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Genetic architecture of population differences in oviposition behaviour of the seed beetle *Callosobruchus maculatus*

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Abstract

Few studies have examined the genetic architecture of population differences in behaviour and its implications for population differentiation and adaptation. Even fewer have examined whether differences in genetic architecture depend on the environment in which organisms are reared or tested. We examined the genetic basis of differences in oviposition preference and egg dispersion between Asian (SI) and African (BF) populations of the seed beetle, *Callosobruchus maculatus*. We reared and tested females on each of two host legumes (cowpea and mung bean). The two populations differed in mean oviposition preference (BF females preferred cowpea seeds more strongly than did SI females) and egg dispersion (SI females distributed eggs more uniformly among seeds than did BF females). Observations of hybrid and backcross individuals indicated that only the population difference in oviposition preference could be explained by complete additivity, whereas substantial dominance and epistasis contributed to the differences in egg dispersion. Both rearing host and test host affected the relative magnitude of population differences in egg dispersion and the composite genetic effects. Our results thus demonstrate that the relative influence of epistasis and dominance on the behaviour of hybrids depends on the behaviour measured and that different aspects of insect oviposition are under different genetic control. In addition, the observed effect of rearing host and oviposition host on the relative importance of dominance and epistasis indicates that the genetic basis of population differences depends on the environment in which genes are expressed.

Introduction

Models of evolutionary change in response to selection often assume that quantifying the additive genetic component of variation is adequate for predicting evolutionary responses (Falconer, 1989). In fact, models assuming only additive-genetic effects can generally explain microevolutionary change for large populations (Charlesworth *et al.*, 1987). However, dominance (interactions among alleles at a single locus) and epistasis (interactions among alleles at different loci; Cheverud & Routman, 1995) can cause inbreeding depression, outbreeding depression (due to the break up of epistatic complexes) and can cause genetic variance–covariance matrices to change in response to selection (e.g. through the conversion of epistatic variance to additive genetic variance; reviews in Meffert, 2000; Agrawal *et al.*, 2002; Meffert *et al.*, 2002). Nonadditivity limits our ability to extrapolate from simple models of selection to population differentiation and speciation (Johnson, 2000; Wade, 2000, 2002; Wolf *et al.*, 2000). Yet, the relative contribution of dominance and epistasis to variation in many kinds of traits is still unknown. Whereas simple quantitative-genetic breeding experiments can detect the presence of nonadditive effects, multi-generation breeding designs or line crosses are required to quantify the magnitude of dominance and epistasis (Lynch & Walsh, 1998; Meffert, 2000).

Behavioural traits are well known to exhibit low heritabilities relative to morphological traits (Roff & Mousseau, 1987; Meffert *et al.*, 2002). These low

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heritabilities could result from strong selection on behavioural traits, from high environmental variance (Price & Schluter, 1991; Houle, 1992), or from important contributions to variance of nonadditive interactions among alleles and loci (Roff, 1997). Some evidence suggests that behavioural traits are more affected by nonadditive genetic variation than are morphological traits (Crnokrak & Roff, 1995; Roff, 1997) but few studies have looked at the relative contributions of dominance and epistasis to phenotypic variation in behaviour (review in Meffert *et al.*, 2002). Here, we examine the relative contributions of nonadditive genetic effects to behaviour differences between two populations of the seed beetle, *Callosobruchus maculatus* (F.).

In herbivorous insects, patterns of host plant use affect spatial distributions and population dynamics (Thomas & Singer, 1987; Summerville *et al.*, 2002). The diet breadth of herbivores is often quite evolutionarily labile; herbivores frequently expand onto new hosts, contract in their diet to exclude ancestral hosts, or shift onto novel hosts (e.g. Radtkey & Singer, 1995; Fox & Savalli, 2000). Host finding and oviposition behaviours of females are often genetically variable within populations (e.g. Jaenike, 1987; Jaenike & Holt, 1991; Fox, 1993; Messina, 1993) and, in many species, populations have diverged in behaviours associated with host finding and oviposition (e.g. Dres & Mallet, 2002). Evolutionary divergence of diet affects the amount of gene flow between populations and can lead to speciation (discussed in Craig *et al.*, 2001). However, we know little about the underlying genetic architecture of population or species differences in host finding and oviposition behaviour. A few recent studies have employed line cross analysis to examine the genetic architecture of population differences in oviposition preference. Some have detected significant nonadditive effects, including dominance and epistasis, and have demonstrated substantial variation in the number of genes affecting differences in oviposition preference between populations or species (Lu & Logan, 1995; Keese, 1996; Craig *et al.*, 2001). For species in which females are heterogametic (such as butterflies and moths) sex chromosomes have been shown to have a disproportionate effect on female oviposition (Thompson *et al.*, 1990; Janz, 1998). However, we have too few studies to generalize regarding the genetic architecture of population differences and its implications for population differentiation and adaptation.

For insect herbivores, the larval environment and early adult experiences can affect adult behaviour and reproduction (Barron, 2001) potentially affecting the architecture of inheritance of behavioural and reproductive traits. For example, the heritability of oviposition preference and egg dispersion can depend on the host upon which insects were reared (Lazarević *et al.*, 1998). However, little is known about how the genetic architecture of population differences is influenced by larval and adult experiences (but see Armbruster *et al.*, 1997 and references therein). We therefore examine whether genetic architecture of differences between seed beetle populations depend on the environment in which each population is reared or tested.

