

Environment-dependent reversal of a life history trade-off in the seed beetle *Callosobruchus maculatus*

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Abstract

Environmental manipulations have consistently demonstrated a cost of reproduction in the capital-breeding seed beetle, *Callosobruchus maculatus*, as females deprived of seeds or mates lay fewer eggs and thereby increase their longevity. Yet fecundity and longevity tend to be positively correlated within populations, perhaps as a consequence of individual differences in resource acquisition. We conducted a split-brood experiment that combined a manipulation of seed availability (seeds present or absent) with a quantitative-genetic analysis of fecundity and lifespan in each environment. Each trait was significantly heritable in each environment. Seed availability not only altered mean fecundity and longevity between environments, but also modified how the traits were correlated within environments. The signs of both the phenotypic and genetic correlations switched from positive when seeds were present to negative when seeds were absent. This reversal persisted even after the effect of body mass (a potential indicator of resource acquisition) was statistically controlled. Cross-environment genetic correlations were positive but significantly less than one for each trait. We suggest that the reversal of the fecundity–longevity relationship depends on a shift in the relative importance of resource-acquisition and resource-allocation loci between environments. In particular, a cost of reproduction may be apparent at the individual level only when seeds are scarce or absent because differences in reproductive effort become large enough to overwhelm differences in resource acquisition. Despite their common dependence on resources acquired during larval stages, fecundity and lifespan in *C. maculatus* do not appear to be tightly coupled in a physiological or genetic sense.

Introduction

Life-history evolution can be constrained by trade-offs among various traits that contribute to fitness (Roff, 2002). Perhaps the most widely studied constraint is the cost of reproduction, in which an increase in current reproduction reduces survival or future reproduction (Williams, 1966; Reznick, 1985; Bell & Koufopanou, 1986). At a physiological level, reproductive costs may be caused by the competitive allocation of resources

between reproduction and somatic maintenance (as in the familiar Y-model of allocation; Zwaan *et al.*, 1995; Sgrò & Partridge, 1999). Yet several studies have failed to detect a mortality cost associated with increased reproduction, and others have found that the effects of reproductive effort on survival depend on the environment in which each trait is measured (Reznick *et al.*, 2000; Ackermann *et al.*, 2001). It has become increasingly evident that life-history trade-offs need to be assessed in multiple environments (Stearns *et al.*, 1991; Bégin & Roff, 2001).

Conclusions about the cost of reproduction may also depend on the technique used to detect it (Partridge, 1992; Rose & Bradley, 1998; Sinervo & Svensson, 1998).

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Phenotypic correlations will not indicate a trade-off if high variation in resource acquisition masks the effects of variation in resource allocation (van Noordwijk & de Jong, 1986). Manipulating an organism's environment can alter the distribution of phenotypes and thereby establish a functional relationship between reproductive rate and survival, but it is not clear if such a relationship accurately predicts evolutionary responses (Chippindale *et al.*, 1997). Even genetic covariances may not produce an accurate picture of evolutionary trade-offs if traits do not interact in a simple bivariate manner (Charlesworth, 1990) or if the number of loci affecting resource acquisition is much larger than the number affecting resource allocation (Houle, 1991). In this study, we combined a quantitative-genetic approach with an environmental manipulation to examine the relationship between fecundity and longevity in the seed beetle *Callosobruchus maculatus* (F) (Coleoptera: Bruchidae).

The simple life cycle of *C. maculatus* makes it a good subject for determining life history trade-offs (Lessells, 1991; Smith, 1991), but this insect also illustrates some of the complexities associated with estimating the cost of reproduction. Beetles have been associated with human stores of legume seeds for thousands of generations (Messina, 1998). In storage, adults are facultatively aphagous and 'capital' breeders (Stearns, 1992); females depend entirely on resources acquired during larval stages for survival and reproduction. Phenotypic correlations between fecundity and longevity tend to be positive (suggesting no trade-off), but studies of closely related *Callosobruchus* species have produced disparate results with respect to the sign and magnitude of the genetic correlation (Møller *et al.*, 1989a; Nomura & Yonezawa, 1990; Tanaka, 1993). In contrast, experimental manipulations consistently suggest a trade-off, as females deprived of seeds or mates lay fewer eggs and, consequently, live longer than nondeprived females (Møller *et al.*, 1989b; Tatar *et al.*, 1993; Wilson, 1994). By varying both nutrient availability and reproductive effort, Tatar & Carey (1995) elegantly demonstrated that the survival cost in *C. maculatus* could be mitigated by facultative adult feeding.

