{I,c}}{(v_{O,c})}$, where v_I and v_O is viability of inbred and outbred larvae, respectively. This yielded a fitness cost of deleterious recessives equal to: $\Delta\omega_{C=0}$ = 0.20 (95% CI: 0.05-0.37) with no competition, and: $\Delta\omega_{C=6}$ = 0.84 (0.67-0.94) at high competition, implying a roughly four times greater strength of purifying selection.

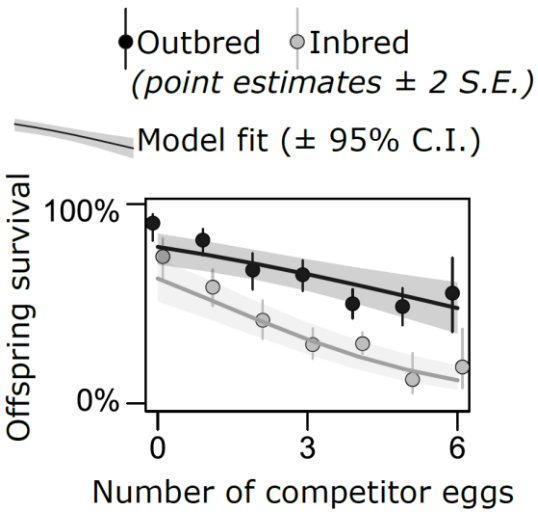

Figure 4: The fitness consequences of larval competition
Eggs placed on seeds with more competitor eggs suffered lower survival. This effect was stronger in inbred (grey) compared to outbred (black) larvae, resulting in stronger selection against deleterious alleles at high competition.

Learning and maternal care by mothers of different genetic quality

We compared the ability of inbred and outbred females to assess the environmental cue and improve maternal care by learning. A larger proportion of the females in the predictable environment were found in the patch with uninfested seeds compared to females in the two unpredictable environments (χ^2_2 = 177.2, p < 0.001), replicating the results seen in the previous experiment (compare Fig. 2 and Fig. 5). Outbred females performed better care compared to inbred females (χ^2_1 = 16.6, p < 0.001). Interestingly, however, the difference diminished with time both within (χ^2_2 = 117.8, p < 0.001) and between (χ^2_2 = 223.0, p < 0.001) runs, suggesting that inbred females took longer to find the patch with uninfested seeds, but then performed like outbred females in the last run of each trial (Fig. 5). This indicates that learning can diminish innate genetic differences in maternal care, given enough time. Importantly, this ameliorating effect of learning was strongest in the predictable environment (Environment:Inbreeding interaction: χ^2_2 = 14.6, p < 0.001; Environment:Inbreeding:Run interaction: χ^2_4 = 24.3, p < 0.001, Fig. 5, Supplementary Table 5).