The seed beetle *C. maculatus* is a cosmopolitan pest of legume seeds, both in human stores and in the field. Populations vary substantially in their host associations, and vary in a suite of life history and behavioural traits associated with these host plant differences (e.g. Messina, 1991; Messina & Slade, 1997; Savalli *et al.*, 2000; Kawecki & Mery, 2003; Fox *et al.*, in press). We examined the genetic architecture of behavioural differences between two populations known to differ in traits such as body size, adult lifespan, larval competitiveness, oviposition behaviour and amount of paternal investment (e.g.Savalli *et al.*, 2000; Fox *et al.*, in press). Some of these trait differences may have arisen as a result of differences in host seed properties. For example, recent selection experiments suggest that variation in seed size can account for differences in the tendency to distribute eggs uniformly among seeds (Messina & Karren, 2003). Selection favours strong avoidance of occupied seeds when larvae develop inside small seeds that can support the development of only one or two larvae, whereas such selection is weaker in populations that use larger seeds that can support the development of multiple larvae (Messina, 1991; Messina & Karren, 2003). We used line cross analyses to examine the relative influences of additive and nonadditive genetic effects on population differences in two important aspects of oviposition behaviour: oviposition preference (the distribution of eggs between two hosts when both are presented simultaneously) and egg dispersion (the tendency to reduce larval competition by distributing eggs uniformly among available seeds). We also estimate the number of genes accounting for population differences in behaviour.

Methods

Natural history and study population

Callosobruchus maculatus females cement their eggs to the surface of host seeds, particularly beans of the genus *Vigna*. First instar larvae burrow through the seed coat and into the seed. Larval development and pupation are completed entirely within a single seed. Female adults mate and begin to lay eggs within hours of emerging from the seed. They are facultatively aphagous, i.e. they require neither food nor water in the adult stage.

We examined the inheritance of differences in oviposition behaviour between two populations that were collected from and maintained on different legume hosts. The South Indian (SI) population was collected in 1979 from infested pods of mung bean, *V. radiata* (L.) Wilczek, and the closely related black gram, *V. mungo* (L.) Hepper,

in Tirunelveli, India (Mitchell, 1991). The Burkina Faso (BF) population was collected in 1989 from infested pods of cowpea, *V. unguiculata* (L.) Walp., in Ouagadougou, BF (Messina, 1993). These two populations differ in body size, lifetime fecundity, patterns of egg dispersion, oviposition preference and adult longevity (see *Introduction*). Both populations were maintained in laboratory growth chambers on seeds of *V. radiata* (SI) or *V. unguiculata* (BF) at >1000 adults per generation for >100 generations (BF) or >200 generations (SI) prior to this experiment.

Experimental design

South Indian and BF beetles were mated to produce F_1, F_2 and backcross progeny. The crosses were created over three generations so that all beetles were scored for their oviposition behaviour simultaneously. All matings were performed reciprocally. Thus, for example, F_1 offspring were obtained from both SI ♀ × BF ♂ and BF ♀ × SI ♂ crosses (these are designated F_1 and F_{1R}, respectively). In total we created 14 crosses: two purebreds (SI ♀ × SI ♂ and BF ♀ × BF ♂), two F_1 crosses (F_1 and F_{1R}), two F_2 crosses (F_1♀ × F_1♂, F_{1R}♀ × F_{1R}♂), four SI backcrosses (SI ♀ × F_1♂, SI ♀ × F_{1R}♂, F_1♀ × SI ♂, F_{1R}♀ × SI ♂) and four BF backcrosses (BF ♀ × F_1♂, BF ♀ × F_{1R}♂, F_1♀ × BF ♂, F_{1R}♀ × BF ♂). The reciprocal crosses allowed us to test for the presence of maternal genetic effects and cytoplasmic effects on line cross means.

As the two populations of beetles are adapted to different host species, we established two independent sets of crosses. In one set, all larvae were reared on mung seeds, the host of the SI population, throughout the three generations of crosses. In the second, all larvae were reared on cowpea seeds, the host of the BF population. This allowed us to test for effects of rearing hosts on the relative importance of additive, dominance and digenic epistatic inheritance.

All crosses were set up with a minimum of 120 pairs (created with unmated beetles that emerged from isolated seeds). Matings were performed in 35 mm Petri dishes containing *c.* 20 cowpea seeds or *c.* 35 mung seeds. Females were allowed to oviposit, with males present, for 48 h, after which the parents were discarded. Larvae were reared to the adult stage at one egg per seed (excess eggs were scraped off), at 25 °C, 15 : 9 light : dark, in a single growth chamber. The positions of the dishes in the growth chamber were rotated daily. Prior to emergence, all offspring were divided into two groups. Emerging offspring from the first group (two beetles per family) were used to measure egg dispersion in single-host arenas, whereas offspring from the second group (two beetles per family) were used to measure oviposition preference in two-host arenas. The remaining offspring were used to quantify the genetic architecture of body size, adult lifespan, egg size and fecundity (results to be presented elsewhere).

