

## A QUANTITATIVE GENETIC ANALYSIS OF OVIPOSITION PREFERENCE AND LARVAL PERFORMANCE ON TWO HOSTS IN THE BRUCHID BEETLE, *CALLOSOBRUCHUS MACULATUS*

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**Abstract.**—The presence of positive genetic correlations between oviposition or feeding preference for hosts, and performance on those hosts, is of fundamental importance to models of host race formation, sympatric speciation, and the maintenance of genetic variation within phytophagous insect populations. In this paper, I estimate the amount of genetic variation in oviposition preference and larval performance present in two California populations of a cosmopolitan pest of stored legumes, *Callosobruchus maculatus* (Bruchidae: Coleoptera), and examine whether positive genetic correlations exist between preference and performance. High levels of genetic variation in both preference and performance were detected in one population (Bay Area population,  $h^2 = 0.73$  for oviposition preference), but not in another population (Davis population). A second estimate of the amount of genetic variation for oviposition preference in the Bay Area population, after three generations of laboratory rearing, supports the hypothesis that the absence of significantly nonzero heritabilities in the Davis population is probably due to the three generations of laboratory rearing prior to the start of the experiment. No positive genetic correlations were detected between preference and any performance character measured. Data are also presented on the genetic correlations between performance on azuki (*Vigna angularis*) and cowpea (*Vigna unguiculata*). Genetic correlations were found to be positive for all characters in both populations of *C. maculatus* (range 0.132 to 0.542).

**Key words.**—*Callosobruchus maculatus*, genetic variation, larval performance, oviposition preference, plant-herbivore interactions.

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The existence of genetic correlations between oviposition or feeding preference for different hosts, and performance on these hosts, has been an issue of debate in theoretical models of the evolution of diet breadth, host race formation, sympatric speciation (Kondrashov, 1983, 1986; Rice, 1984, 1987; Futuyma and Peterson, 1985; Kondrashov and Mina, 1986; Tauber and Tauber, 1990; Diehl and Bush, 1990) and the maintenance of genetic variation (Hedrick, 1990; Jaenike and Holt, 1991) in herbivorous insects. In populations where genetic variation for both preference and performance exist, selection is expected to favor individuals which prefer to feed on the resources they perform best on, or females which prefer to oviposit on resources most suitable to their offspring (Rausher, 1983; Thompson, 1988a). Thus, selection may produce genetic correlations between preference and performance either by generating linkage disequilibrium or by favoring alleles which pleiotropically influence both preference and performance.

Empirical studies have demonstrated that variation in host preference and host spec-

ificity exists both within and among insect populations that use multiple resources, and that large proportions of this variation are often genetic (reviewed by Futuyma and Peterson, 1985; Jaenike, 1990a; Jaenike and Holt, 1991; Thompson and Pellmyr, 1991; Via, 1991a). Genetic variation generally also exists in the ability of insects to use these resources (reviewed in Via, 1991a). Thus, genetic correlations between preference and performance may be expected to arise in these populations.

No genetic correlations between preference and performance have been found in several insect-plant systems (Tabashnik, 1986; Thompson, 1988b; Thompson et al., 1988; Jaenike, 1989, 1990b), while positive genetic correlations have been found in others (Taylor and Condra, 1983; Via, 1986; Singer et al., 1988; Ng, 1988). To date, however, the number of studies has been too few to allow generalizations.

In the cowpea weevil, *Callosobruchus maculatus* (Fabricius) (Bruchidae: Coleoptera), genetic variation in oviposition preference (Wasserman and Futuyma, 1981; Wasserman, 1986) and performance on dif-

ferent hosts (Moller et al., 1989) exists both within and among populations. Wasserman and Futuyama (1981) found no evidence for a correlated response in performance when they selected on oviposition preference of *C. maculatus*, although a substantial response for oviposition preference was observed. Their result may be due either to the absence of a correlation between oviposition preference and performance, or to a lack of genetic variation in their beetle population because their beetle population was derived from a colony reared in the lab for over thirty years (> 500 generations) on a single host (Taper, 1990). More recently, Milanovic et al. (1991) demonstrated that larvae of *Acanthoscelides obtectus*, another bruchid beetle, developed significantly faster on two bean species when their mothers were allowed to choose which host to oviposit on than when females were forced to lay on one or the other host, suggesting a preference-performance correlation.