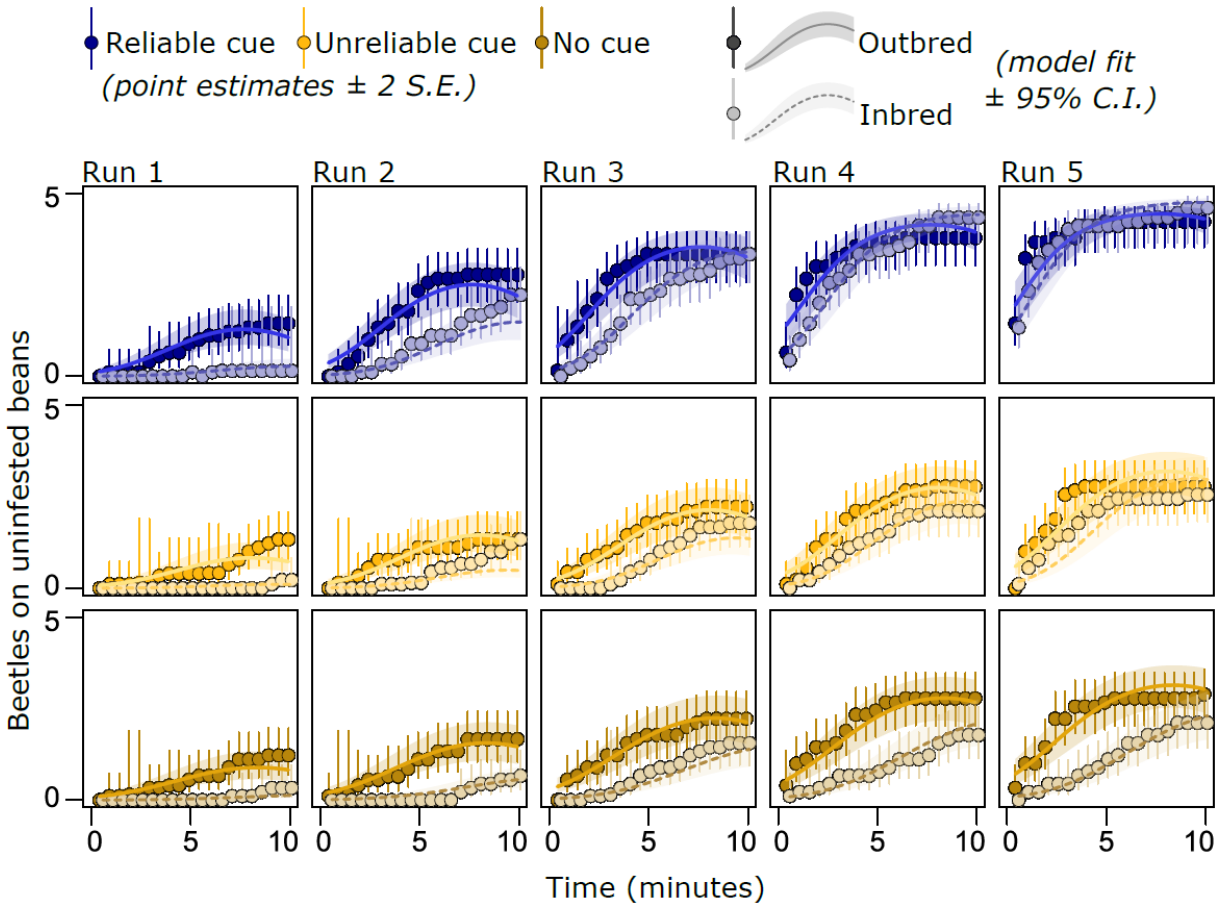

Figure 5: Host search in females of different genetic quality

Females learnt the location of the patch with uninfested host seeds as runs progressed. The rate of learning was again highest in females exposed to the reliable cue (blue) compared to those exposed to the unreliable cue (yellow) or no cue (brown). Inbred females were poorer at finding uninfested seeds. However, learning reduced this difference between outbred and inbred females, especially if females received the reliable cue.

When inspecting the number of eggs laid on host seeds, we found that females in the predictable environment laid both a larger fraction of eggs (χ^2_2 = 72.8, p < 0.001) and overall more eggs (χ^2_2 = 98.3, p < 0.001) on uninfested seeds compared to females in the two unpredictable environments, again replicating the results seen in the previous experiment (compare Fig. 3 and Fig. 6). Outbred females performed better compared to inbred females, both with regards to the fraction (χ^2_1 = 13.4, p < 0.001) and total number (χ^2_1 = 33.2, p < 0.001) of eggs laid on uninfested seeds. For the fraction of eggs on uninfested seeds, we found no effect of the environmental cue on the difference between inbred and outbred females (Environment:Inbreeding interaction: χ^2_2 = 3.88, p = 0.14). However, for the total number of eggs on uninfested seeds, the difference between inbred and outbred females was smaller in the predictable environment (Environment:Inbreeding interaction: χ^2_2 = 11.7, p = 0.003, Fig. 6). This result lends further supports to the hypothesis that predictable environments that leave opportunity for learning can ameliorate individual fitness differences in maternal care owing to genetic quality. Thus, our results show that adaptive behavioural plasticity in the predictable environment diminishes genetic differences in both maternal care and offspring survival, reducing the strength of selection and weakening IGEs between mothers and their offspring.