The experiment described here was motivated by a previous study in which *C. maculatus* females were subjected to four different levels of seed availability (Messina & Slade, 1999). As expected, mean longevity was inversely related to mean fecundity across the four environments. Within environments, however, phenotypic correlations were inconsistent; individual fecundity and longevity were positively correlated when seeds were abundant, uncorrelated when seeds were few, and negatively correlated when seeds were absent (Messina & Slade, 1999; in the absence of seeds, mated females may 'dump' eggs on any smooth substrate; Wilson & Hill, 1989; Fox & Tatar, 1994). Thus, applying the same technique (phenotypic correlation) to groups of females with the same average level of larval resource acquisition

(females were randomly assigned to the four seed-availability treatments after they became adults) produced opposite conclusions regarding the cost of reproduction.

This study examined whether the genetic covariance between fecundity and longevity similarly varies between environments. Plasticity of the genetic correlation (i.e. a change in the genetic correlation between environments) would suggest that the two traits are not tightly integrated physiologically (Stearns *et al.*, 1991), and that correlated responses to selection will be environment-dependent (Windig, 1994). We were particularly interested in whether the reversal of the fecundity-longevity relationship could be explained by higher among-individual variation in resource allocation when seeds are rare. At a phenotypic level, some *C. maculatus* females (egg-dumpers) show only a modest drop in realized fecundity in the absence of seeds, whereas others die without laying an egg (Wilson & Hill, 1989; Messina, 1991, 1998; Tatar & Carey, 1995). If high variation in resource allocation produces a negative genetic covariance between fecundity and longevity in the absence of seeds, and low variation yields a positive relationship, then this result would run counter to the usual prediction that genetic trade-offs are *less* likely to be observed in stressful or novel environments (Service & Rose, 1985).

We used a half-sib/full-sib, split-brood design to compare the heritabilities of fecundity and longevity and their genetic correlation at two extremes of seed availability. Because adult mass at emergence is frequently used as a potential indicator of resource acquisition, and is known to affect fecundity and longevity in *C. maculatus* (Credland *et al.*, 1986; Møller *et al.*, 1989a), we also determined whether the contribution of mass to the fecundity-longevity relationship differed between environments. To examine whether a shift in the genetic correlation between environments reflects genetic variation for plasticity (i.e. whether genotypes vary in their responses to seed deprivation; Schlichting & Pigliucci, 1998), we calculated cross-environment correlations for fecundity and longevity, and devised specific tests to determine whether the correlations differed from zero or one. A correlation coefficient that is not statistically distinguishable from zero signifies that trait expression is genetically independent between environments, whereas a correlation that is indistinguishable from one suggests complete genetic dependence.

Materials and methods

Origin and maintenance of the population

A population of *C. maculatus* was derived from infested pods of cowpea, *Vigna unguiculata* (L.) Walp, near Ouagadougou, Burkina Faso (Messina & Slade, 1999). Three generations after it was brought into the

laboratory, the population was found to possess high additive-genetic variation for body size ($h^2 = 0.90 \pm 0.20$) and lifetime fecundity ($h^2 = 0.63 \pm 0.15$) (Messina, 1993). We conducted the current breeding experiment after the population had been maintained in the laboratory at large population sizes for 70 generations. The population was therefore likely to have reached genetic equilibrium with respect to standard culture conditions.

Each generation was formed by adding 1500–2500 newly emerged adults (estimated by volume) to a 2-L jar containing *c.* 750 g of cowpea seeds of the 'California black-eye' variety. Adults were collected in the middle of the emergence period (28–32 days after the start of the previous generation) in order to reduce directional selection for development time or adult mass (Møller *et al.*, 1990; Sgrò & Partridge, 2000). We maintained stock cultures and conducted the experiment in a growth chamber at 24 °C and continuous light. The laboratory environment provides a reasonable approximation of the 'natural' environment of *C. maculatus*, which appears to have evolved specific traits for exploiting legume seeds both in the field and in storage (Messina, 1998).