Egg dispersion was measured in 60-mm Petri dishes containing either 30 cowpea seeds or 30 mung seeds (hereafter referred to as oviposition hosts). Females were collected within 24 h of emerging from an isolated seed (to ensure they were unmated) and then paired with a random male from the same cross type. Unfortunately, this design does not allow us to disentangle male from female effects on female oviposition behaviour. However, we had no *a piori* reason to expect large effects due to the source of the male (Messina & Slade, 1997). After mating, females were transferred to a dish containing either cowpea or mung seeds. Females were allowed to oviposit for 24 h (±10 min). Egg dispersion was calculated as the uniformity index (U) devised by Messina & Mitchell (1989). This index is derived from the number of 'mistakes' that a female makes, where the number of mistakes is defined as the number of eggs that would need to be transferred among seeds to produce the most uniform distribution possible (given a particular number of eggs). This observed number of mistakes is compared with the expected number of mistakes committed by a female laying eggs randomly (according to a Poisson distribution) on the same seeds.

$$U = \frac{\text{Expected mistakes} - \text{Observed mistakes}}{\text{Expected mistakes}}.$$

The index usually ranges between 0 and 1, where 0 represents a random distribution and 1 represents a completely uniform distribution. U will be less than 0 if a female clumps her eggs. U is not biased at low or high fecundities (Messina & Mitchell, 1989). However, random and uniform distributions are indistinguishable when mean egg number is low (the sampling variance in U increases with decreasing fecundity). We thus included in our analysis only females that laid more than 10 eggs. Although U is not biased at low fecundities, female behaviour is influenced by egg densities. In this study, U was weakly, but significantly correlated with the number of eggs females laid in their first 24 h of oviposition (linear regression, R^2 between 0.05 and 0.10, $P < 0.05$ in most cross–treatment combinations). We removed the effect of egg number from estimates of average U for each combination of oviposition and rearing host by calculating least-square means.

Oviposition preference was estimated in test arenas (60 mm Petri dishes) consisting of 20 cowpea seeds and 35 mung seeds. Females were collected within 24 h of emergence (to ensure they were unmated) and then paired with a random male from the same cross type. After mating, females were transferred to test arenas and allowed to lay eggs for *c.* 24 h. Oviposition preference was defined as the proportion of eggs laid on cowpea. Because mung and cowpea seeds are of unequal surface area and were used in unequal numbers within a test arena, we cannot extend the oviposition scores obtained from a female to an absolute estimate of rank order

preference for a seed (i.e. we cannot conclude a female prefers mung over cowpea, or vice versa, even if she lays more eggs on that host) but we can use the preference estimates as an unbiased estimate of differences among crosses (Singer, 1986).

Genetic analysis

All means were averaged across females within a family and then averaged across families within a cross to control for nonindependence of sisters. Composite genetic effects explaining the differences between the line means were estimated as described in Lynch & Walsh (1998; chapter 9). We used the genetic model of Kearsey & Pooni (1996), which has parameterization as described in Table 1 of Gilchrist & Partridge (1999) and uses the expected mean of F_∞ offspring as a point of reference. The parameterization of this model differs only slightly from that described by Lynch & Walsh (1998), who use expected phenotype of F_2 offspring as a point of reference. The two models can be easily translated to alternate parameterizations (Basford & De Lacy, 1979; note that we also used the Lynch & Walsh parameterization, for comparison, and all results were qualitatively the same).

We tested for goodness of fit to genetic models using the weighted residual sum of squares (Lynch & Walsh, 1998; Bradshaw & Holzapfel, 2000). The weighted residual sum of squares (RSS) is

$$\mathrm{RSS}_w = \sum_{i=1}^{k} \frac{e_i^2}{\mathrm{SE}_i^2},$$

where k is the number of crosses, e_i^2 is the difference between the observed and predicted composite genetic effects and SE_i^2 are the standard errors of the estimated composite genetic effects (Lynch & Walsh, 1998; Bieri & Kawecki, 2003). For normally distributed data RSS_w is χ^2 distributed with degrees of freedom equal to the number of lines minus the number of parameters in the model. A significant χ^2 indicates that the fitted model was inadequate to explain the observed line cross means.

As we are interested in eight different parameters [additive (α), dominance (δ), additive–additive epistasis (α^2), additive–dominance epistasis ($\alpha\delta$), dominance–dominance epistasis (δ^2), an additive genetic maternal effect (am), a dominance genetic maternal effect (dm) and a cytoplasmic effect (c)], there are $2^8 = 256$ possible models. Traditional joint-scaling techniques avoid the need to compare all models by adding parameters sequentially starting with additivity, then adding dominance, then epistasis, etc., until the line means predicted by the model no longer differ from the observed line means (based on the comparison of RSS_w to a χ^2 distribution, as described above; Mather & Jinks, 1982; Bradshaw & Holzapfel, 2000). However, the order in which terms are introduced into the model affects the ability to detect effects added later and this technique does not always produce the most parsimonious model.

Table 1 Akaike's Information Criterion most parsimonious models and estimated composite genetic effects contributing to differences in oviposition preference and egg dispersion between *Callosobruchus maculatus* populations (South India and Burkina Faso).

Oviposition preference	Reared on Cowpea (column A)		Reared on Mung (column B)	
μ_0	0.59 ± 0.01		0.59 ± 0.01	
α	0.27 ± 0.01		0.24 ± 0.02	
δ	–		–	
α^2	–		–	
$\alpha\delta$	–		0.18 ± 0.08	
δ^2	–		–	
χ^2	7.27*ns*		1.99*ns*	
	Reared on Cowpea		Reared on Mung	
Egg dispersion	Oviposition on Cowpea (column C)	Oviposition on Mung (column D)	Oviposition on Cowpea (column E)	Oviposition on Mung (column F)
μ_0	0.18 ± 0.20	0.97 ± 0.01	0.74 ± 0.03	0.92 ± 0.02
α	−0.11 ± 0.03	−0.06 ± 0.01	−0.11 ± 0.03	−0.04 ± 0.02
δ	1.25 ± 0.48	–	0.07 ± 0.05†	0.05 ± 0.03†
α^2	0.45 ± 0.20	−0.07 ± 0.02	–	–
$\alpha\delta$	–	0.13 ± 0.06	–	–
δ^2	−0.71 ± 0.29	–	–	–
χ^2	3.44*ns*	3.16*ns*	10.36*ns*	7.68*ns*

χ^2 values are calculated only for those values shown; *ns* indicates that the model adequately explains the data.