In this paper, I quantify the amount of genetic variation in oviposition preference for two hosts within two populations of *C. maculatus* collected from stored beans, and then examine whether this variation is genetically correlated to offspring performance on these two hosts. I also present data on the correlation between performance across hosts, and examine whether there is evidence of a trade-off in performance between these two hosts.

#### MATERIALS AND METHODS

*Natural History of Callosobruchus maculatus.*—*C. maculatus* is a cosmopolitan pest of stored legumes. Females colonize seeds both in the field and in storage, cementing their eggs to the surface of the host seeds. Approximately four to five days later (at 28°C), the eggs hatch and the first instar larvae burrow into the seed, directly beneath the egg. Larval development and pupation are completed entirely within a single seed. Emerging adults require neither food nor water to reproduce, although adults will feed (pers. obs.) if damaged seeds are available (adult beetles cannot feed through the undamaged testa of the bean). In these experiments, adults were offered neither food nor water.

*Experimental Populations.*—The two

populations used in these experiments were collected from stored beans in California. The first was collected from stored cowpeas (*Vigna unguiculata*) on the University of California, Davis, campus, and is referred to as the Davis population. This population represents beetles which have invaded a storage container at the harvest site, immediately following the post-harvest fumigation. Because seeds are not regularly maintained at this site, this population does not represent a permanent storage population, but instead represents recent colonists from surrounding agricultural areas. This population was initiated with more than 100 males and 100 females, and maintained on cowpea for three generations before the experiment began.

The second population was collected from stored azuki beans (*Vigna angularis*) from a single warehouse in the San Francisco Bay Area of California, and is referred to as the Bay Area population. Unlike the Davis population, this population likely represents an established warehouse population with access to very large patches (storage bins) of various host types, and which regularly receives immigrants from incoming bean shipments. This population was begun with more than 1,000 eggs attached to azuki seeds, and was subsequently maintained on azuki. Adults emerging from the original eggs were used as the parental generation of the following experiment.

All beetles were maintained, and all experiments were performed, at  $27^{\circ} \pm 1^{\circ}\text{C}$ , LD 13:11. Experiments using each population were performed simultaneously, with all rearing dishes randomly intermixed throughout two incubators.

*Measurement of Preference and Performance.*—Oviposition preference in *C. maculatus* was estimated in test arenas consisting of 14 cowpea seeds and approximately 33 azuki seeds (estimated by weight = 2.7 g) distributed randomly in a 60 × 10 mm plastic dish. Pilot experiments with other seed ratios in both 60 mm and 100 mm plastic dishes indicated that this ratio produced a relatively normal distribution of oviposition preference within each population. Within approximately 12 hours of adult emergence, virgin females were mated, placed individually in test arenas, and

allowed to oviposit on seeds for approximately 24 hours. Oviposition preference was defined as the proportion of eggs laid on cowpea (number of eggs on cowpea/total number of eggs laid). Because azuki 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 azuki over cowpea, or vice versa, even if she lays more eggs on that host). Oviposition scores can be used only to compare among females. Preference designs of this type are discussed by Singer (1986).

Because *C. maculatus* is known to avoid seeds that already have eggs oviposited on them (Messina, 1990), and most females laid more than 20 eggs in a 24 hour period, the use of only 14 cowpea seeds in the preference arenas potentially biases this estimate of preference away from 1.0 by biasing females toward oviposition on azuki (of which there were more seeds in the test arena). In their exploration of *C. maculatus* oviposition preferences, Wasserman and Futuyma (1981) found a strong correlation between lifetime fecundity and preference for the more abundant host. Their preference tests, however, consisted of only 10 seeds of the less preferred host, and each female was allowed to oviposit in the test arena for her entire lifetime. The preference tests reported here utilized more seeds and allowed females to oviposit for only 24 hours. No correlation was found between the number of eggs laid during the 24 hour test period and preference. In addition, a high repeatability of oviposition preference across days (even as fecundity declined), the large number of eggs laid on some cowpea seeds (up to seven or eight eggs on a single cowpea), and similar within population distributions of preference obtained with larger arenas (unpubl. data) each suggest that this bias is small or absent in this experiment.

