

TRADEOFFS IN PERFORMANCE ON DIFFERENT HOSTS: EVIDENCE
FROM WITHIN- AND BETWEEN-SITE VARIATION IN
THE BEETLE *DELOYALA GUTTATA*

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Host races of phytophagous insects are sympatric populations that have different host preferences and between which gene flow is restricted because of the difference in host preference. Sympatric, host-associated sibling species are sympatric populations that use different host plants and that do not interbreed because of the presence of isolating mechanisms not related to host preference (Jaenike, 1981; see Mayr, 1970, and Bush, 1969, for slightly different definitions of these terms).

Although the existence of host races and host-associated sibling species of phytophagous insects has been suspected for over 50 years (e.g., Thorpe, 1930), the evolutionary mechanism of host race formation remains controversial. In particular, there is disagreement about the importance of sympatric divergence in generating host races and species. White (1978) has argued that sympatric speciation must be invoked to explain, in part, the great diversity of specialized herbivorous insects, while Bush (1974, 1975) has forcefully advocated the operation of sympatric divergence in the creation of sympatric host races of tephritid flies. By contrast, Futuyma and Mayer (1980; see also Futuyma, 1983a) have argued that there is no reliable experimental evidence to support these claims and that models of sympatric speciation are based on assumptions that are probably not met by most phytophagous insects.

Several authors have developed formal models of sympatric divergence and speciation (Maynard Smith, 1966; Dickinson and Antonovics, 1973; Caisse and Antonovics, 1978; Pimm, 1979; Felsenstein, 1981). Although these models do

not account for the evolution of differences in host plant preference associated with purported sympatric speciation in phytophagous insects, Bush and Diehl (1983) and Rausher (1984) have suggested how modification of these models could remedy this problem.

A common assumption of all these models is that fitness on one host is negatively correlated with fitness on a second. This type of negative correlation is manifested in these models in the assumption that genetic variation exists at loci that exhibit a "crossing" genotype \times host plant interaction, i.e., at loci at which some genotypes have high fitness on one host but low fitness on a second host while other genotypes have low fitness on the first but high fitness on the second host. This negative correlation seems to be necessary for sympatric speciation because it permits linkage disequilibrium to be established between loci influencing, say, viability on different hosts and loci influencing host preference. The resulting coadapted preference-viability gene complexes represent incipient host races or species. Moreover, the breakdown of these coadapted gene complexes by recombination provides the selection pressure that improves reproductive isolation, whether isolation is achieved via mating on the host (e.g., Bush, 1974, 1975) or by a separate assortative mating locus in linkage disequilibrium with loci affecting preference and fitness (e.g., Felsenstein, 1981).

Without a crossing interaction, one homozygote genotype would have maximal fitness on both host species. Consequently, unless reproductive isolation were achieved instantaneously by a mutation

conferring complete reproduction isolation, that homozygote genotype would spread and become fixed throughout the entire population and only variation in host preference would remain. There would then be no further selection favoring increased reproductive isolation and hence speciation. Thus, it seems that whether sympatric speciation is common among phytophagous insects will depend in part on how frequently species exhibit negative correlations between fitnesses on different hosts.

Several recent attempts have been made to determine whether selection for high fitness on a particular host species entails in some way a decline in fitness on other host species. Most of these investigations have compared measures of larval growth performance on different host species for diet specialists and diet generalists (Schroeder, 1976, 1977; Smiley, 1978; Scriber and Feeny, 1979; Auerbach and Strong, 1981; Futuyma and Wasserman, 1982). The rationale underlying these experiments, although seldom stated in these terms, is that it is not possible to maximize fitnesses on two hosts simultaneously owing to negative genetic correlations between them. Consequently, for species using many hosts natural selection is likely to favor at least moderate viability and fecundity on each of several hosts used and fitness on no one host will be maximal. By contrast, some insects may specialize and feed on only one (or a few closely related) host; improvement of fitness on that host is not constrained by selection also favoring improvement of fitness on other hosts. As a result, if viability and fecundity of a generalist and specialist are compared on the host species of the specialist, the fitness of the specialist should be higher.