Model parameters: μ_0, mean; α, additive; δ, dominance; α^2, additive–additive epistasis; $\alpha\delta$, additive–dominance epistasis; δ^2, dominance–dominance epistasis; χ^2, goodness of fit of the model to the real data – a low χ^2 indicates a better fit.

†Indicates a parameter in the most parsimonious model that when deleted did not significantly reduce the fit of the model to the observed line means (see Methods).

To find the most parsimonious model, we used Akaike's Information Criterion (AIC) (following Bieri & Kawecki, 2003; see Burnham & Anderson, 1998). This technique chooses a model that is the best compromise between the amount of variance explained and the number of parameters in the model. The technique is explained thoroughly by Bieri & Kawecki (2003). In short, the model with the lowest AIC is the most parsimonious, where $AIC = -2\ \ln(L) + 2K$, where L is the log-likelihood of the model given the data and K is the number of parameters fitted in the model. Bieri & Kawecki (2003) showed that $AIC = RSS_w + 2K$ + constant. The constant is the same for all models and thus need not be calculated to compare different genetic models.

As the number of possible models is so large (256), we first reduced the number of candidate models. Because additive maternal, dominance maternal and cytoplasmic effects were not significant in our preliminary joint-scaling analyses, we dropped them from all other analyses. Then, to further reduce the number of candidate models, we pooled the three forms of digenic epistasis and compared eight models for each trait (following Bieri & Kawecki, 2003): a model with only the overall mean (μ_0), an additive model ($\mu_0 + \alpha$), a dominance model ($\mu_0 + \delta$), an epistasis model ($\mu_0 + \alpha^2 + \alpha\delta + \delta^2$), an additive–dominance model ($\mu_0 + \alpha + \delta$), an additive epistasis model ($\mu_0 + \alpha + \alpha^2 + \alpha\delta + \delta^2$), a dominance epistasis model ($\mu_0 + \delta + \alpha^2 + \alpha\delta + \delta^2$) and an additive–dominance epistasis model ($\mu_0 + \alpha + \delta + \alpha^2 + \alpha\delta + \delta^2$). We chose the model with the lowest AIC as the most parsimonious. Only if the most parsimonious model included epistasis did we expand our model into all possible models including the three forms of digenic epistasis. For example, if the additive epistasis model was most parsimonious, we expanded this into the following seven models: $\mu_0 + \alpha + \alpha^2$, $\mu_0 + \alpha + \alpha\delta$, $\mu_0 + \alpha + \delta^2$, $\mu_0 + \alpha + \alpha^2 + \alpha\delta$, $\mu_0 + \alpha + \alpha^2 + \delta^2$, $\mu_0 + \alpha + \alpha\delta + \delta^2$ and $\mu_0 + \alpha + \alpha^2 + \alpha\delta + \delta^2$, and again chose the model with the lowest AIC as our most parsimonious. None of the most parsimonious models included a significant cytoplasmic or Y-chromosome effect, so we reduced the 14 crosses into 9 crosses by pooling the two F_2 crosses ($F_1♀ \times F_1♂$, $F_{1R}♀ \times F_{1R}♂$) into a single F_2, SI $♀ \times F_1♂$ and SI $♀ \times F_{1R}♂$ into BC_1, $F_1♀ \times$ SI $♂$ and $F_{1R}♀ \times$ SI $♂$ into BC_{1R}, BF $♀ \times F_1♂$ and BF $♀ \times F_{1R}♂$ into BC_2 and $F_1♀ \times$ BF $♂$ and $F_{1R}♀ \times$ BF $♂$ into BC_{1R}. This provided better estimates of the line means for use in the reduced models (those lacking cytoplasmic effects).

It is possible that the most parsimonious model includes parameters that contribute little, such that removing the parameter would not significantly decrease the fit of the model. We tested whether the removal of individual terms significantly reduced the fit of the model to the observed line means using a likelihood ratio test (Lynch & Walsh, 1998). The degree of reduced fit of the model is estimated as $\Lambda = RSS_{w\ (\text{reduced model})} - RSS_{w\ (\text{full model})}$. The parameter Λ is χ^2 distributed at large sample sizes, with degrees of freedom equal to the difference in the number of parameters in the two models.

We compared our AIC most parsimonious models with results from a joint-scaling analysis in which terms are added sequentially to the model until the best fit model is obtained (Mather & Jinks, 1982; Lynch & Walsh, 1998; Bradshaw & Holzapfel, 2000). Following standard procedures we sequentially estimated the composite genetic effects for a model containing only the overall mean (μ_0) and the additive genetic effect (α_1; additive model), $\mu_0 + \alpha_1$ + dominance genetic effect (δ_1; additive-dominance model), $\mu_0 + \alpha_1 + \delta_1$ + the additive digenic epistatic effect (α^2), $\mu_0 + \alpha_1 + \delta_1 + \alpha^2$ + the additive–dominance digenic epistatic effect ($\alpha\delta$) and then $\mu_0 + \alpha_1 + \delta_1 + \alpha^2 + \alpha\delta$ + dominance digenic epistatic effect (δ^2). For each model we calculated RSS_w and tested whether the model was adequate to explain the observed line means (see above). A significant χ^2 indicates that the fitted model was inadequate to explain the observed line cross means. We tested whether each sequential model improved the fit to the data using a likelihood ratio test (Lynch & Walsh, 1998). The degree of improvement in the model is estimated as $\Lambda = \chi^2_{\text{initial model}} - \chi^2_{\text{enlarged model}}$. The parameter Λ is χ^2 distributed at large sample sizes, with degrees of freedom equal to the difference in the number of parameters in the two models. When addition of a parameter did not significantly improve the fit of the model to the data, that parameter was dropped from the analysis. We tested for additive and dominance genetic maternal effects, plus cytoplasmic effects, but they did not improve the fit of any model.