Experimental design

We used a half-sib/full-sib, split-brood design, in which full-sib females were divided between environments with or without seeds. To obtain sires and dams, we collected several hundred infested seeds from the stock culture and isolated each seed in a small vial. Vials were inspected twice daily for newly emerged adults. Each newly emerged, unmated sire was put into an empty Petri dish with five newly emerged, unmated dams for 24 h. We collected a total of 105 sires over six consecutive days; each collection day was treated as a separate block in subsequent statistical analyses. After the 24-h mating period, each dam was transferred to a 10-cm Petri dish containing approximately 100 cowpea seeds. This number of seeds ensured that the offspring (test) generation developed without competition within seeds (Messina, 1991). The positions of dishes in the growth chamber were randomized with respect to sire identity.

Dishes were inspected for hatched eggs on seeds after 12 days. If fewer than four dams per sire produced hatched eggs (most likely because two or more dams were not inseminated during the 24-h mating period), all offspring from that sire were eliminated. This reduction left 94 sires mated to either five dams (56 sires) or four dams (38 sires), or 432 full-sib families. When offspring began to emerge, we inspected the dishes twice daily, and collected 10–12 female offspring from each full-sib family. We used only offspring that had emerged during the 6 h since dishes were last inspected.

Each offspring female was weighed on an electrobalance, paired with an unrelated male, and placed into a 6-cm dish containing either no seeds or 25 cowpea seeds.

Females from the same full-sib family were alternately assigned to the seeds and no-seeds treatments until there were four to six individuals in each environment. Most full-sib families (91%) were represented by either five (337 families) or six (57 families) females per environment. We placed a total of 2201 females in dishes with seeds and 2207 females in dishes without seeds. Dishes were randomly arranged in the growth chamber with respect to sire identity, dam identity, and seed availability. Female survival was determined daily. After a female died, we recorded the total number of eggs laid on the seeds or dish.

Statistical analyses

Data were analysed by restricted maximum likelihood (REML), as implemented by the MIXED procedure in SAS version 8 for Windows (SAS Institute Inc., 1992; Littell *et al.*, 1996). For univariate analyses within treatments, effects were blocks, sires within blocks, and dams within sires. All effects were considered random. Trait means and their standard errors were obtained by requesting the solution for the model intercept ('SOLUTION' option on the 'MODEL' statement). Additive-genetic (V_A), maternal-effect (V_M), and environmental (V_E) variances were estimated as four times the sire variance, the dam variance minus the sire variance, and the residual (within-dam) variance minus twice the sire variance, respectively (Falconer & Mackay, 1996). This formulation assumes that dominance variance is negligible; if dominance variance is present, the estimates of V_M and V_E will be inflated by $1/4V_D$ and $3/4V_D$, respectively (Falconer & Mackay, 1996). In our experiment, the maternal-effect variance includes both strictly maternal effects (e.g. via egg provisioning) and common-environment effects owing to full sibs developing in the same dish. The remaining environmental variance (V_E) includes the effects of unshared, individual environments. Standard errors of V_A , V_M , and V_E were calculated from the asymptotic variances and covariances of the observational variance components (obtained by the 'ASYCOV' option), using the standard formula for the variance of sums. Heritabilities were estimated as $V_A / (V_A + V_M + V_E)$; standard errors of the heritabilities were estimated by the delta method (Weir, 1996), using Mathematica software (Wolfram, 1996; program available on request).

Likelihood-ratio tests were used to determine whether V_A and V_M differed from zero. Under the null hypothesis, twice the difference in log-likelihoods between the full model and a model with a given variance constrained to be zero should have a χ^2 distribution with one degree of freedom. As the test in this case is one-tailed, the resulting probabilities were halved. V_A was constrained to zero by leaving the sire effect out of the model. A more complicated procedure was used to constrain V_M to zero; the relevant SAS program is in the Appendix (see Supplementary material section).