All of the empirical studies cited above are difficult to interpret because they employ interspecific comparisons. As Fox and Morrow (1981) point out, however, inferences about evolutionary constraints acting within populations that are based on interspecific comparisons can be invalid because patterns of variation

among species can differ both in sign and in magnitude from analogous patterns of variation within species (Simpson, 1953; Gould, 1966; Antonovics, 1976; Lande, 1979). Consequently, in order to determine whether negative genetic correlations of the kind necessary for sympatric speciation are common in nature, it is necessary to examine patterns of host-associated viability, fecundity, and growth performance within and between populations of a single species. The recent demonstrations by Gould (1979) that selection for high fitness of mites on cucumbers reduces fitness on lima beans represent a significant initial movement in such a direction.

The experiments reported in this paper represent an initial attempt to determine whether components of fitness are negatively correlated across host plants in the tortoise beetle *Deloyala guttata* (Chrysomelidae: Cassidinae). Because this insect was chosen without any prior knowledge of its genetic properties, I take it to be as likely as any other phytophagous insect to exhibit such negative correlations. Consequently, detection of such correlations in this species would suggest they are probably common in other species. I emphasize, however, that I am *not* asking whether sympatric divergence or speciation has actually occurred in *D. guttata*. Rather, I am using *D. guttata* as a model organism to ask whether certain genetic properties believed to be necessary for sympatric speciation are common in phytophagous insects in nature.

METHODS

Study Organisms

The tortoise beetle *Deloyala guttata* is distributed throughout the southeastern United States. Little is known about its feeding and oviposition habits throughout this region other than that it is found on plants in the morning glory family (Convolvulaceae). In North Carolina I have found it feeding and ovipositing frequently on *Ipomea pandurata* and *I. purpurea* and occasionally on *I. hederacea*.

The beetle is multivoltine with at least two and possibly three generations per year in the Piedmont of North Carolina. Both adults and larvae feed on foliage of the host plants.

Of the two host species used in this study, *I. pandurata* is native to the eastern United States. This species is a trailing perennial vine that is a common inhabitant of disturbed areas. By contrast, *I. purpurea* is naturalized from tropical America and grows as a weedy annual in disturbed areas throughout much of the eastern United States. Although little is known about differences in the chemical composition of these plant species, it is clear that they are not physiologically, nutritionally, and chemically equivalent substrates for growth and reproduction by *D. guttata*, since components of the beetle's fitness on and its behavioral responses to the two hosts are not the same. For example, mean pupal weight, percent survival, and fecundity differ for beetles reared on the two hosts (see Results). Moreover, oviposition preference between the two hosts is influenced by adult experience (Rausher, 1983a), which would not occur if beetles perceived both hosts as the same. The two hosts thus constitute different environments for the beetle and may therefore be expected to select for different adaptive characteristics.

Collections of beetles and plants were made at two study sites in Orange Co., North Carolina. One site, Duke Field (DF), is an old field bordered on three sides by forest and one side by a road and a cultivated field. Many *I. pandurata* plants grew in this field. The *I. pandurata* population is at least several and probably at least ten years old. Although *I. purpurea* occurs at this site, it is rare and is restricted to the edge of the road. It showed few signs of beetle damage and no beetles were seen on this plant. The second site, Wilbur Way (WW), was a cornfield, approximately 6.5 km north of the DF site. At WW *I. purpurea* was very common, while *I. pandurata* was very

rare (only 1 plant was seen) and showed no signs of use by *D. guttata*.

All beetles were collected as late-instar larvae and were reared to the adult stage on leaves collected from the two study sites. Beetles from DF were all collected from *I. pandurata*, whereas beetles from WW were collected from *I. purpurea*.

Before the experiments outlined below were performed, the beetles from both sites were randomly mated with other beetles from the same site and the offspring were reared by families for one generation on *I. purpurea*. The purpose of this generation of laboratory rearing was to minimize maternal effects as causes of differences among families in subsequent experiments. Because families were reared separately, residual maternal effects could remain due to differences among rearing containers. However, any residual maternal effects should influence only within-population comparisons and not between-population comparisons, since statistical analysis of between-population effects takes into account the between-family variance component due to maternal effects.