To compare composite genetic effects between treatments, i.e. the two rearing hosts and the two oviposition hosts, we calculated the Wald chi-square statistic in which $\chi^2 = (b_1 - b_2)^2/[SE\ (b_1)^2 + SE\ (b_2)^2]$, where b_1 and b_2 are the composite genetic effects in each environment, and SE (b_1) and SE (b_2) are the standard errors of those composite genetic effects (Allison, 1995). The sum of the Wald chi-square provides a test of whether two models are different; the sum is χ^2 distributed with K degrees of freedom, where K is the number of parameters in the model (not the sum of the number of parameters in the two models being compared). Because the parameter estimates are sensitive to which parameters are included in the model, we compared models with the same parameterization; for example, if a parameter was significantly different from 0 in only one of the two models to be compared, it was nonetheless included in both models for the purpose of hypothesis testing. The line difference in μ_0 was not included in this analysis.

We also estimated n_e (the effective number of factors) using the Castle–Wright method (Castle–Wright estimator; Lynch & Walsh, 1998). n_e provides an estimate of the number of freely segregating loci of equal effects that

would yield the observed pattern of line means and variance. This Castle–Wright estimator is based on the segregational variance (σ_s^2), which is estimated from the variance of the SI, BF, F_1, F_2, BC_{SI} and BC_{BF} crosses. σ_s^2 is estimated from the increase in variance in the F_2, BC_{SI} and BC_{BF} relative to the F_1 hybrids and both parental lines (SI and BF).

Results

In total, oviposition preference (in the paired host test) was scored for 924 females (410 reared on cowpea and 514 reared on mung). Egg dispersion was scored for 1065 total females (221 mung–mung, 299 mung–cowpea, 229 cowpea–mung and 316 cowpea–cowpea).

Descriptive patterns in parental populations

Most females laid eggs during their first 24-h period of oviposition – only 5% of females failed to lay at least one egg during this period. There was no effect of rearing host on the probability that a female failed to lay eggs (chi-square test tests, n.s. for all analyses). However, BF females were more likely to lay eggs when provided cowpea than when provided mung bean ($P < 0.05$), whereas SI females were equally likely to lay eggs regardless of host species (n.s.).

Egg dispersions of females from both populations deviated significantly from a random distribution (mean $U > 0$, $P < 0.001$ for all analyses). As expected, SI females laid their eggs much more uniformly than did BF females (Fig. 1; $F_{1,215} = 36.47$, $P < 0.001$). Both populations laid their eggs more uniformly on mung seeds (the smaller seed species) than on cowpea seeds ($F_{1,215} = 68.77$, $P < 0.001$). Interestingly, females from both populations reared from mung seeds also laid their eggs more uniformly than did females reared from cowpea seeds, regardless of the oviposition host (although highly significant, the magnitude of this effect is fairly small; Fig. 1; $F_{1,215} = 8.17$, $P < 0.01$).

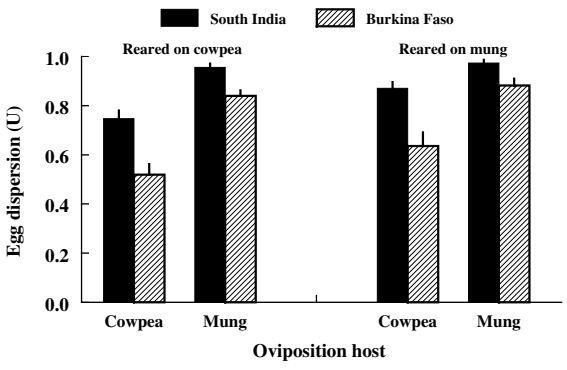

Fig. 1 Mean egg dispersions (*U*-scores; least-squares mean ± SEM) of *Callosobruchus maculatus* females as a function of geographic origin, rearing host and test host.

When presented with both cowpea and mung seeds simultaneously, BF females strongly preferred cowpea whereas SI females strongly preferred mung seeds; BF females laid 84 ± 1% of their eggs on cowpea, whereas SI laid only 34 ± 2% of their eggs on cowpea ($F_{1,198} = 626.19$, $P < 0.001$). There was no effect of rearing host on oviposition preference ($F_{1,198} = 0.01$, n.s.), nor was there a population–rearing host interaction ($F_{1,198} = 0.61$, n.s.).

Patterns of inheritance

Composite genetic effects

Results of the line cross analyses are presented in Figs 2 and 3; estimates of the composite genetic effects are presented in Table 1. Although reciprocal crosses are presented in the figures, there was no evidence that cytoplasmic or genetic maternal effects influenced any of the hybrid means so they are not discussed further.