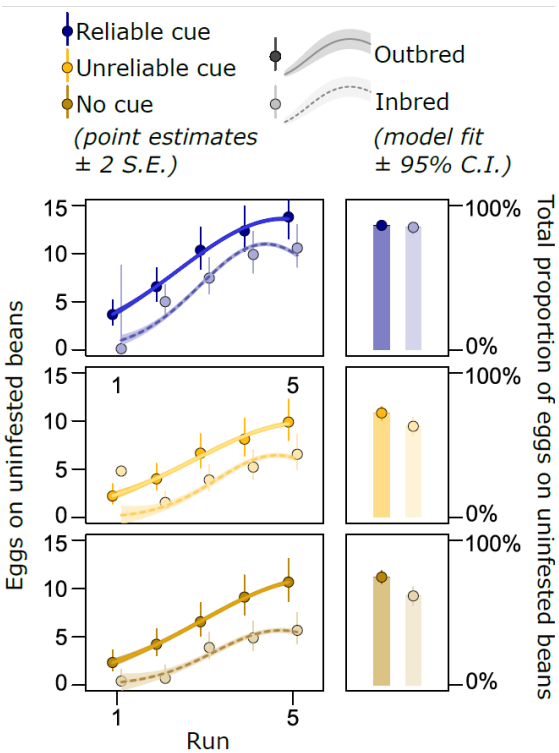

Figure 6: Host choice in females of different genetic quality
Females got better at locating the patch with uninfested seeds as runs progressed. The rate of improvement was again highest in females exposed to the reliable cue (blue). Inbred females laid fewer eggs on the uninfested seeds. However, when receiving the reliable cue, inbred and outbred females showed smaller differences in the number and proportion of eggs placed on uninfested seeds compared to when receiving the unreliable (yellow) or no (brown) cue.

Genetic load in predictable and unpredictable environments

We quantified the relative fitness cost associated with recessive deleterious alleles in each of the three environments by comparing fitness of inbred and outbred genotypes. Fitness was calculated by weighting the total number of eggs laid on infested and uninfested seeds (Fig. 6) by the predictions for larval survival at no competition (uninfested seeds) and three competitors (the mean number of *C. phaseoli* eggs on infested seeds) (Fig. 4). Expected fitness was higher in the predictable environment compared to the two unpredictable environments (Fig. 7A). Moreover, and echoing the previous findings, the reduction in fitness due to recessive deleterious alleles was lower in the predictable environment with a reliable cue (Δω= 48%, CI: 29-61%) than in the environments with a unreliable cue (Δω= 60%, CI: 45-70%, P_{MCMC} = 0.062) and no cue (Δω= 64%, CI: 52-74%, P_{MCMC} = 0.006), although the difference was marginally non-significant in the first comparison (Fig. 7B, C).

Hence, in accordance with theory, the predictable environment rendered higher fitness and population growth, while at the same time relaxing selection against deleterious alleles. Based on our experimental estimates of selection, we predicted the long-term fitness consequences of behavioural plasticity in the predictable (reliable cue) and unpredictable (no cue) environment by parameterizing an existing model by Kawecki et al. (1997) (23) with our experimental data (full details are given in Supplementary 6). This model estimates the genetic load at mutation-selection balance in a meta-population experiencing two different environments that differ in the strength of selection on deleterious alleles. Based on our experimental data, we set the mean strength of selection in the unpredictable environment to be 0.64/0.48 times stronger in the unpredictable environment (i.e. s_k = 1.33s_j, Fig. 7B, C). The results how that, while fitness is always greater in the predictable environment with a reliable cue, the frequency of deleterious alleles increases in the population as the environment becomes more predictable due to the alleviating effect of adaptive behavioral plasticity on the strength of selection (Fig. 7D). The resulting fitness effects of this accumulated genetic load are more pronounced at high mutation rate and in the unpredictable environment. Thus, in certain scenarios (high predictability of environmental variation and high mutation rate), it could be envisioned that species evolving in predictable environments will be unable to colonize unpredictable environments due to competitive exclusion by resident species.