Experiment 1

This experiment was designed to estimate the heritabilities of various fitness components on each host, and to determine whether genotype \times host interactions exist within the populations and whether populations differ genetically in these fitness components when reared on either or both hosts. In addition, this experiment provided estimates of the average within-population genetic correlation between performance on the two hosts for each fitness component.

The four fitness components examined were survivorship to pupation, larval development time (time to pupation), pupal weight, and fecundity. Development time is potentially an important component of fitness in the field because it determines how long larvae are exposed to predators, parasites, and other mortality agents. Pupal weight was measured

because adult longevity and fecundity in insects is often correlated with size (Morris, 1963; Englemann, 1970). Fecundity was estimated by the number of eggs laid over the first two weeks of reproductive activity. Females may live for as long as one month in the laboratory but egg production normally decreases markedly after about two weeks (Rausher, 1983a). Fecundity measured over two weeks thus represents a reasonable approximation of lifetime fecundity.

For the experiment, seven males and seven females from each site were selected from the adults of the laboratory-reared generation of beetles. Each individual of a particular sex was from a different full-sib family, which was selected randomly without replacement from the available families. The beetles were then paired randomly with mates from the same site and eggs were obtained by allowing females to oviposit on cut leaves. Within-family (sib-sib) matings were avoided to prevent possible inbreeding effects from complicating the analysis. The hatchling larvae from each pair (full-sib families) were then allocated to either of two treatments: half to growth on *I. pandurata* and half to growth on *I. purpurea*. A total of 634 larvae were used in this experiment. The mean number of larvae per plant species per family was 22.7 ± 3.5 (SD). The range was 18–30.

The larvae within each treatment were assigned with a random number table to individually-labeled leaves on potted plants in a growth chamber set to a photoperiod of 18L:6D, a temperature regime of 29 C:21 C Light:Dark (± 1 C), and a constant relative humidity of 85%. Larval density was one larva per leaf; the leaves were large enough to permit a larva to complete its development on only one leaf. The bases of the leaf petioles were coated with tanglefoot to prevent larvae from moving off the leaves upon which they had been placed. Just prior to pupation larvae turn from pale yellow to green and void their guts. All larvae were checked twice daily to determine

whether this change had occurred. Any larvae that had so changed were removed and placed individually in petri dishes for pupation. All individuals were weighed within 24 h of pupation. Upon eclosion, adults were mated and females were then placed in a petri dish with a portion of leaf of the species on which they were reared at larvae. Leaves were replaced every two days and eggs were counted at replacements.

Experiment 2

A second experiment was performed to examine variation in standard indices of larval growth rate and growth efficiency (Waldbauer, 1968; Scriber, 1977). This experiment was designed to determine, for the indices listed in Table 1, whether genetic variation exists within populations for larvae grown on a particular host, whether a genotype \times host interaction exists within populations, and whether a negative genetic correlation exists within populations between a particular index on one host species and the same index on the other host species.

Twelve mating pairs were set up from the adults of the laboratory-reared generation. The 12 males and females represented different randomly-selected families from the DF site. The larval offspring from each of the 12 pairs were allocated to either of two experimental treatments: rearing on *I. pandurata* or rearing on *I. purpurea*. The larvae were reared under the growth chamber conditions of Exp. 1 on cut foliage replaced every 2 days until they molted to the fifth (last) instar, when they were used in the experiment.

Prior to weighing, the larvae were starved for three hours, a time that proved sufficient to allow them to void their guts of previously ingested foliage, and then weighed. A separate cohort of larvae was sacrificed at the beginning of the experiment, dried, and reweighed to determine an initial dry weight/wet weight ratio. Since the families did not differ significantly in this ratio, a common value was

TABLE 1. Growth performance indices measured in Experiment 2. Indices calculated as described in Waldbauer (1968) and Scriber (1977).