For oviposition preference (proportion of eggs laid on cowpea seeds in a two-host arena), the additive model was the AIC most parsimonious model when females were reared from cowpea, whereas the model including additive genetic effects (α) + additive–dominance epistasis ($\alpha\delta$) was most parsimonious when females were

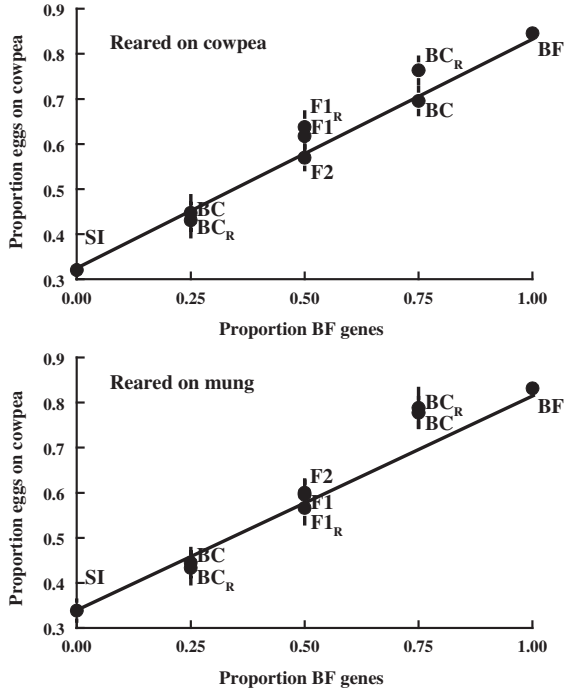

Fig. 2 Mean oviposition preference (proportion of eggs laid on cowpea ± SEM) of females from the Burkina Faso (BF) population, South Indian (SI) population and their hybrids. Reciprocal crosses are designated with an R. The line indicates the expected hybrid means if inheritance of population differences in oviposition preference were purely additive.

reared from mung (Fig. 2; Table 1). The joint-scaling analysis gave similar results; for oviposition preference of females reared from cowpea, the additive model was adequate to explain the observed line means, and the addition of epistasis did not improve the fit of the model, whereas for oviposition preference of females reared from mung seeds, the additive model was also adequate to explain the observed line means, but the inclusion of $\alpha\delta$ epistasis significantly improved the fit of the model ($\Lambda_1 = 5.67$, $P < 0.05$). There was no evidence that the overall models differed between rearing hosts or that rearing host affected any of the individual parameter estimates (Wald chi-square test, n.s. for all tests; Table 1, column A vs. B).

The genetic architecture of population differences in egg dispersion was more complicated. When females were reared on mung, the additive + dominance model was the AIC most parsimonious (for both oviposition hosts; columns E and F of Table 1). However, dropping dominance did not significantly reduce the fit of the model to the data. This was consistent with the joint-scaling method, in which the additive model was adequate to explain the observed line means ($\chi^2_7 < 14$, $P = 0.07$ for both oviposition hosts; $P > 0.05$ indicates that the fitted model did not differ significantly from the observed line means) and the addition of dominance did not improve the fit of the data to the model ($\Lambda_1 < 2.69$, n.s.). When females were reared on cowpea we detected substantial epistasis, regardless of oviposition host (columns C and D of Table 1). When these females laid on cowpea, dominance (δ) and both additive–additive (α^2) and dominance–dominance (δ^2) epistasis were included in the AIC most parsimonious model; dropping any term significantly reduced the fit of the model to the observed line means. Likewise, when beetles oviposited on mung, the AIC most parsimonious model included two types of epistasis (α^2 and $\alpha\delta$), but did not include dominance (δ); dropping either type of epistasis significantly reduced the fit of the model. Interestingly, for these females laying on mung, the model estimated based on the joint-scaling method detected significant dominance but was unable to detect either type of epistasis. This is because the order of addition of terms to the model (first μ_0, then α, δ, α^2, etc.), reduces the power to detect later-added terms. In addition, certain types of epistasis can be detected as dominance when epistasis is not present in the model, inflating the risk of erroneously detecting dominance instead of epistasis in the joint-scaling model.

Pair-wise comparison of the models demonstrated that there was a significant effect of oviposition host on the genetic architecture of egg dispersion when females were reared on cowpea (sum of the Wald chi-squares, $\chi^2_5 = 13.8$, $P < 0.05$), but the oviposition host effect was marginally nonsignificant when females were reared on mung ($\chi^2_5 = 8.9$, n.s.). There was also a highly significant effect of rearing host on genetic architecture when females laid eggs on cowpea ($\chi^2_5 = 23.0$, $P < 0.001$), but no significant effect when eggs were laid on mung ($\chi^2_5 = 3.4$, n.s.). Comparison of individual genetic parameters for egg dispersion indicated that the magnitude of the additive genetic composite effect (α) differed significantly between oviposition hosts, regardless of rearing host (column C vs. D and E vs. F in Table 1; Wald chi-square test, $\chi^2_1 > 3.9$, $P < 0.05$). Consistent with visual inspection of parameter estimates, both dominance (δ) and α^2 epistasis differed significantly between oviposition hosts for beetles reared from cowpea (columns C vs. D in Table 1; $\chi^2_1 = 3.6$ for both, $P = 0.058$). In addition, consistent with inspection of Table 1 was the result that dominance (δ), α^2 epistasis and δ^2 epistasis differed significantly between rearing hosts for egg dispersion on cowpea (columns C vs. E in Table 1; $\chi^2_1 > 6.65$, $P < 0.01$ for each). However, the amount of dominance and epistasis did not differ significantly between rearing hosts for egg dispersion on mung (columns D vs. F in Table 1; $\chi^2_1 < 1.2$, n.s. for each).

Effective number of factors (number of genes)

The observed variances in oviposition preference of the hybrid crosses can be explained by a minimum of three to four independently segregating loci with fixed differences between the SI and BF populations (estimated $n_e = 3.5 \pm 0.11$ when reared on cowpea seeds, 2.9 ± 0.14 when reared on mung seeds). Only one independently segregating locus was required to explain the variance in egg dispersion among the hybrid lines (estimates of n_e range from 0 to 1.1).

