

Heritability and 'evolvability' of fitness components in *Callosobruchus maculatus*

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Heritabilities of traits closely related to fitness (e.g. life-history traits) tend to be lower than those of morphological traits in natural populations. It is unclear, however, whether this pattern reflects relatively low additive-genetic variation, relatively high residual variation (i.e. non-additive and environmental effects) or both. A standard, half-sib breeding design was used to estimate narrow-sense heritabilities and coefficients of additive-genetic variation (CV_A) for a life-history trait (total fecundity), a morphological trait (wing length) and a behavioural trait (allocation of eggs among available resources) in two outbred populations of the seed beetle *Callosobruchus maculatus*. Heritabilities of fecundity and wing length were high in both populations whereas the heritability of egg-laying behaviour was low but non-zero. In contrast, estimates of 'evolvability', which depend on CV_A , were highest for fecundity, intermediate for egg-laying behaviour and lowest for wing length. These results resemble those from a recent survey of *Drosophila* studies and suggest that the typically low heritabilities of behavioural or life-history traits are better explained by high residual variation than by low additive-genetic variation. Phenotypic and genetic correlations were generally not significant except for a positive relationship between wing length and fecundity. No evidence was obtained of a trade-off or underlying functional relationship between the number of eggs laid and the pattern of egg dispersion among available resources.

Keywords: egg-laying behaviour, fecundity, fitness components, heritability, seed beetles.

Introduction

Traits that are closely related to fitness, such as life-history traits, often exhibit lower narrow-sense heritabilities (h^2) than do morphological, physiological or behavioural traits in natural populations (Gustafsson, 1986; Mousseau & Roff, 1987; Roff & Mousseau, 1987; Falconer, 1989). The explanation for this robust pattern is unclear (Price & Schluter, 1991). One interpretation considers the low heritabilities of life-history traits as a corollary of Fisher's fundamental theorem (1958) which states that a population at genetic equilibrium should possess little or no additive-genetic variance (V_A) for total fitness. Thus, traits with a major effect on fitness should also exhibit relatively little additive genetic variation. As recent analyses have shown, however, Fisher's theorem concerns only fitness itself and cannot predict the amount of genetic variation associated with a particular fitness component, even for a population at equilibrium (Lande, 1982; Barton & Turelli, 1989; Price & Schluter, 1991).

An alternative explanation is that life-history traits possess as much additive-genetic variation as other traits but are typically subject to a greater amount of environmental variation. This conclusion rests on the simple observation that life-history traits are affected by all of the environmental variation associated with their underlying metrical traits plus any additional environmental variation acting on the trait itself. In Darwin's finches, for example, large body size (a metrical trait) leads to greater longevity but adult survival is also affected by several other non-heritable causes (Price & Schluter, 1991). Because a low heritability estimate can reflect low additive-genetic variation, high residual variation (non-additive plus environmental effects) or both, Houle (1992) has argued that h^2 is a potentially misleading indicator of the comparative 'evolvability' of a trait (although it is clearly useful in predicting the absolute response to selection, which equals the product of h^2 and the selection differential). Using the coefficient of additive-genetic variation ($CV_A = 100\sqrt{V_A/\bar{x}}$; Charlesworth,

1984) as an alternative measure, Houle (1992) re-analysed a large number of quantitative-genetic studies and concluded that life-history traits are in fact characterized by high, standardized genetic variability.

The typical level of genetic variation associated with different kinds of traits remains a largely empirical issue. In this study a half-sib breeding design was used to compare h^2 and CV_A for a morphological trait (wing length), a life-history trait (total fecundity) and a behavioural trait (allocation of eggs among resources) in two outbred populations of beetle *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). These traits were chosen because they vary widely between populations and earlier studies have examined their respective contributions to fitness. Also compared were phenotypic and genetic correlations between traits to assess whether there are any short-term constraints to their independent evolution (Stearns *et al.*, 1991; Arnold, 1992).

Biology of *C. maculatus*

Callosobruchus maculatus infests seeds of wild and cultivated legumes, especially *Vigna* spp. It has probably been associated with human stores of grain legumes in Africa for several thousand years (Mitchell, 1983). Adults occur in two phenotypic morphs; a sedentary morph is short-lived and highly fecund whereas a dispersing morph displays migratory behaviour and delayed reproduction (Utida, 1972). This polymorphism permits use of host legumes at both the developing pod stage (attacked by the dispersing morph) and the dried seed stage (attacked by the sedentary morph). Storage populations are usually founded by few individuals but expand rapidly on dried seeds (Hagstrum, 1985; Huignard *et al.*, 1985). Analyses of recently collected, field populations (as in this study) can thus provide information on the genetic variation present when infested seeds are brought into storage.