Index	Method of calculation ¹
Relative consumption rate (RCR)	$\frac{\text{Biomass foliage ingested}}{\text{Mean larval biomass} \times 24 \text{ h}}$
Relative growth rate (RGR)	$\frac{\Delta \text{ larval biomass}}{\text{Mean larval biomass} \times 24 \text{ h}}$
Gross growth efficiency (ECI)	$\frac{\Delta \text{ larval biomass}}{\text{Biomass foliage ingested}}$
Approximate digestibility (AD)	$\frac{\text{Biomass foliage ingested} - \text{Biomass feces}}{\text{Biomass foliage ingested}}$
Net growth efficiency (ECD)	$\frac{\Delta \text{ larval biomass}}{\text{Biomass foliage ingested} - \text{Biomass feces}}$

¹ Mean larval biomass = $\frac{1}{2}(\text{Initial larval biomass} + \text{Final larval biomass})$.

used to calculate the initial dry weight of the experimental larvae.

After being weighed, each larva was placed in a 15 cm diameter plastic petri dish with a disc of moistened filter paper and a small piece of leaf of the host species on which the larva had been reared during the first four instars. This leaf piece was obtained by cutting in half a larger piece of leaf. The half offered to the larva was weighed to determine initial fresh weight. The other half was weighed, freeze-dried, and reweighed to determine a dry weight/wet weight ratio for that leaf. This ratio was then used to estimate the dry weight of the leaf fragment offered to the larva. All leaf weighings were done prior to all larval weighings to minimize the length of time over which larvae were weighed.

The dishes with larvae were placed in the growth chamber (same conditions as in Exp. 1) for 24 h. The leaves were then removed from the dishes and the larvae were starved for 3 h to permit gut voidance. The larvae were then weighed, freeze-dried, and reweighed to determine final dry weight and weight gain. The remaining leaf fragment and feces were also collected, dried, and weighed to estimate the indices in Table 1.

Because estimation of growth indices is highly labor-intensive, large numbers of individuals could not be handled on a single day. Consequently, the experiment

described above was replicated on three different days, with approximately 4–5 larvae from each family being fed each host species in each replicate. The overall experiment thus has a three-way factorial design with host species, family, and day (replicate) as main effects, the family and day effects being considered random and the host effect fixed.

Statistical Analyses

The significance of between-family and between-site main effects, as well as of host species \times family and host species \times site interactions, was assessed using analysis of variance. In such analyses between-family main effects within populations may be due to any combination of genetic differences and maternal effects and include a dominance component of variance (Falconer, 1960). Consequently, heritabilities calculated for each significant family main effect by the standard ratio for full-sib families, $2\sigma_f^2/(\sigma_f^2 + \sigma_e^2)$ represent upper bounds (Falconer, 1960). Heritabilities of percent survival were calculated by the method of Bull et al. (1982) for binary data. Because only one value of survivorship is available per family on each host, ANOVA could not be used to analyze the effects of family and host on survivorship. Instead, a two-way *G*-test (Sokal and Rohlf, 1969) was used to determine whether families differed sig-

nificantly in survivorship on each host. An analogous three-way log likelihood ratio analysis (Fienberg, 1970; Bishop et al., 1975) was used to determine whether relative survivorship on the two hosts differed among families, i.e., whether there was a family \times host interaction for per cent survival. Finally, differences between sites in survivorship were assessed using a two-way ANOVA on the family values, with host and site as main effects.

Two types of correlation estimates were calculated in this study: family mean correlations and variance component correlations (Arnold, 1981). Family mean correlations are calculated by applying the standard product-moment correlation formula to the family means for each host:

$$r_m = \frac{\text{Cov(I,II)}}{\sqrt{\text{Var(I)} \times \text{Var(II)}}},$$

where Cov(I,II) is the covariance of family means on the two hosts and Var(I) and Var(II) are, respectively, the variances of family means on *I. pandurata* and on *I. purpurea*. This procedure tends to underestimate the absolute value of the true genetic correlation because the expected mean squares of the variances in the denominator are inflated by the presence of the within-family (error) variance component, whereas the covariance in the numerator is not so inflated (Yamada, 1962). Nevertheless, since estimated variances of r_m tend to be smaller than those of the variance component estimate, r_g , the use of r_m often allows a more powerful statistical test of whether the genetic covariance is significantly different from zero.