To illustrate this point further, we modelled the relative survival of the competitor, *C. phaseoli*, in the survival experiment (Fig. 4), depending on the density of eggs and the inbreeding status of *C. maculatus*. This showed that the survival of *C. phaseoli* depends on if *C. maculatus* is inbred or not (Inbreeding:egg density interaction: χ_1^2 = 5.38, p = 0.020, Supplementary Fig. X). To quantify this dependence in more detail, we estimated the competitive outcome between the two species when coinhabiting the same seed. This model confirmed that the outcome of the species-interaction depends on the inbreeding status of *C. maculatus* in such as way that *C. phaseoli* has a competitive

disadvantage against outbred *C. maculatus* larvae, but an advantage when *C. macultatus* is inbred (Inbreeding:egg density: χ_1^2 = 7.83, p = 0.005, Fig. 7E). Based on estimates of interspecific competition coefficients and carrying capacities for each species based on the survival data, we calculated competition isoclines and mapped them on the model predictions of competitive outcome between the two species (Fig. 7E). When *C. phaseoli* is competing against outbred *C. maculatus*, a non-stable equilibrium is reached, with the more abundant species excluding the rare colonizing species. However, when *C. phaseoli* is competing against inbred *C. maculatus* it is the superior competitor and is predicted to exclude *C. maculatus*, irrespective of starting population sizes.