Egg-laying females attach eggs singly to host seeds. Hatching larvae chew through the seed coat and complete their development within a single seed. Emerging adults require neither food nor water. The beetle's short generation time (22–28 days at 28°C) and simple requirements make it well suited for quantitative-genetic analyses (e.g. Wasserman & Futuyma, 1981; Taper, 1990; Fox, 1993) and the laboratory is a reasonable approximation of the 'natural' storage environment. Nearly all previous experiments, however, have been conducted using long-term, laboratory strains or synthetic populations.

Traits that are known to vary within or between populations of *C. maculatus* were examined (e.g.

Messina, 1990; Mitchell, 1990; Smith, 1991). The length of the adult forewing (or elytron) is strongly correlated with fresh weight at emergence (e.g. Wilson & Hill, 1989) which in turn has been phenotypically and genetically correlated with total (lifetime) fecundity (Credland *et al.*, 1986; Møller *et al.*, 1989; Messina, 1991). Sibly *et al.* (1991) recently suggested that body size is subject to indirect optimizing selection under typical laboratory conditions as a consequence of a size-mediated trade-off between development rate and fecundity.

The contribution of a behavioural trait to fitness is often unknown but several studies have investigated egg-laying behaviour and its consequences in *C. maculatus*. Ovipositing females discriminate against seeds that already bear eggs and also distinguish between seeds bearing few eggs vs. many eggs (Messina & Renwick, 1985). Such behaviour leads to a non-random, uniform dispersion of eggs among seeds and reduces the frequency and intensity of larval competition (Messina, 1991). Mitchell (1975, 1983) has calculated the fitness advantage of a typical, uniform egg dispersion in relation to a random one. The tendency to lay eggs uniformly varies substantially among populations (Messina & Mitchell, 1989), perhaps as a result of concomitant variation in larval competitiveness in seeds (Messina, 1991). The mechanism of avoidance of occupied hosts is unknown but probably involves a marking pheromone (Credland & Wright, 1990). A study of the closely related species, *C. chinensis*, indicated moderate within-individual repeatability in the avoidance of pheromone-treated seeds (Tanaka, 1991).

Materials and methods

Samples of two African populations of *C. maculatus* were obtained in November 1989. The population from Niamey, Niger (hereafter referred to as NN) was derived from infested pods of a local variety ('TN 88/63') of cowpea, *Vigna unguiculata* (L.) Walp., at the University of Niamey Experiment Station. The Burkina Faso population (OBF) was derived from pods of *V. unguiculata* ('Kamboince' variety) in a field near Ouagadougou, approximately 350 km from Niamey. Laboratory populations were established by transferring more than 100 adults emerging from field infested seeds onto clean seeds of the California black-eye variety of *V. unguiculata*. In subsequent generations, more than 1500 emerging adults were transferred onto ≈ 600 g of seeds. The breeding design was implemented after three laboratory generations. Populations were maintained and experiments con-

ducted in a dark incubator at 28°C and 50–60 per cent relative humidity.

Breeding design

Each population was subjected to a conventional, half-sib/full-sib breeding design (Falconer, 1989). Unmated sires and dams (sedentary morph only) were obtained by isolating several hundred seeds from the stock culture in separate small vials. Each newly emerged sire was combined with five dams in an empty Petri dish for 24 h. After this mating period, each dam was transferred to a separate dish bearing 100 cowpea seeds. This number of seeds ensured that all of a dam's offspring experienced little or no competition within seeds (Tucic *et al.*, 1991). After 12 days, dishes were inspected for hatched eggs on the surfaces of seeds. If fewer than four dams per sire produced hatched eggs (possibly because some dams were not inseminated successfully), then all offspring of that sire were eliminated from the experiment. Similarly, if all five dams mated to a given sire produced hatched eggs, the offspring of one dam were randomly eliminated. These steps maintained a balanced design (four dams/sire) and caused only a minor loss of replication.

Five to seven female offspring were collected per dam within 6 h of adult emergence. Each offspring was paired with an unrelated, newly emerged male and placed in a separate 5 cm Petri dish bearing 40 seeds. A pilot experiment indicated that total fecundity was similar when females were given 40 or 100 seeds (see also Messina, 1991). Each offspring then distributed her lifetime supply of eggs on the seeds. After she had died (within 10 days of adult emergence), the dish was frozen overnight (to kill the offspring's own progeny) and stored until it was convenient to measure the relevant traits. To maintain a balanced design, offspring were randomly eliminated in excess of four per dam.