Discussion

The relative influence of nonadditive genetic effects on oviposition behaviours varied between the behavioural traits that we examined indicating that these traits differ substantially in their underlying genetic control. The populations differed in both oviposition preference and egg dispersion, but only the difference in oviposition preference was explainable by complete additivity (Fig. 2); substantial dominance and epistasis contributed to the population differences in the dispersion of eggs (Fig. 3).

Two previous studies have examined the genetics of population differences in oviposition behaviours of *C. maculatus*, although neither examined the effects of rearing environment on the patterns of inheritance, nor did they examine the relative contribution of epistasis to population differences. Messina & Slade (1997) examined the inheritance of population differences in host acceptance (measured as lifetime fecundity) and oviposition preference (measured in a paired host design similar to the one used here) between these same SI and BF populations. They found that the population difference in oviposition preference was additively inherited but found evidence of dominance for the population

difference in host acceptance. However, they were unable to test for epistasis because they created only F_1 offspring (F_2 and/or backcross progeny are needed; Lynch & Walsh, 1998). Similarly, Messina (1989) performed crosses between this same SI population and a Brazilian strain of *C. maculatus* that was associated with cowpea (like the BF population used here). As in our crosses here, he detected significant dominance of alleles for uniform egg dispersion (dispersion was measured on mung bean only). Although he did not test for epistasis, he created the necessary crosses. When these data were re-analysed we detected significant dominance and all three types of digenic epistatic interactions (α^2,$\alpha\delta$ and δ^2).

Few other studies have used line crosses to examine the genetics of population differences in oviposition behaviours. However, most of those have detected at least some dominance and often some epistasis (Jaenike, 1987; Guldemond, 1990; Lu & Logan, 1995; Sheck & Gould, 1995; Keese, 1996; Craig *et al.*, 2001) suggesting that nonadditive genetic effects are quite common. Two exceptions for which there was an absence of dominance and epistasis affecting population differences in oviposition preference include the brown planthopper (*Nilaparvata lugens*; Sezer & Butlin, 1998) and the soapberry bug (*Jadera haematoloma*; Carroll *et al.*, 2003). In both of these species oviposition preference was assessed using a paired preference design analogous to our design. In a literature review of genetic experiments, Meffert *et al.* (2002) found that 64% of behavioural traits are influenced by at least one nonadditive genetic effect, and that dominance was present for about 40% of the behavioural traits examined.

The effects of alleles on phenotypes of traits depend on the environment in which those alleles are expressed (Falconer, 1989). We thus expect, and frequently observe, differences among environments in the heritability of traits and the relative contributions of additive vs. nonadditive genetic effects to variation within populations (Roff, 1997; Czesak & Fox, 2003). However, the effect of the environment on the genetic architecture of population differences is generally unknown (but see Armbruster *et al.*, 1997; Fenster & Galloway, 2000; and references therein), although it is of substantial importance when examining traits that have evolved due to environment-specific selection. The two populations of *C. maculatus* studied here have evolved on different host species and many of the population differences in oviposition behaviour are likely due to host-associated differences in selection. We therefore examined whether the genetic architecture of population differences depends on either the host in which females developed or on the host used for egg laying. Both rearing and test host affected the mean values of traits and affected the genetic architecture of population differences in egg dispersion (Fig. 3; Table 1). The identity of the rearing host changed both whether epistasis was detectable and the magnitude of the different composite genetic effects for egg dispersion. In addition, for females reared from cowpea, the host upon which females laid eggs affected whether dominance was detectable and which forms of epistasis influenced line means. This result suggests that, for some traits, we should be cautious when extrapolating from experimental tests for nonadditive effects and the specific values we estimate for parameters to the

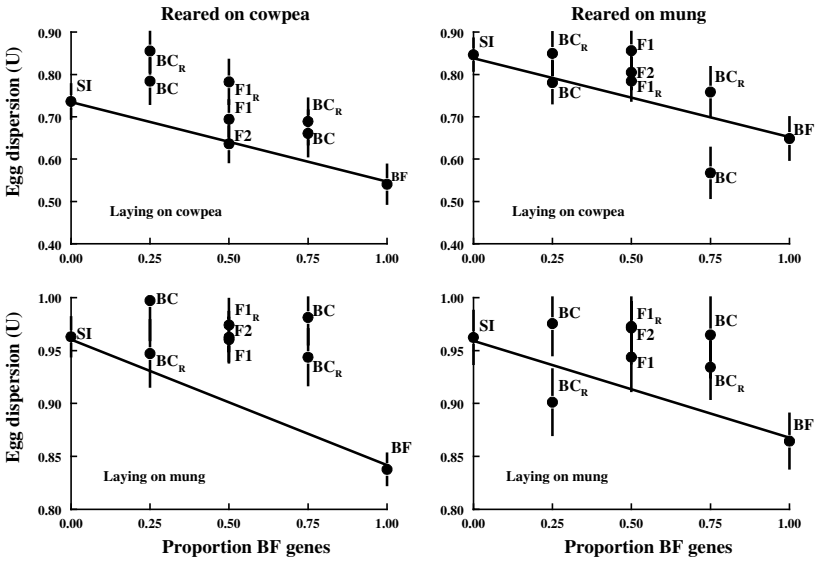

Fig. 3 Mean egg dispersions (*U*-scores; least-squares mean ± SEM) of females from the Burkina Faso (BF) population, South Indian (SI) population and their hybrids. Higher values of *U* indicate a more uniform dispersion of eggs. Reciprocal crosses are designated with an R. The line indicates the expected hybrid means if inheritance of population differences in eggs dispersion were purely additive.

relative importance of those nonadditive effects in different environments.