Up to 20 offspring from each preference-tested female were reared on each host species (one larva per seed). Because *C. maculatus* glues its eggs to host seeds, it was not possible to transfer eggs from one seed to another without damaging the eggs. Some females laid a majority (or all) of their eggs

on one host, resulting in very few or no eggs on the less preferred host. These females were placed in dishes with seeds of the less preferred host on the third day to increase the number of offspring reared on that host. A maternal age effect, such that eggs laid by older females develop slower or produce smaller offspring, would result in smaller or slower developing larvae on the less preferred host, biasing a correlation between preference and performance away from the null hypothesis. However, Wasserman and Asami (1985) demonstrated that this type of maternal effect was not evident until females reached at least five days of age. Here, all offspring developed from eggs laid within the first three days following adult emergence.

Development time was estimated for every emerging beetle as the time from egg hatch (the time when larvae were first observed burrowing into the bean) to adult emergence. Pronotum width, elytron length, body weight, and oviposition preference (of females) were measured within 12 hours of offspring emergence from seeds. These measures of body size are positively correlated with egg load (Wilson and Hill, 1989) and lifetime fecundity (Moller et al., 1989; Credland et al., 1986; C. Fox, unpubl. data).

*The Heritability of Oviposition Preference.*—The heritability of oviposition preference was calculated as the regression of family average preference on parental preference. To control for an influence of rearing host on host preference, estimates of family means were corrected for unequal numbers of full sibs on each host such that average offspring preference = (average preference of sibs reared on azuki + average preference of sibs reared on cowpea)/2.

*The Genetic Correlation between Preference and Performance.*—The genetic correlations between preference and performance were estimated by calculating the product moment correlation between the family means of offspring preference and offspring performance, with performance defined as the average family performance on azuki minus the average family performance on cowpea (following Via, 1986), hereafter referred to as performance(azuki-cowpea). These family mean correlations are only approximations of the true genetic cor-

TABLE 1. Estimates of the heritability of oviposition preference in two populations of *Callosobruchus maculatus* calculated as the regression of mean offspring preference on maternal preference (see Materials and Methods section for details).

Population/ generation	Slope (SE)	Herita- bility estimate
Bay Area/1st Gen	0.363 (0.062)***	0.726
Bay Area/4th Gen	0.439 (0.134)**	0.878
Davis	0.174 (0.090) NS	0.348

\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , NS = not significant at  $P = 0.05$ .

relations because each variance and covariance used in their estimation contains a fraction of the within family "error" variance or covariance, but they are expected to converge on the true genetic correlation with increasing numbers of offspring per family (Via, 1984b). Also, because all individuals within a family are full sibs, these analyses are potentially biased by maternal effects, dominance, and other environmental effects. Standard errors of the family mean correlations were calculated by bootstrapping the correlations 1,000 times and then correcting the resulting standard errors for bias (Efron, 1982).

*The Genetic Correlation between Performance on Azuki and Performance on Cow-*

*pea.* — Genetic correlations for the same trait across environments were calculated as product moment correlations of the family means for a trait on pairs of hosts. As noted above, these correlations are only approximations of the true genetic correlations, and are potentially biased by maternal effects and other non-additive genetic variance components.

No data transformations were necessary to satisfy the normality assumptions of the multivariate models. All significance tests are at the 0.05 level.

RESULTS

A total of 305 female offspring from 30 families were reared from the Davis population (141 reared on azuki, 164 on cowpea), and 417 female offspring from 41 families in the Bay Area population (233 reared on azuki, 184 on cowpea).