Length of the right elytron was measured at $50\times$ with an ocular micrometer. For lifetime fecundity the total number of eggs laid on the seeds was recorded, as well as the small number of eggs that were occasionally laid on the dish itself. Egg-laying behaviour was measured by quantifying the distribution of eggs among seeds. The uniformity index, U , was used, described by Messina & Mitchell (1989); the advantage of this index is that it is statistically independent of the number of eggs laid. Briefly, U depends on the number of 'mistakes' committed by a female in spreading her eggs among seeds, where the number of mistakes equals the minimum number of eggs that would have to be transferred among seeds to transform the observed distribution into a uniform one. This observed number of mistakes (O) is then compared with the expected

number of mistakes (E) that would be committed by a female laying the same number of eggs at random (i.e. a Poisson distribution). $U = (E - O)/E$, and thus typically ranges between zero, which indicates a random egg dispersion ($E = O$), to one, which indicates a completely uniform dispersion ($O = 0$). If a female tended to aggregate her eggs among seeds ($O > E$), U is negative.

The experiment was replicated twice (i.e. performed in two blocks) for each population. In the NN population, traits in offspring of 50 sires from the first block and 34 sires from the second block were measured, which yielded a total of 1344 offspring. In the OBF population, 42 and 31 sires were used from the first and second blocks, respectively, which yielded a total of 1168 offspring.

Analysis

Data were subjected to a three-level, nested, random-effects analysis of variance with the following linear model:

$$Y_{ijkl} = \mu + B_i + S_{j(i)} + D_{k(ij)} + W_{l(ijk)}$$

where μ is the overall population mean, B_i is the effect of the i th block, $S_{j(i)}$ is the effect of the j th sire within block i , $D_{k(ij)}$ is the effect of the k th dam within the sire j and block i , and $W_{l(ijk)}$ is the effect of the l th offspring within dam k , sire j , and block i . The ANOVA was performed using PROC NESTED in SAS (SAS Institute, 1988). Because the experiment was balanced at all levels except the highest one (block), this analysis yields unbiased estimates of variance components. It was confirmed that the observational variance components from PROC NESTED were identical to those produced by the VARCOMP (REML) procedure in SAS. Probability plots indicated that wing length and total fecundity were approximately normally distributed and thus these variables were not transformed for ANOVA. U -scores were first subjected to the transformation, $(1 + U)/2$, which placed all scores between 0 and 1 (raw scores ranged from -0.58 to 1.00) and were then subjected to the angular transformation (Sokal & Rohlf, 1981).

Narrow-sense heritabilities were calculated as $4V_S/V_P$, where V_S is the between-sire variance component and V_P is the total phenotypic variance, as derived from the sum of the observational variance components. Standard errors of h^2 were calculated using the formula in Becker (1984). To assess the importance of common-environment or non-additive effects, heritabilities were also estimated from resemblances of full-sibs, where $h^2 = 2(V_S + V_D)/V_P$, and V_D is the between-dam variance component. CV_A was calculated as described above (where $V_A = 4V_S$), as well as

the coefficient of residual variation, $CV_R = 100 \sqrt{(V_P - V_A)/\bar{x}}$.

Phenotypic (Pearson) correlations (r_p) were estimated between traits within each population. Genetic correlations (r_A) were estimated as $Cov_{XY}/\sqrt{(V_X \times V_Y)}$, where the numerator equals the between-sire component of covariance for traits X and Y (or one-fourth of the additive-genetic covariance) and the denominator includes the between-sire variance components for each trait. Standard errors of r_A were determined using the approximate formula in Falconer (1989). Environmental correlations (r_E) were derived from the equation, $r_p = h_X h_Y r_A + e_X e_Y r_E$, where h is the square-root of the heritability and $e = \sqrt{(1 - h^2)}$.

Results

Phenotypic means and variances were similar between populations for all traits (Table 1), although NN

Table 1 Means (and standard deviations) of three traits in *C. maculatus* populations from Niger (NN) and Burkina Faso (OBF).