Genetic, maternal-effect and environmental correlations between each pair of traits were estimated separately for each seed-availability treatment using programs described in the Appendix. The genetic correlation (r_g) is equivalent to the variance component correlation among sires; r_g and its asymptotic standard error is output directly by program 2A. Modifying the program to constrain r_g to zero or one is straightforward (see Appendix); the resulting likelihood-ratio tests are two-tailed and one-tailed, respectively. For graphical depiction of genetic correlations, empirical best linear unbiased predictors (EBLUPs; Littell *et al.*, 1996) of sire breeding values were calculated (see Program 2A, Appendix). Breeding values are two times the sire EBLUPs provided by SAS. Maternal-effect (r_m) and environmental (r_e) correlations were calculated from the output of program 2B, which calculates covariances between traits among sires (COV_S), among dams within sires (COV_D), and within dams (COV_W). For a given pair of traits, $COV_D - COV_S$ estimates the maternal-effect covariance; this value divided by the square root of the product of the maternal-effect variances (see above) produces an estimate of r_m . Similarly, $COV_W - 2COV_S$ estimates the environmental covariance; this value divided by the square root of the product of the environmental variances estimates r_e . Standard errors of r_m and r_e were estimated by the delta method. (As a check, r_g and its standard error were estimated from the output of program 2B in a similar fashion; the results matched the output of program 2A). No method could be found for constraining r_m or r_e , so likelihood-ratio tests could not be performed for these parameters. For comparison with r_g , r_m and r_e , phenotypic correlations (r_p) were calculated as simply the raw product-moment correlations.

One of our main goals was to determine whether genetic correlations were affected by seed availability. Towards this goal, Program 2C (see Appendix) was used to constrain r_g in both treatments to the same value, r_g^* . We varied r_g^* in increments of 0.01 to find the value that maximized the log-likelihood of the model. This log-likelihood was compared with that of the unconstrained model, in which r_g was free to differ between treatments. The resulting test is two-tailed and has 1 d.f.

We estimated genetic correlations of fecundity and longevity across seed availability treatments, and tested whether they differed from zero and one, using Program 3 in the Appendix. We also estimated the genetic correlation between fecundity in the presence of seeds and the percentage of reduction in fecundity caused by the absence of seeds (see Results). For this purpose, we first calculated the mean fecundity of each dam's progeny in each treatment. The mean fecundity with seeds present and the percentage of reduction in fecundity between treatments were then treated as if they were two traits measured on a single offspring of each dam. This method allows us to calculate the genetic correlation between the two measures, but does not

separate maternal and environmental contributions to the traits.

Parameter estimates and EBLUPs were calculated using untransformed data. Likelihood-ratio tests were performed after square-root transformation. Sire means were approximately normally distributed after square-root transformation (Shapiro-Wilk's test, $P > 0.05$), but not always before transformation. Unfortunately, no transformation could be found to make residuals normally distributed. The worst violation of normality was for fecundity in the seeds-absent treatment, which was right-skewed, with a single mode at zero containing 13.4% of the observations. Nonetheless, because the dataset is nearly balanced, the REML variance and covariance estimates are close to the (unbiased) methods-of-moments estimators based on sums of squares. Standard errors and hypothesis tests may be biased to an unknown degree. Because of long run times, bootstrapping was not feasible, and the validity of jackknifed standard errors of quantitative-genetic parameters with non-normally distributed data has not been established.

Results

Trait means, heritabilities and variance components

Callosobruchus females displayed a clear cost of reproduction between environments; seed deprivation caused a more than three-fold decrease in mean fecundity and a 70% increase in mean longevity (Table 1). Each trait possessed significant additive-genetic variation in each environment, although the heritability of longevity was lower than that of fecundity. Mass at adult emergence was also heritable (Table 1; all females were included in this analysis because mass was measured before females were assigned to treatments). There was a significant contribution of maternal effects ($V_M > 0$) to each trait in each environment, but the maternal-effect variance component was consistently lower than the additive-genetic component (Table 1). In our experiment, V_M potentially includes strict maternal effects, effects of a shared environment among full-sib larvae, as well as any nonadditive genetic effects. Comparisons across variance components indicate that estimates of h^2 were similar between environments for longevity because both genetic and nongenetic variances rose substantially in the absence of seeds (see also Fig. 1). For fecundity, h^2 was somewhat lower in the absence of seeds because of a decrease in V_A and an increase in V_E (Table 1).