*The Heritability of Oviposition Preference.* — Heritability estimates were positive in each population, although significantly so only for the Bay Area population (Table 1). An analysis of variance of oviposition preference (Table 2) similarly demonstrated large family effects for both populations.

The heritability of oviposition preference was also estimated for the Bay Area popu-

TABLE 2. A partition of the variance of oviposition preference in two populations of *Callosobruchus maculatus*. Analyses of Variance were performed using SAS GLM procedure (SAS, 1985), calculating Type IV sums of squares, with Family as a random effect and Host as a fixed effect. *F*-ratios are calculated as MS(Family)/MS(Error) for the Family main effect, MS(Host)/MS(Family-Host) for the Host main effect, and MS(Family-Host)/MS(Error) for the Family-Host interaction effect (Neter et al., 1985). The "proportion variance" column indicates the proportion of the total variance explained by the source. Variance components were estimated using the Restricted Maximum Likelihood method of SAS Varcomp (SAS, 1985), assuming random effects for all variables (defining Host as a fixed effect prevents SAS Varcomp from calculating the necessary variance components).

Population/ generation	Source	Sum-of-squares	df	F-ratio	Proportion vari- ance
Bay Area (1st Gen)	Family	4.482	40	2.87***	0.201
	Host	0.174	1	4.10*	0.010
	Family-Host	1.691	40	1.08 NS	0.001
	Error	12.606	323		0.778
Bay Area (4th Gen)	Family	6.635	38	6.60***	0.330
	Host	0.323	1	9.10**	0.040
	Family-Host	1.350	38	1.34 NS	0.046
	Error	7.485	283		0.584
Davis	Family	2.279	29	2.40***	0.161
	Host	0.055	1	1.41 NS	0.031
	Family-Host	1.119	29	1.18 NS	0.002
	Error	7.581	232		0.805

NS =  $P > 0.05$ , \*  $P < 0.05$ , \*\*\*  $P < 0.001$ .

TABLE 3. Estimates of additive genetic variances of oviposition preference for two populations of *C. maculatus*, based on the heritability estimates in Table 1. Additive genetic variances are calculated as the product of the heritability estimate and the phenotypic variance of the parental generation. The remaining variance is the phenotypic variance minus the additive genetic variance. Mean preference for the parental population (left), and the mean, across families, of offspring mean preference (right), are presented.

Population	Mean pref	Phenotypic variance	$h^2$	Additive genetic variance	Remaining variance
Bay Area/1st Gen	0.534/0.551	0.052	0.726	0.038	0.014
Bay Area/4th Gen	0.282/0.365	0.027	0.878	0.024	0.003
Davis	0.687/0.607	0.052	0.348	0.018	0.034

lation after three generations of laboratory rearing on azuki (not simultaneously with all other estimates). Although this later estimate of heritability was very large in the Bay Area population ( $h^2 = 0.886$ , Table 1), the estimated additive genetic variance was lower than in the first generation (Table 3). The high heritability estimate was due to a large reduction in the estimated non-additive genetic variance (including environmental variance), possibly due to laboratory rearing. The Davis population, despite having also been reared in the lab for three generations, showed a much higher amount of non-additive variance (Table 3). Although estimates of variance components in each generation were performed in the same incubator under the same environmental conditions, differences among the generations may be due either to unobservable envi-

ronmental differences or changes in the genetic structure of the population across generations.

Because only females can be preference tested in this experiment, regressions of offspring average preference on mid-parent or paternal preference is not possible. Maternal effects, such that offspring preferences resemble their mother's preference due to a maternal environment influence, would thus result in overestimates of the amount of heritable variation. Because mothers choose their offsprings' larval host, one such maternal effect might be an influence of larval or early emergence experience with hosts on host preference. An analysis of variance and partitioning of the variance in oviposition preference into a family, rearing host, and interaction component shows that the effect of rearing host accounts for only a very small

TABLE 4. Means and standard deviations for development time, body size and survivorship of *Callosobruchus maculatus* reared on two hosts (seeds). All means are averages of family means. Statistical comparisons within populations are using Wilcoxon signed rank tests on paired family means. Between population comparisons are using Mann-Whitney *U*-tests (unpaired data). Means sharing letters *within* a population are homogeneous, such that those having no letters are different from the same character on the other host. Underlined means denote homogeneity across populations, within a host species (i.e., among population comparisons are significant for all characters except survivorship). Only families which produced adults from both hosts are included in development time and morphological averages (see Table 7). All families are included in survivorship estimates.