By contrast, the variance component estimate, given by

$$r_g = \frac{\sigma_{g_{1,11}}}{\sqrt{\sigma_{g_1}^2 \sigma_{g_{11}}^2}},$$

where $\sigma_{g_{1,11}}$ is the genetic component of covariance in performance on the two hosts and $\sigma_{g_1}^2$ and $\sigma_{g_{11}}^2$ are, respectively, the genetic components of variance in performance on *I. pandurata* and on *I. purpurea*, is a less-biased estimate of the true genetic correlation. The variable r_g

and its variance were estimated by the jackknife technique (Gray and Schucany, 1972) by deleting the data for each family in turn and obtaining the between-family variance components from the appropriate ANOVA. For each partial data set, the covariance of family means provided an unbiased estimate of the genetic covariance (Yamada, 1962). All analyses were performed on a data set from which significant sex and site main effects were first removed (there were no significant interactions to be removed); r_m and r_g were then calculated from the remaining residuals. The correlations obtained thus represent average within-site genetic correlations that are not confounded by between-site effects.

All ANOVAS were performed using the GLM procedure of the Statistical Analysis System (Barr et al., 1979). Because in most analyses the data were unbalanced, Type IV sums of squares were used in tests of significance because this method is appropriate for tests with unbalanced data. The three-way log likelihood ratio analysis was performed using an APL program written by and available from the author.

RESULTS

Experiment 1

Within-population Variation.—Development time, pupal weight, and per cent survival all exhibited significant between-family variation (Tables 2, 3 and 4), although all estimates of heritability are low (Table 4). By contrast, there is no evidence for a family \times host species interaction for any of the four characters (Tables 3 and 4; the relevant entry in Table 4 is the survivorship \times host \times family 3-way interaction). Thus, while there is some evidence suggesting the existence of genetic variation affecting three of the four fitness components examined, no evidence indicates that genotypes respond in different ways on the two host species.

Falconer (1952, 1960) has argued that a single trait measured in two environ-

TABLE 2. Mean values of Development Time (DEVT), Pupal Weight (PUPALWT), and Two-Week Fecundity (FECUND) by host, sex, and family. Development Time is measured in days, pupal Weight in mg, and Fecundity in number of eggs laid. Standard errors are in parentheses. PA: *Ipomoea pandurata*. PU: *I. purpurea*.