Because the mean values of fecundity and longevity were very different in the two environments, the mean-standardized, additive-genetic coefficient of variation ($CV_A = 100 \times \sqrt{V_A} / \bar{x}$) may be more appropriate than h^2 for comparing the amount of genetic variation expressed in each environment (Houle, 1992). For fecundity, CV_A was much higher when seeds were absent than when they were present, although the point

Table 1 Means, heritabilities and variance components (\pm SE) for mass at adult emergence (all females), and for fecundity and longevity of females with or without seeds ($n = 2201$ and 2207 females, respectively).

Traits	Seed availability	Mean	h^2	V_A	CV_A	$V_M \dagger$	V_E
Mass (mg)	–	4.88 \pm 0.08	0.48 \pm 0.10	0.237 \pm 0.055	9.99	0.050 \pm 0.019*	0.212 \pm 0.028
Fecundity	Present	64.5 \pm 3.4	0.60 \pm 0.12	176.9 \pm 41.7	20.62	31.1 \pm 14.6**	86.8 \pm 21.7
	Absent	20.5 \pm 1.2	0.40 \pm 0.10	115.9 \pm 30.5	52.42	23.7 \pm 11.6**	150.1 \pm 16.8
Longevity (days)	Present	8.90 \pm 0.06	0.28 \pm 0.08	0.66 \pm 0.19	9.11	0.16 \pm 0.08*	1.57 \pm 0.11
	Absent	15.27 \pm 0.21	0.25 \pm 0.08	4.66 \pm 1.56	14.15	2.15 \pm 0.70***	12.00 \pm 0.92

\dagger Likelihood-ratio test of whether V_M differs from zero: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. All V_A values differ from zero at $P < 0.0001$.

h^2 , heritability; V_A , additive-genetic variance; CV_A , additive-genetic coefficient of variation; V_M , maternal-effect / common-environment variance; V_E , unshared environmental variance.

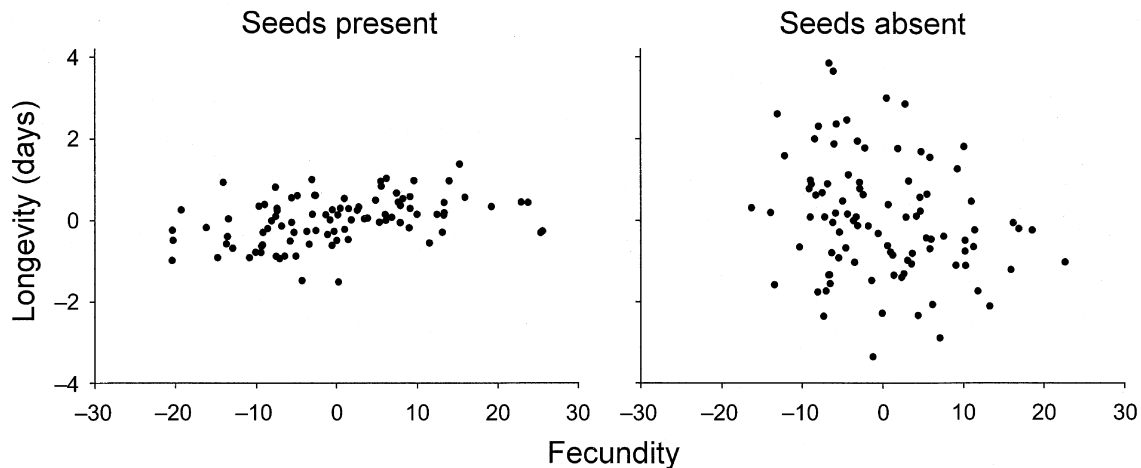


Fig. 1 Scatter plots of estimated breeding values (EBLUPS) for fecundity and longevity when seeds were present or absent. To facilitate comparisons of genetic variances between treatments, standardized values were plotted on the same axis scales.

estimate of h^2 was lower in this environment (Table 1). A similar but smaller difference in CV_A was obtained for longevity. The total (phenotypic) coefficient of variation was also considerably higher when seeds were absent than when they were present (for fecundity: 85.3% vs. 29.7%; for longevity: 28.5% vs. 17.4%).