Host	Sex	Development time (days)	Emergence weight (mg/10)	Pronotum width (mm/10)	Elytron length (mm/10)	Survivorship (Hatch to emergence)
Bay Area population						
Azuki	F	23.12 (0.98) A	45.17 (3.65) A	6.11 (0.21) A	9.36 (0.29) A	<u>0.92</u> (0.10)
	M	22.45 (0.85)	29.20 (2.48) C	5.45 (0.17) C	8.27 (0.27) C	
Cowpea	F	23.50 (1.87) A	46.03 (4.31) A	6.13 (0.21) A	9.43 (0.30) A	<u>0.86</u> (0.14)
	M	23.10 (1.21)	29.26 (2.95) C	5.42 (0.21) C	8.25 (0.34) C	
Davis population						
Azuki	F	23.79 (0.84)	53.83 (3.53) B	6.48 (0.18) B	10.03 (0.24) B	<u>0.88</u> (0.24)
	M	23.80 (1.76)	38.87 (3.04)	5.97 (0.18) D	9.56 (0.26) D	
Cowpea	F	24.65 (1.69)	55.69 (3.56) B	6.52 (0.17) B	10.08 (0.24) B	<u>0.86</u> (0.13)
	M	24.22 (1.82)	40.11 (2.95)	5.98 (0.14) D	9.25 (0.22) D	

proportion of the variance in oviposition preference in either population (Table 2). The experimental design does not allow the source of this rearing host effect to be examined, because beetles emerged into dishes containing the seed they were reared on and were allowed to sit on this bean for up to 12 hours before they were collected for preference testing. Thus, a larval host effect cannot be distinguished from an effect of early adult experience. However, the influence of experience has been controlled for in all analyses presented here (see Materials and Methods).

*The Genetic Correlation between Preference and Performance.*—In both populations, beetles developed faster and had higher survivorship when reared on azuki, but adults were larger when reared on cowpea (Table 4). Large differences in the performance characters were observed among populations: beetles from the Bay Area population developed faster, but were smaller, on both hosts than beetles from the Davis population (Table 4).

Before a genetic correlation between preference and performance can be detected within a population, genetic variation in both preference and performance must be present. An analysis of variance for each performance character for *C. maculatus* (Table 5) demonstrates that among-family variance was present for all performance characters in the Bay Area population, and for development time and pronotum width in the Davis population. However, when estimating the correlation between family mean preference and family mean performance, I have defined a family's mean performance as the difference between their average performance on azuki and their average performance on cowpea [performance(azuki-cowpea), see Materials and Methods]. Demonstration of among family variance is not sufficient to demonstrate the presence of genetic variance in performance(azuki-cowpea). Both the family and host components of the analysis of variance may be positive, but if an interaction between them is absent, performance(azuki-cowpea) will be a constant for all families, and there is no genetic variance in this character [note that if only the among family component is positive (i.e., the host effect

TABLE 5. Analysis of variance for performance characters of *Callosobruchus maculatus* females reared on two hosts (seeds) in the laboratory. All analyses are performed using SAS GLM (SAS, 1985), calculating type IV sums of squares, with Family as a random effect and Host as a fixed effect. *F*-ratios were calculated as in Table 2.