Trait	NN	OBF
Elytral length (mm)	1.80 (0.10)	1.75 (0.12)
Total fecundity	50.05 (16.62)	45.16 (16.03)
<i>U</i> -score†	0.54 (0.25)	0.69 (0.19)
No. of females	1344	1168

†*U* estimates how a female distributes her eggs among seeds, where 0 = a random dispersion of eggs and 1 = a uniform dispersion.

females were slightly bigger and more fecund than OBF females (statistical comparisons between strains are precluded because the experiments were not carried out simultaneously). Most females in each group spread their eggs among seeds in a pattern that was intermediate between a random dispersion (i.e. according to Poisson distribution of eggs among 40 seeds) and uniform dispersion (Table 1).

Nested ANOVA indicated a significant between-sire effect, and thus additive-genetic variance, for all three traits in both populations (Table 2). The between-dam effect was also consistently significant. Heritabilities were highest for wing length, intermediate for total fecundity and lowest for egg-laying behaviour, although the estimates for wing length and fecundity were similar in the NN population (Table 3). Heritabilities derived from the between-dam variance component (not shown) were comparable to those based on the between-sire component, such that the full-sib and half-sib estimates of h^2 were only marginally different (Table 3). Little evidence was thus obtained of additional variance due to dominance or common-environment effects.

A different perspective is provided when the mean-standardized coefficient of additive-genetic variation is substituted for h^2 as a comparative measure of variability or evolvability. In both populations, CV_A was very high for total fecundity, intermediate for egg-laying behaviour and lowest for wing length (Table 3). Thus, the heritabilities of the behavioural trait were lower than those of the morphological trait because of relatively high residual variance rather than relatively low additive-genetic variance. The comparable heritabilities of wing length and fecundity in the NN strain mask

Table 2 Nested, random-effects analysis of variance for three traits in two populations of *C. maculatus*

Source	d.f.	Elytral length		Total fecundity		<i>U</i> -score†	
		<i>SS</i>	<i>F</i>	<i>SS</i>	<i>D</i>	<i>SS</i>	<i>F</i>
NN strain							
Block	1	0.37	8.3**	32482	27.5***	0.30	4.2*
Sire (block)	82	3.63	3.5***	96834	3.6***	5.80	2.1***
Dam (sire)	252	3.18	2.0***	83464	2.1***	8.33	1.3***
Error	1008	6.35		158081		25.40	
OBF strain							
Block	1	1.31	16.4***	37494	34.8***	0.002	0.01 ns
Sire (block)	71	5.69	3.9***	76461	3.1***	8.04	1.5*
Dam (sire)	219	4.49	2.8***	74904	2.7***	16.46	1.3*
Error	876	6.47		111022		50.08	

†As defined in Table 1.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ns, not significant.

large differences between the traits in both additive-genetic and residual variance (Table 3).

Phenotypic correlations between wing length and fecundity were positive in both populations whereas correlations between behaviour and wing length or fecundity were not significant (Table 4). Wing length and fecundity were also correlated genetically in the OBF population. For all other genetic correlations, 95 per cent confidence intervals overlapped zero, with fairly large standard errors (Table 4; the matrix of genetic covariances, not shown, closely resembled the correlation matrix). The weak correlations between egg-laying behaviour and fecundity were also opposite in sign between populations. Environmental correlations were generally low, except for a negative relationship between wing length and fecundity in the OBF strain.

Table 3 Narrow-sense heritability (h^2), additive-genetic coefficient of variation (CV_A) and residual coefficient of variation (CV_R) for three traits in two populations of *C. maculatus*. Heritabilities were derived from the between-sire variance component (h^2_s) or the combined between-sire and between-dam components (h^2_{s+D})

Trait	$h^2_s \pm \text{SE}$	h^2_{s+D}	CV_A	CV_R
NN strain				
Elytral length (mm)	0.76 ± 0.17	0.69	4.95	2.75
Total fecundity	0.70 ± 0.15	0.64	29.12	18.90
U -score†	0.32 ± 0.09	0.30	8.88	13.08
OBF strain				
Elytral length (mm)	0.90 ± 0.20	0.85	6.98	2.32
Total fecundity	0.63 ± 0.15	0.69	30.01	22.86
U -score	0.15 ± 0.07	0.21	9.59	22.96

†As defined in Table 1.

Discussion

Interfertile populations of *C. maculatus* from different geographical regions are widely divergent in several behavioural, physiological and life-history traits (Messina, 1989, 1990; Mitchell, 1990). This study reveals significant additive-genetic variation within two west African populations for three fitness-related traits, including lifetime fecundity (Table 2). The mechanisms underlying the maintenance of such variation are unclear as nothing is known about the selection histories or effective population sizes of *C. maculatus* in the region. One possibility is that the demographic instability associated with the storage-to-field life cycle provides little opportunity for directional or optimizing selection (Utida, 1972; Huignard *et al.*, 1985). Genetic variation for fecundity observed here is higher than that observed in a long-term laboratory strain of *C. maculatus* (Smith, 1991) but the mean number of eggs laid was relatively low (see Table 1 of Mitchell, 1990). These differences suggest that typical laboratory culture practices may select for higher fecundity than occurs in natural populations.