Trait correlations within environments

As in the previous study, the sign of the phenotypic correlation between fecundity and longevity switched from positive when seeds were abundant to negative when seeds were absent (Table 2). Mass at emergence was positively correlated with both traits in each environment, but the only strong relationship was between mass and fecundity in the presence of seeds (Table 2). Controlling for the effect of mass reduced the correlation coefficients between fecundity and longevity, but the two traits remained positively correlated when seeds were present (partial $r_p = 0.29$) and negatively correlated when seeds were absent (partial $r_p = -0.21$; $P < 0.001$ in each case).

The pattern of genetic correlations closely resembled the pattern of phenotypic correlations. The sign of the correlation between fecundity and longevity was reversed between environments (Table 2; Fig. 1), and this effect of seed availability on r_g was highly significant ($-2\ln\lambda = 8.46$; $P < 0.01$). Like the phenotypic correlation, the genetic correlation between mass and fecundity was considerably higher when seeds were present than when they were absent (Table 2; $-2\ln\lambda = 3.23$; $P = 0.07$). Controlling for the positive effects of mass reduced the correlation coefficient between fecundity and longevity by an equal amount in each environment: partial $r_g = 0.21$ in the presence of seeds and -0.59 in the absence of seeds. All genetic correlations in Table 2 were significantly different from one (likelihood-ratio tests; $P < 0.001$), which indicates at least partial genetic independence between each pair of traits in each environment.

In contrast to the phenotypic and genetic correlations, the maternal-effect correlation between fecundity and longevity was positive both in the presence and absence of seeds, although the strength of the correlation was

Table 2 Phenotypic, genetic, maternal-effect and environmental correlations (\pm SE) for traits of females with or without seeds.

Correlation	Seed availability	Fecundity vs. longevity	Fecundity vs. mass	Longevity vs. mass
Phenotypic	Present	0.32***	0.41***	0.14***
	Absent	-0.18***	0.17***	0.17***
Genetic	Present	0.35 \pm 0.16*	0.57 \pm 0.13***	0.32 \pm 0.18*
	Absent	-0.44 \pm 0.19*	0.28 \pm 0.17	0.34 \pm 0.19
Maternal	Present	0.94 \pm 0.28	0.04 \pm 0.33	-0.05 \pm 0.34
	Absent	0.61 \pm 0.37	-0.22 \pm 0.40	0.11 \pm 0.29
Environmental	Present	0.31 \pm 0.08	0.25 \pm 0.12	0.04 \pm 0.07
	Absent	-0.20 \pm 0.06	0.08 \pm 0.09	0.05 \pm 0.07

*0.05 < P < 0.10, *** P < 0.001, for whether the phenotypic or genetic correlation differs from zero. Likelihood-ratio tests were used to determine the significance of the genetic correlations.

weaker in the no-seeds environment (Table 2 presents point estimates and standard errors but we could not perform likelihood-ratio tests on r_m values). There was little evidence of maternal-effect contributions to correlations between mass and either fecundity or longevity (Table 2). The final component of the phenotypic covariance between traits is the unshared environmental covariance, which results from the two traits being exposed to the same individual environment. Correlations due to individual environmental deviations resembled the phenotypic and genetic correlations; fecundity and longevity were positively correlated in the presence of seeds and negatively correlated in the absence of seeds (Table 2). In addition, mass and fecundity were positively correlated in the presence of seeds.

Cross-environment correlations

A cross-environment genetic correlation considers a trait measured in two environments as two traits, and its magnitude signifies the degree to which the trait is under the same genetic control in each environment. As expected, neither fecundity nor longevity displayed complete genetic independence between environments; cross-environment correlations were significantly greater than zero (Table 3). The correlations were also significantly different from one, however, which indicates familial differences in the degree to which seed deprivation reduced fecundity or increased longevity. Genetic variation for plasticity appeared to be higher for longevity than for fecundity (Table 3).