Source	Development time			Pronotum width			Elytron length			Emergence weight		
	SS	df	F	SS	df	F	SS	df	F	SS	df	F
Family	413.7	40	4.59***	3.06	40	3.21***	6.57	40	3.06***	3,815	40	2.66***
	11.2	1	1.90 NS	0.04	1	0.75 NS	0.18	1	1.57 NS	59	1	1.44 NS
	236.9	40	2.63***	2.17	40	2.28***	4.54	40	2.12***	1,651	40	1.15 NS
	744.1	330		7.94	333		17.93	334		11,974	334	
Family	305.9	29	2.46***	0.78	29	2.02**	2.19	29	1.16 NS	1,813	29	1.31 NS
	42.0	1	10.09**	0.01	1	0.63 NS	0.00	1	0.05 NS	167	1	3.79 NS
	120.9	29	0.97 NS	0.42	29	1.09 NS	1.70	29	0.90 NS	1,283	29	0.93 NS
	1,043.4	243		3.20	241		15.62	241		11,653	244	

NS = *P* > 0.05, \*\* *P* < 0.01, \*\*\* *P* < 0.001.

TABLE 6. The family mean correlations between preference and performance in two populations of *Callosobruchus maculatus*. Standard errors (in parentheses) were calculated by bootstrapping the correlations 1,000 times, and correcting for bias (Efron, 1982). Signs of the correlations were corrected, if necessary, so that a positive correlation reflects that the beetles prefer the host they perform best on. Negative correlations reflect the opposite. The Davis correlations were calculated using 30 families, the Bay Area correlations with 41 families. None of the correlations are significantly different from zero.

Population	Family mean correlations between preference and:				
	Development time	Body weight	Pronotum width	Elytron length	Survival to adult
Bay Area	0.033 (0.142)	-0.187 (0.169)	-0.100 (0.195)	-0.155 (0.191)	-0.041 (0.164)
Davis	-0.187 <sup>1</sup> (0.178)	-0.222 (0.197)	-0.113 (0.256)	-0.201 (0.194)	-0.072 (0.170)

<sup>1</sup> 1 extreme outlier was deleted from this analysis.

is non-significant), performance (azuki-cowpea) will equal zero for all families]. An interaction between the family and host effects, however, would indicate that performance (azuki-cowpea) is not constant for all families, and that genetic variation is present for this character. This interaction term is intuitively important: if both among-family and among-host variances are positive, but the interaction between them is not, then all families will perform better on one host than the other, and all families would be selected to prefer that host.

For *C. maculatus*, among-family variance was present for almost all characters in each population (Table 5). However, the family  $\times$  host interaction was significantly non-zero for only development time, pronotum width, and elytra length in the Bay Area population, and for no characters in the Davis population (Table 5). Thus, a positive genetic correlation between preference and performance (azuki-cowpea) would only be expected to exist for these three characters.

There was no evidence in either population of a genetic correlation between ovi-

position preference and performance. Family mean correlations ranged from -0.222 to 0.033, but none of these estimates differed significantly from zero (Table 6). These estimates of genetic correlations are also potentially biased by maternal effects, which have been controlled for only as described above for the heritability estimates. Maternal age effects have not been controlled for, but if present would tend to bias results towards positive genetic correlations (see Materials and Methods section).

*The Genetic Correlation between Performance on Azuki and Performance on Cowpea.* — The family mean correlations of performance across hosts were positive for all characters in both populations (Table 7, range 0.132 to 0.542).

## DISCUSSION

*Heritability of Oviposition Preference.* — Genetic variation in oviposition preference within phytophagous insect populations has been demonstrated for a number of species using several techniques (reviewed by Futuyma and Peterson, 1985; Jaenike, 1990a;

TABLE 7. Family mean correlations of performance across hosts for *C. maculatus*. All standard errors were calculated by bootstrapping the family means correlations 1,000 times, and correcting for bias (Efron, 1982). *N* = the number of families which produced offspring on both hosts. Survivorship correlations are calculated independent of sex (dead larvae were not sexed).