The coefficient of additive-genetic variation may be more appropriate than heritability for comparing potential responses to selection among different kinds of quantitative traits (Price & Schluter, 1991). Houle (1992) provided alternative formulae for the evolvability of traits under different selection regimes (e.g. linear-directional selection vs. truncation selection) and found that under each regimen evolvability was more closely related to CV_A than to h^2 . By the CV_A criterion, the evolvability of fecundity was particularly high in this study but both fecundity and egg-laying behaviour were subject to a proportionally high amount of residual variation (CV_R in Table 3). The high CV_A for fecundity and low CV_A for wing length

Table 4 Phenotypic (r_p), genetic (r_A), and environmental (r_E) correlations between traits in two populations of *C. maculatus*

	r_p	$r_A (\pm \text{SE})$	r_E
NN strain			
Elytral length vs. total fecundity	0.14**	0.17 ± 0.15	0.07
Elytral length vs. U -score†	0.04	0.02 ± 0.18	0.07
Total fecundity vs. U -score	0.001	-0.14 ± 0.17	0.15
OBF strain			
Elytral length vs. total fecundity	0.38**	0.64 ± 0.10	-0.53
Elytral length vs. U -score	0.01	0.02 ± 0.23	-0.002
Total fecundity vs. U -score	-0.03	0.19 ± 0.23	-0.15

†As defined in Table 1.

** $P < 0.00001$; other phenotypic correlations not significant; d.f., 1342 for NN and 1166 for OBF.

observed in this study (Table 3) matches the results of a survey of *Drosophila* experiments in which the median CV_A estimate for wing length was 1.96 vs. a median estimate of 11.9 for fecundity (Houle, 1992). The direction of this difference is the reverse of the one obtained by comparing narrow-sense heritabilities of morphological vs. life-history traits (Roff & Mousseau, 1991).

Most of the residual variation in fecundity and egg-laying behaviour was probably due to environmental effects (or genotype–environment interactions) rather than non-additive, genetic variance, as the between-dam variance components for these traits were similar to the between-sire components (Falconer, 1989). An interesting example of environmental effects on fecundity is provided by Wasserman (1986), who showed that variation in mating behaviour among *C. maculatus* males (e.g. differences in copulation attempts, copulation duration and courtship chases) can lead to significant variation in female egg production. Similarly, several environmental variables may affect the phenotypic value for a behavioural trait such as the pattern of egg-laying among seeds; one likely source is variation in the quality of the seeds themselves which is known to influence oviposition preferences (Mitchell, 1990).

Correlations between traits were not significant except for a positive relationship between size and fecundity (Table 4). This relationship is frequently observed in ectothermic invertebrates (Mousseau & Roff, 1987; Møller *et al.*, 1989). The scarcity of other significant relationships, together with the small number of traits and low sample sizes (less than 100 half-sib families per population), precluded a formal comparison of genetic covariance matrices between populations (Cowley & Atchley, 1992; Shaw, 1992). Within the OBF population, the environmental correlation between wing length and fecundity was opposite in sign to the genetic correlation, and was also substantially different from the corresponding environmental correlation in the NN population (Table 3). These results caution against using phenotypic correlations to infer genetic relationship (Willis *et al.*, 1991).

No obvious trade-offs were detected between egg-laying behaviour and either size or fecundity although the absence of significant genetic correlations does not automatically imply that particular pairs of traits can evolve independently (Charlesworth, 1990; Houle, 1991). A negative relationship between the number of eggs laid and the pattern of egg distribution might be expected *a priori* if distributing eggs uniformly among hosts entails a significant cost in resources that might otherwise be allocated to egg production. For example, females producing more uniform egg distributions may

expend more time or energy searching among seeds for unoccupied hosts or may need to produce a relatively greater amount of marking pheromone (Messina *et al.*, 1991). Such functional relationships between traits might be more accurately assessed in large populations of *C. maculatus* that have been maintained in the laboratory for many generations and are thus more likely to be at genetic equilibrium (Service & Rose, 1985). It is not clear, however, that these populations held under constant conditions will adequately represent natural populations which, in the case of *C. maculatus*, occupy environments with high spatial and temporal variability.

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