Table 3 Cross-environment genetic correlations (\pm SE) for fecundity and longevity between the seeds and no-seeds environments, and likelihood-ratio tests ($-2\ln\lambda$) for whether each correlation differs from zero or one.

Trait	Correlation	Different from 0?	Different from 1?
Fecundity	0.76 \pm 0.10	21.14**	4.29*
Longevity	0.44 \pm 0.18	4.36*	11.93**

* P < 0.05, ** P < 0.001.

A genotype \times environment interaction for fecundity is consistent with earlier studies showing wide variation in individual (phenotypic) responses to seed deprivation. To explore how genetic variation for plasticity might be maintained, we calculated the genetic correlation between fecundity in the presence of seeds and the percentage of reduction in fecundity caused by the absence of seeds. This correlation was negative ($r_g = -0.52 \pm 0.19$) and significantly different from zero ($P < 0.01$). Thus, genotypes that were highly fecund when seeds were abundant appeared to be less able to 'withhold' eggs (or cease egg production) in an adaptive manner when there were no suitable oviposition sites.

Discussion

Previous experiments demonstrated that manipulating host availability does not merely affect mean fecundity and longevity among groups of *C. maculatus* females; it simultaneously modifies how the traits are correlated among individuals within groups (Messina & Slade, 1999). This study extends those results by demonstrating that the genetic correlation between fecundity and longevity also switches from positive to negative, depending on whether seeds are abundant or absent. Although we examined only two extreme environments, we suspect that the genetic correlation between fecundity and longevity is near zero at intermediate levels of seed availability. Genetic correlations between these traits appear to mirror phenotypic correlations (Table 2), and the phenotypic correlation gradually shifted from positive to negative across four levels of seed availability in the earlier study (Messina & Slade, 1999).

Our results add to growing evidence that the expression of genetic variance and covariance can vary as much between assay environments as between geographical populations or closely related species (Giesel, 1986; Spitze *et al.*, 1991; Tucic *et al.*, 1991; Gebhardt & Stearns, 1993; Bégin & Roff, 2001). Strong environmental sensitivity will complicate attempts to identify constraints on the simultaneous evolution of multiple characters. On the other hand, it may help explain the maintenance of genetic variation for life history traits or other traits

closely related to fitness (Tucic *et al.*, 1991). If direct or correlated effects of alleles on fitness are environment-dependent and averaged across multiple environments, populations will be less likely to evolve towards particular optimal genotypes. Analyses of quantitative-trait loci in *Drosophila* suggest that allelic effects on lifespan depend strongly on larval density (Leips & Mackay, 2000).

Because *C. maculatus* is a capital breeder, a positive genetic correlation between fecundity and longevity may be attributed to differences in resource acquisition; some females may garner enough resources during larval stages to permit both high fecundity and long adult lifespan (Møller *et al.*, 1989a). Why then does this relationship disappear (and reverse itself) under conditions of seed deprivation? There is no *a priori* expectation that high plasticity in two or more traits should lead to plasticity of trait correlations (Schlichting & Pigliucci, 1998). Our results are consistent with a shift in the relative importance of resource-acquisition and resource-allocation loci between environments (Tanaka, 1996; Reznick *et al.*, 2000; Tatar, 2001). When many seeds are available, genetic or environmental effects on allocation are likely to be small, as all females lay their entire complement of eggs within a few days of adult emergence (Messina & Slade, 1999). When seeds are scarce or absent, variation in resource allocation increases (some females readily 'dump' eggs, while others lay few or no eggs) and the importance of acquisition differences is reduced. Hence, the cost of reproduction becomes apparent even at the individual level. The absence of host seeds in this study increased CV_A for fecundity (Table 1), and the total (phenotypic) CV for fecundity rose from 29.7% in the presence of seeds to 85.3% in the absence of seeds.