Population	Sex	<i>N</i>	Development time	Emergence weight	Pronotum width	Elytron length	Survivorship (Hatch to emergence)
Bay Area	F	41	0.241 (0.156)	0.355 (0.166)	0.299 (0.140)	0.331 (0.141)	0.131 (0.187) <sup>1</sup>
	M	42	0.617 (0.202)	0.579 (0.095)	0.652 (0.097)	0.708 (0.080)	
Davis	F	30	0.542 (0.188)	0.132 (0.175)	0.327 (0.152)	0.302 (0.182)	0.247 (0.141) <sup>2</sup>
	M	33	0.091 (0.227)	0.432 (0.134)	0.147 (0.211)	0.326 (0.172)	

<sup>1</sup> *N* = 42 for Bay Area population survivorship data.

<sup>2</sup> *N* = 33 for Davis population survivorship data.

Jaenike and Holt, 1991; Via, 1991a). Available heritability estimates range from less than 0.10 for *Drosophila buzzatii* and *D. aldrichii* (Barker, 1992), 0.11 in *D. mojavensis* (Lofdahl, 1987), and 0.45 for *D. suboccidentalis* (Courtney and Chen, 1988), to as high as 0.9 in *Euphydryas editha* (Singer et al., 1988). The estimate of  $h^2$  for oviposition preference of 0.72 for the Bay Area population of *C. maculatus* (first generation) is unusually high for a behavioral character (Mousseau and Roff, 1987; Roff and Mousseau, 1987), but within the range of reported values for host preferences of herbivorous insects.

The maintenance of this observed variation in oviposition preference, however, is poorly understood. Both the presence of preference-performance genetic correlations and density dependent selection within different habitats can theoretically maintain high levels of genetic variation (Jaenike and Holt, 1991). In the two populations examined here, genetic correlations between preference and performance are not greater than zero, and thus cannot be maintaining the variation in oviposition preference observed in these populations.

*The Genetic Correlation between Preference and Performance.*—In the Bay Area population of this study, substantial genetic variation was present for at least three characters, development time, pronotum width, and elytra length (Table 4), yet no genetic correlation between preference and performance was detected. It is important to note that absence of a correlation for preference and one measure of performance may tell us little or nothing about the other possible correlations. In this project I have not measured all possible components of performance, and thus any positive correlations that might exist between preference and another performance character will not be detected.

The absence of a positive genetic correlation in these two populations is consistent with the results of Wasserman and Futuyma (1981), who also found no evidence for a positive correlation after 11 generations of selection on *C. maculatus* oviposition preference for two hosts, azuki (also used here) and pigeon pea (*Cajanus cajan*). Positive correlations between preference and perfor-

mance have been demonstrated for only three species of herbivores: *Drosophila pseudoobscura* (Taylor and Condra, 1983), *Euphydryas editha* (Ng, 1988; Singer et al., 1988) and *Liriomyza sativae* (Via, 1986). For at least four others (Wasserman and Futuyma, 1981; Tabashnik, 1986; Thompson, 1988b; Thompson et al., 1988; Jaenike, 1989, 1990b) no positive correlations have been detected.

*The Genetic Correlation between Performance on Azuki and Performance on Cowpea.*—In this project, I found no evidence for a trade-off between performance on azuki and performance on cowpea. This result for *C. maculatus* is consistent with most studies of performance trade-offs among hosts for other insects. Although many studies of this type have found substantial amounts of genetic variation for performance on each of the hosts they compared, little evidence has been found for genetic trade-offs (e.g., Via, 1984a, 1984b; Rausher, 1984; Weber, 1985; Hare and Kennedy, 1986; Futuyma and Philipi, 1987; James et al., 1988; Pashley, 1988; Karowe, 1990). Only Gould (1979), Pashley (1988), Fry (1990, 1992) and Via (1991b) have found any convincing evidence that trade-offs may exist across hosts.

Although positive, the genetic correlations calculated for *C. maculatus* are small (all less than 0.55). Via (1991a) notes that this is generally true for herbivorous insects, and suggests that genetic trade-offs may not constrain the evolution of performance on different hosts. Rather, performance on one host may be nearly genetically independent of performance on other hosts. My results are consistent with this hypothesis, particularly when considering that the correlations estimated here may be biased by maternal effects.

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## LITERATURE CITED

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