A. DF Population			Family						
Host	Sex	Character	18	19	25	50	61	65	66
PA	M	DEVT	14.2 (6)	15.2 (6)	14.6 (3)	15.1 (4)	14.7 (6)	14.6 (9)	13.9 (5)
		PUPALWT	10.7 (2)	9.9 (1)	10.1 (2)	9.8 (3)	9.9 (3)	11.0 (1.2)	9.7 (4)
	F	DEVT	15.1 (6)	14.8 (4)	15.9 (6)	16.9 (1.0)	14.0 (1.0)	14.7 (6)	15.6 (6)
		PUPALWT	13.9 (5)	12.6 (5)	12.0 (6)	12.0 (5)	12.7 (4)	11.3 (4)	11.0 (5)
PU	M	FECUND	15.0 (6.0)	51.0 (9.3)	102.0 (13.4)	57.3 (11.9)	87.5 (21.5)	90.3 (7.6)	61.6 (14.0)
		DEVT	13.0 (3)	13.0 (6)	13.6 (1.1)	15.8 (1.0)	15.2 (5)	13.7 (3)	13.6 (3)
		PUPALWT	11.1 (2)	10.7 (3)	10.1 (4)	9.7 (2)	9.8 (5)	9.4 (7)	9.6 (4)
	F	DEVT	14.4 (9)	14.5 (4)	14.0 (4)	17.1 (1.2)	—	14.7 (4)	14.4 (4)
		PUPALWT	13.1 (2)	12.5 (5)	13.3 (3)	11.4 (5)	—	11.2 (3)	11.2 (6)
		FECUND	53.3 (14.1)	63.2 (15.6)	88.6 (14.5)	69.8 (21.6)	—	77.5 (12.8)	83.8 (14.9)
B. WW population			Family						
Host	Sex	Character	309	317	318	325	327	330	349
PA	M	DEVT	16.9 (1.6)	14.9 (5)	15.3 (1.8)	15.4 (1.4)	14.0 (3)	15.0 (—)	14.2 (5)
		PUPALWT	9.7 (5)	10.9 (5)	10.8 (2)	10.3 (1)	10.7 (2)	9.7 (—)	10.5 (2)
	F	DEVT	16.8 (1.1)	15.7 (8)	14.6 (5)	15.4 (1.4)	14.9 (4)	15.5 (5)	15.1 (4)
		PUPALWT	11.8 (1.3)	12.8 (4)	12.6 (3)	11.9 (5)	13.9 (6)	11.3 (1.6)	12.9 (4)
		FECUND	25.7 (7.2)	28.7 (12.2)	43.3 (11.6)	44.0 (23.1)	32.6 (6.7)	21.0 (—)	49.0 (23.6)
PU	M	DEVT	16.5 (1.4)	15.5 (7)	14.8 (8)	15.0 (6)	14.8 (4)	28.0 (—)	13.6 (4)
		PUPALWT	9.7 (3)	10.4 (4)	10.3 (6)	10.0 (4)	10.4 (7)	7.1 (—)	10.3 (4)
	F	DEVT	17.5 (3.0)	15.5 (1.3)	15.3 (5)	17.1 (1.1)	14.8 (8)	13.0 (—)	15.3 (5)
		PUPALWT	12.3 (8)	11.8 (4)	12.3 (2)	11.2 (3)	11.9 (7)	12.9 (—)	11.8 (4)
		FECUND	86.5 (10.5)	61.0 (47.0)	68.9 (15.1)	90.3 (1.1)	70.2 (24.7)	84.0 (—)	57.0 (—)

TABLE 3. Results of analysis of variance for development time, pupal weight and fecundity in Experiment 1.

Source	Development time		Pupal weight		Fecundity	
	<i>d.f.</i>	<i>F</i>	<i>d.f.</i>	<i>F</i>	<i>d.f.</i>	<i>F</i>
Sex	1;283	6.25**	1;283	208.91***	—	—
Host	1;12	.01	1;283	4.62*	1;76	16.68***
Site	1;12	3.29	1;12	.13	1;12	1.44
Site × Host	1;282	3.62	1;282	3.25	1;76	6.17**
Family (within site)	12;282	3.63***	12;282	4.10***	12;76	1.10
Family × Host	12;270	1.16	12;270	0.92	11;65	.83

* $P < .05$, ** $P < .02$, *** $P < .001$.

ments can be considered as two different traits and that the genetic correlation between these two traits is related to the magnitude of the genotype × environment interaction associated with the single trait. Robertson (1959) and Yamada (1962) formalized this suggestion and demonstrated that, relative to between-family main effect variance, a large interaction variance implies a negative genetic correlation, while a small interaction variance implies a positive genetic correlation. This line of reasoning suggests that the genetic correlation for the fitness components examined in this experiment should be high and positive.

This expectation is substantiated by the calculated genetic correlations (Table 5). The best estimates (r_g) of the true genetic correlations across hosts for pupal weight and development time are .668 and .719, respectively. For pupal weight the 95% confidence interval of the family mean correlation does not overlap zero, indicating that there is a statistically significant ($P < .05$) positive genetic covariance between pupal weight on the two

hosts and that the genetic correlation is significantly greater than zero. For development time, by contrast, there is no evidence for a non-zero genetic covariance. Nevertheless, the best estimate (r_g) of the genetic correlation suggests it is high and positive; it is clearly not strongly negative.

Finally, because only one value of survivorship is available per family on each plant, r_m is the only estimate available for the genetic correlation for percent survival. This estimated value of .51 is significantly greater than zero, as judged by the 95% confidence interval (Table 5). Moreover, since this value underestimates the true genetic correlation, it appears that that correlation is again positive and high.