The role of body mass provides further support for a reduction in the importance of resource acquisition when seeds are absent. Phenotypic, genetic and environmental correlations all indicated that female mass (a common indicator of resource acquisition) had a stronger positive effect on fecundity in the presence, than in the absence of seeds (Table 2). The effect of body size on fecundity and longevity also appears to be environment-specific in *Drosophila* (Nunney & Cheung, 1997; Norry & Loeschke, 2002). We note, however, that the reversal of the fecundity-longevity relationship in this study persisted even after the effect of mass was statistically controlled. Thus, females may have possessed mass-independent differences in 'vigour' that contributed to the positive relationship between fecundity and lifespan when seeds were present, but became less important when seeds were absent.

Our suggestion that seed availability modifies the relative importance of acquisition and allocation loci presupposes that there is little pleiotropy between the two kinds of loci. As Houle (1991) noted, this assumption seems reasonable for a capital breeding, holometabolous

insect, in which larvae and adults are characterized by very different behaviours and metabolic tasks (but see Foley & Luckinbill, 2001). In addition, we presume that the lack of a trade-off between fecundity and longevity in the presence of seeds reflects individual differences in resource acquisition (that are at least partly independent of body mass). It is possible, however, that fecundity and longevity are functionally constrained even when seeds are abundant, but this constraint is not evident in strictly bivariate analyses that ignore how each trait is related to other (unmeasured) fitness components (Charlesworth, 1990).

Wide variation in resource allocation has been observed previously among seed-deprived females of *C. maculatus* (Wilson & Hill, 1989; Messina, 1991; Tatar & Carey, 1995). Although we did not estimate reproductive schedules (daily egg counts) in this study (Tanaka, 1996; Müller *et al.*, 2001), an earlier experiment with the same beetle population demonstrated that deprived females were nearly bimodal in their egg-laying rates during the first few days after adult emergence (Messina & Slade, 1999). Some of this variation in oviposition plasticity appears to be genetically based, as the cross-environment correlations for both fecundity and longevity were significantly less than one (Table 3). Because seed shortages are likely to occur both in field and storage environments (Wilson & Hill, 1989) and only eggs laid directly on seeds yield viable offspring, it is not clear why *all C. maculatus* females do not remain in a nonreproductive or 'waiting' mode (and thereby increase longevity) until seeds are discovered (Carey *et al.*, 1998 present an analogous situation for Mediterranean fruit flies deprived of protein). One explanation is suggested by the negative genetic correlation between lifetime fecundity in the presence of seeds and the percentage of reduction in fecundity between the seeds and no-seeds environments. This correlation implies that highly fecund genotypes are less able to shut down egg deposition when seeds are absent, or, equivalently, that high egg-laying plasticity entails a fecundity cost in an environment with seeds (DeWitt *et al.*, 1998). Highly fecund genotypes lay more eggs, even when seeds are absent, because they cannot exert as much control over rates of egg maturation (Wilson & Hill, 1989).

There has been considerable discussion of the effects of novel or stressful environments on the expression of genetic variation or covariation underlying life history traits (Bell & Koufopanou, 1986; Hoffmann & Merilä, 1999; Reznick *et al.*, 2000). Several studies have suggested that evolutionary trade-offs will be disrupted in novel environments, perhaps because they derive from an antagonistic pleiotropy that developed in the ancestral environment (Service & Rose, 1985; Holloway *et al.*, 1990; Guntrip *et al.*, 1997). In this study and the previous one (Messina & Slade, 1999), a fecundity-longevity trade-off became apparent only in the no-seeds environment, which can be considered novel (or stressful) in

comparison with the longstanding culture conditions experienced by the population. It may therefore be premature to generalize with respect to the effect of novelty *per se* on trait covariances (Spitze *et al.*, 1991; Kawecki, 1995). Plasticity of genetic and phenotypic correlations between fecundity and longevity does suggest that the two traits are not tightly integrated in a physiological or pleiotropic sense, despite their common dependence on levels of resource acquisition (Stearns *et al.*, 1991). Further insights into the integration of lifespan and fecundity can be gained by examining whether individual loci have joint or independent effects on these fitness components (e.g. Tucic *et al.*, 1998; Hsin & Kenyon, 1999; Clancy *et al.*, 2001).

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEB/JEB535/JEB535sm.htm>

An Appendix with four SAS programs that describe how quantitative-genetic parameters were estimated in this study.

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