The number of loci influencing population differences in oviposition behaviours of females is known for only a few species, and in those organisms is generally few (e.g. Jaenike, 1987; Lu & Logan, 1995; Sezer & Butlin, 1998). For example, only one or two loci account for differences in oviposition behaviour between host races of the brown planthopper, *N. lugens* (estimated to be <1 before statistical correction, 2 following correction; Sezer & Butlin, 1998). Likewise, population differences in oviposition behaviour of *Drosophila tripunctata* are due to one or two loci (Jaenike, 1987). Sheck & Gould (1996) showed that different host-associated feeding behaviours were controlled by multiple and likely different loci. We estimated that three to four loci affect the difference in oviposition preference between the SI and BF populations of *C. maculatus*. Phenotypic differences in oviposition behaviour between *C. maculatus* populations are thus attributable to very few loci or chromosomal regions. With regard to egg dispersion, a single major locus could affect either the composition of the marking pheromone that signals the presence of an egg on a seed or, more likely, the degree of female sensitivity to cues to detect eggs on occupied hosts (Messina *et al.*, 1991). Our analyses likely underestimate the true number of loci accounting for the differences between populations. Estimates of n_e are biased downward when loci affecting a trait do not assort independently, when loci have unequal effects on the trait value, and when loci interact epistatically. Statistical methods are available to correct these estimates of n_e (Zeng, 1992; Lynch & Walsh, 1998) but they require estimates of the coefficient of variation in composite effects among segregating loci (i.e. C_α in Lynch & Walsh, 1998). Such estimates are available for many traits in *Drosophila*, but not for most other organisms. Unfortunately, estimates of C_α vary widely among traits which results in huge variation in corrected estimates of n_e. We have thus left our estimates uncorrected. Models for estimating n_e also assume that the two populations are fixed for different alleles at the relevant loci, which is not always the case.

Although we could not test for sex-linkage, there is no reason to expect that sex chromosomes contribute disproportionately to differences in oviposition behaviour because *C. maculatus* females are not heterogametic. For insect species in which females are heterogametic, oviposition related traits are often sex linked (e.g. Thompson, 1988; Thompson *et al.*, 1990; Scriber *et al.*, 1991; Sperling, 1994; Janz, 1998). This is probably because selection on the heterogametic sex will lead to more rapid fixation of favourable recessive or partially recessive alleles if they are sex-linked rather than autosomal because recessive alleles are shielded from selection when heterozygous but are exposed to selection when hemizygous (Rice, 1984; Charlesworth *et al.*, 1987). Because seed beetles females are homogametic the evolutionary dynamics of female behaviours are no different than any sex-limited autosomal trait. We thus have no *a priori* reason to expect the evolution of sex linkage (but see Mark, 1981). However, for insects that mate on their host plant, in which males may exhibit host preferences, selection may favour the evolution of sex linkage through selection on male behaviour (Craig *et al.*, 2001). It is likely that seed beetles do mate on their host plants, but male host finding has not been studied.

We found no evidence that maternal effects influenced the oviposition behaviour of hybrid *C. maculatus* females. This is consistent with previous results of Messina (1989) who likewise found no evidence of a maternal effect for egg dispersion (in crosses between the SI and a Brazilian population of *C. maculatus*). However, our results contrast with those of Messina & Slade (1997) who found a significant maternal effect on oviposition preference (using a paired host design, similar to ours) in a cross between the SI and BF populations of *C. maculatus*. Despite the result of Messina & Slade, we did not expect to detect significant maternal effects for any of our traits because maternal effects on the traits of offspring tend to be high only when offspring are young, and decline quickly thereafter (Mousseau & Fox, 1998; Heath *et al.*, 1999). Interestingly, large maternal effects were detected for body mass and adult lifespan of hybrids from these same line crosses (C. Fox, unpublished data).

The measurement of dominance and epistasis requires the use of multi-generation breeding designs or line crosses (Lynch & Walsh, 1998; Meffert, 2000). We must be cautious when extrapolating from evidence of significant dominance and epistasis in crosses between populations (as in this study) to the presence of epistasis within populations. For example, previous studies with *C. maculatus* and *Stator limbatus*, another seed beetle, found that dominance and epistasis explained little of the total variation in body size within populations (Fox, 1994, 1998) but line crosses demonstrated substantial amounts of epistasis affecting population differences in body size (C. Fox, unpublished data). The question has been investigated theoretically (Wolf *et al.*, 2000), but few studies have examined empirically how the genetic architecture of population differences changes through the process of population differentiation, although it is clear that large genetic differences and complex genetic architectures of population differences can evolve rapidly in nature (e.g. Gilchrist & Partridge, 1999; Carroll *et al.*, 2001, 2003). Conversely, genetically differentiated populations may fail to converge on similar genetic architectures despite long-term selection for adaptation to similar environments (e.g. Bieri & Kawecki, 2003). For traits affected by many genes there are often a variety of combinations of alleles that generate similar phenotypes, and thus a variety of genetic architectures may underlie similar population differences. For example, markedly different genetic architectures underlie the body size differentiation along latitudinal clines of *D. melanogaster*

on different continents (Gilchrist & Partridge, 1999). Likewise, populations that have similar mean phenotypes may differ genetically. To link observed genetic architectures of population differences to the process of adaptation and population differentiation we must examine empirically the genetic architecture of population differentiation throughout the process of adaptation. This may be feasible only for laboratory artificial or natural selection experiments (e.g. Šešlija & Tucíc, 2003) or by the comparison of transplanted natural populations with ancestral populations (Carroll *et al.*, 2001, 2003).

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