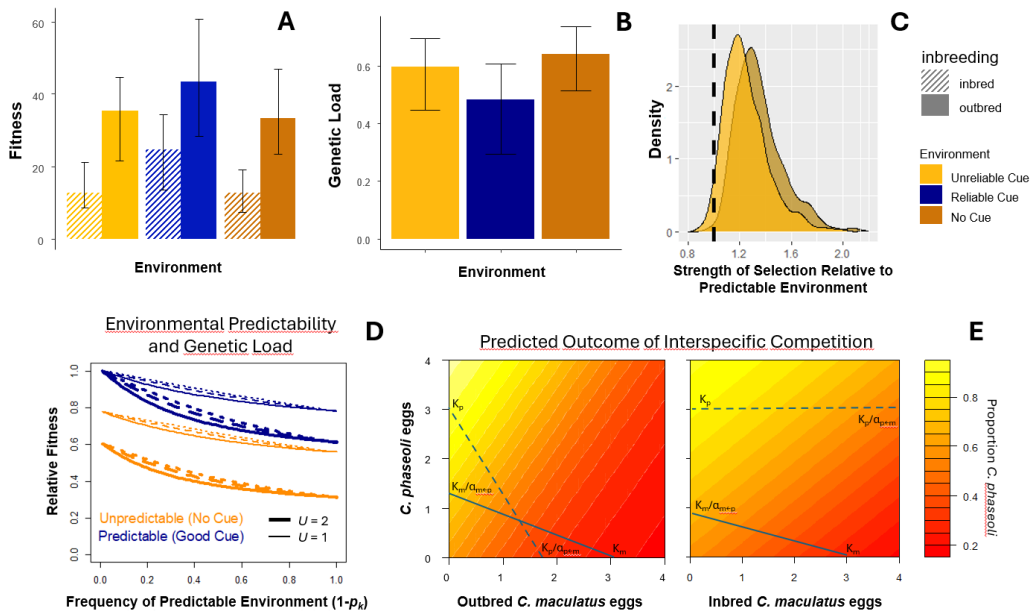

Figure 7: Genetic load in predictable and unpredictable environments.
In A) Expected offspring production is highest in the predictable environment providing a reliable cue compared to the other two environments. B) The strength of selection against deleterious recessive alleles in inbred individuals is reduced in the predictable environment relative to the two unpredictable environments. C) Bayesian posterior densities showing the increase in the strength of selection in the two unpredictable environments compared to the predictable environment. D) Evolution in the predictable environment is predicted to relaxe selection on deleterious alleles, leading to higher fitness but also an accumulation of genetic load in the meta-population. This effect increases for higher deleterious mutation rates (thick lines: U = 2, thin lines U = 1, set to capture the range of probable values in eukaryotes (90)). Load increases further when the predictable environment is more productive (full lines: B_j/B_k = 1.96 based on the difference in expected fitness of inbred individuals in the environment with a reliable cue relative to those in the environment with no cue, hatched lines: B_j/B_k = 1.30 based on the same difference between outbred individuals, and dotted lines: $B_j = B_k$ for comparison). Further details are given in Supplementary 6. Given that the deleterious mutation rate is not negligible, behavioral plasticity and evolution in the predictable environment will increase load in the unpredictable environment to levels with potentially drastic effects on the outcome of interspecific competition. E) This effect is illustrated by comparing the relative success of *C. phaseoli* in the survival experiment when competing against either outbred or inbred *C. maculatus*. Interspecific competition isoclines are drawn based on approximations of each species' carrying capacity (K) and interspecific competition coefficients (α) on a single mung bean, based on the survival data. When *C. phaseoli* is competing against outbred *C. maculatus*, a non-stable equilibrium is predicted, with the competitive outcome dependent on the starting abundance of each species. Thus, the more abundant species is expected to exclude the colonizing species. When *C. phaseoli* is competing against inbred *C. maculatus* it is the superior competitor and will exclude *C. maculatus*, irrespective of starting frequencies.

Discussion

Finetuning of behaviours can allow organisms to avoid perils and shield them from selection. Behavioural plasticity is therefore regarded as a central mechanism allowing animals to cope with fluctuating environments (3,14,34,40). However, by relaxing the strength of selection overall, behavioural plasticity may lead to increases in conditionally deleterious alleles, which' effects may become exposed in the absence of mitigating behaviours. If this process continues for long enough, organism practising extensive behavioural plasticity are predicted to build up substantial conditionally deleterious genetic loads (17,42,58), perhaps to the extent that they no longer will be competitive in situations where adaptive plasticity is restricted by too rapid and unpredictable environmental changes (90,91). Indeed, to accurately finetune behaviours by learning, the organism needs to be able to assess and predict environmental variability (17,26,27), leading to the expectation that organisms occupying environments that differ in their predictability should show systematic differences in the expression of learning and conditional genetic loads.

Here, we sought an experimental proof-of-principle for this hypothesis. By manipulating the predictability of environmental cues given to egg-laying female seed beetles, we show that learning is strongly dependent on reliable information on future host quality and location. This led to adaptive behavioural plasticity and greatly improved maternal care in the predictable environment, in turn reducing genetic selection in juveniles. This relaxed selection is expected to lead to the build-up of a cryptic genetic load over time. We show that increased genetic load is likely to feed back on the female's ability to perform maternal care; inbred mothers were significantly worse at finding uninfested hosts. However, inbred females learned the location of uninfested hosts with time, diminishing genetic differences in maternal care. Importantly, learning was facilitated by reliable cues, contributing further to relaxing selection on genetic load in the predictable environment. Hence, our study presents convincing evidence for a positive feedback loop between environmental predictability, adaptive behavioural plasticity, and the strength of purifying selection.

Our study also represents a rare experimental demonstration of how the strength of indirect genetic effects (IGEs) can be moulded by the environment. We identified effects of recessive deleterious alleles on both the ability of mothers to provide care and on their offsprings' survival, such that (outbred) mothers of high genetic quality provided better care and increased survival of their offspring, who also had higher intrinsic viability. This positive genetic covariance between the mothers trait (care) and the expression of her offsprings' trait (survival) increases genetic variance in offspring fitness relative to a situation without IGEs (40,57,58,60), and should lead to more efficient purging of genetic load. However, this positive covariance was considerably weakened in the predictable environment that reduced genetic differences between both adults and offspring,

demonstrating that environmental variation can be a key component of evolutionary dynamics driven by IGEs.

C. maculatus females use the presence of eggs to choose whether or not to oviposit (63). However, even though a mother can use cues to make informed decision on where to oviposit, she cannot protect the offspring from the choices made subsequently by other mothers ovipositing on the same host. Likewise, larval genotypes that compete will constitute an evolving environment that may favour the evolution of even more (or less) pronounced competitive traits. This illustrates that environmental predictability in this system is likely to evolve as a function of genes and the IGEs exerted between both competing females and their juvenile offspring (77). Similar dynamics have been elegantly demonstrated in burying beetles (22,51,92,93), and as we argue here, the increased opportunity for learning of maternal care may have strong impact on these processes. It is possible that the interplay between environmental predictability and IGEs may be a key driver of geographic differentiation in strategies of host use in this system. Indeed, different geographic strains of *C. maculatus* show genetic differentiation in foraging strategies (94) but see: ((95)) and novel host use (71). Host specialization has been shown to evolve rapidly in this (74,96) and closely related species (97) and future studies could more directly explore the role of IGEs in driving local adaptation in this system, which may provide important insights into the rapid geographic spread of this insect pest.

While our chosen environmental treatments represent realistic situations for egg-laying *C. maculatus* females, they are unlikely to perfectly match the level of environmental predictability and the frequencies of informed and uninformed oviposition choices in natural populations. Nevertheless, because female *C. maculatus* are faced with ephemeral host availability and varying population densities and levels of competition (63,70,71,71,75,76,78), unpredictability in host quality and abundance is likely ubiquitous. Thus, our treatments were chosen to capture this natural variability, yet the results should not be taken literally but as a proof-of-principle that environmental predictability is key in determining the adaptive value of behavioural plasticity and potential for learning, with cascading effects on the strength of selection and genetic load. To illustrate this point further, we also analysed effects on juvenile survival of the competitor *C. phaseoli* when coinhabiting seeds with inbred and outbred *C. maculatus* larvae. This showed that also competing species can be affected by the dynamics between environmental predictability and behavioural plasticity (Fig. 7). Indeed, our adoption and parameterization of the model on genetic load in heterogenous environments by Kawecki et al. (1997) (23) illustrates that behavioural plasticity in predictable environments can build up a sizeable conditionally deleterious genetic load that becomes exposed to selection upon contact with competing species evolving without plasticity. By parameterizing the model with our rather extreme experimental scenario, comparing an environment giving perfect cue reliability with an environment giving no cue at all, in a situation where heavily infested hosts were presented before high quality hosts (thus skewing the placement of eggs towards infested hosts, all else equal), we

likely overestimated the cost associated with environmental unpredictability. Thus, the model predictions should be taken as an illustration of the principle rather than as an attempt to predict genetic load in *C. maculatus*. Nevertheless, it is worth noting that by assuming homogeneous selection across genomic loci within each environment, and by focusing only on deleterious alleles (i.e. no antagonistic pleiotropy across environments), our calculations underestimate the magnitude of the (hidden) genetic load built up in the predictable environment (98).

Another potential caveat of our study is that our lines were almost completely isogenic (highly inbred), and hence, our estimates of the genetic load exposed by homozygosity is in this sense arbitrary and does not reflect the level of exposure of recessive deleterious alleles that would occur by inbreeding in natural populations. However, our rationale was that these lines would serve as a powerful tool to estimate the relative strength of selection across the predictable and unpredictable environments by manipulating mothers and their larvae to be assayed in outbred and inbred state; completely hiding or expressing all the differentially fixed recessive deleterious alleles across the three lines. Hence, all our estimates are meant to be interpreted in relative terms, giving indications of how the strength of purifying natural selection is affected by correlated changes in maternal care and offspring competition. By doing so, our study illustrates the important role that environmental predictability can play in facilitating learning and adaptive behavioural plasticity, in turn leading to correlated changes in natural selection on associated traits and affecting the strength of IGEs. In support of our findings, a recent comparative study across bird species found that unpredictable environments are associated with reduced parental care (38). Another recent study on burying beetles found that parental care led to a build-up of deleterious mutations over 20 generations of laboratory evolution compared to populations evolving without care (22). However, a study on the same species found the contrasting result that parental care increased phenotypic variance in offspring size (99), which is opposite to general expectations (21,47,49,100,101). This highlights the importance of considering the exact type traits and context of parental provisioning and thus motivates further study of the relationship between environmental predictability and IGEs involving parents and offspring (62). In summary, our study highlights the important link between environmental variation, adaptive behavioural plasticity and genetic load, and that IGEs between parental provisioning and offspring fitness can be highly sensitive to environmental conditions. This in turn has important implications for rates of local adaptation and outcomes of species competition across environments that differ in their predictability.

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