Between-population Variation.—Neither development time nor pupal weight exhibit differences between sites and neither show a site × host interaction; however, fecundity does exhibit such an interaction (Table 3). Moreover, this interaction is of the crossing type, as shown in Figure 1a. The differences between sites are in the direction expected if sites represent populations locally adapted to their host plants: beetles from each site have higher fecundity on the host species from which their progenitors were collected. Some evidence suggests that these differences are due to effects expressed first in the larval stage which then carry over to influence early adult fecundity. During the first week of reproduction, fecundity exhibits the same sig-

TABLE 4. Results of log-likelihood ratio analysis for survivorship in Experiment 1.

Source	<i>G</i>	<i>d.f.</i>	<i>P</i>
Survivorship × host	4.01	1	<.05
Survivorship × family	46.75	13	<.005
Host × family	8.10	13	NS
Survivorship × host × family	15.53	13	NS

TABLE 5. Maximum values of heritabilities (h^2) of fitness components and values of genetic correlations between performance on *I. pandurata* and *I. purpurea* for fitness components exhibiting significant genetic variation. Values in parentheses are 95% confidence intervals (for r_m) and standard errors (for r_g).

Character	h^2		r_m	r_g
	On <i>I. pandurata</i>	On <i>I. purpurea</i>		
Development time	.139**	.274***	.365 (-.188,.716)	.719 (.964)
Pupal weight	.230*	.286***	.620 (.130,1.00)	.668 (.454)
Percent survival	.124***	.091**	.510 (.154,.971)	—
Fecundity	.292	.000	—	—

* $P < .05$; ** $P < .01$; *** $P < .005$.

nificant crossing interaction as overall fecundity (Fig. 1b; for site \times host interaction, $F_{1,76} = 11.82$, $P < .001$), whereas during the second week it does not (Fig. 1c; $F_{1,76} = .67$, NS). This pattern is consistent with the hypothesis that differential accumulation of reserves during the larval stage is responsible for the differences in fecundity observed during the first week of reproduction, but that these reserves are exhausted by the beginning of the second week; eggs laid thereafter are produced entirely from food ingested by adults, which do not differ between sites in ability to process foliage from the two types of host.

Percent survival does not appear to differ between sites ($F_{1,24} = 1.14$, NS). There also is no apparent site \times host interaction ($F_{1,24} = .06$, NS).

Experiment 2

The five indices of growth performance assayed in this experiment were analyzed by a Multivariate Analysis of Variance (Timm, 1975) because they tended to be highly correlated with each other. Neither the family main effect nor the host \times family nor host \times family \times day interactions were statistically significant (Tables 6 and 7). These results indicate that there was no detectable genetic variation in characters associated with growth performance on either of the two host plants. Consequently, genetic correlations were not calculated for any of the indices, since

such correlations have no meaning if genetic variability does not exist.

Absence of detectable genetic variation in any of the growth indices measured suggests that the within-population variation in development time and pupal weight found in Exp. 1 is not due to underlying genetic variation in characters associated with larval feeding rates or digestive physiology. Although not tested directly, a more likely explanation for such variation is that individuals differ genetically in the critical size threshold (e.g., Nijhout and Williams, 1974; Nijhout, 1975) at which pupation is initiated. Such differences would most likely affect development time and pupal weight in the same direction on each host species and would thus account for the significant between-family main effect and the lack of significant family \times host interactions, as well as for the positive correlations across hosts, seen in these traits.

DISCUSSION

The purpose of this investigation was to determine whether components of fitness for beetles reared on one host species are negatively correlated with analogous components for beetles reared on a different host. Analysis of within-population variation has revealed no evidence of such negative genetic correlations. Of course, the experimental analyses may not have been sensitive enough to allow detection of small amounts of the type of

TABLE 6. Mean values of growth indices by family and host, averaged over days. Abbreviations as in Tables 1 and 2. BEGWT: Initial dry weight of larva in mg, used as covariate in MANOVA. Values in parentheses are standard errors.

Family	RCR		RGR		ECI		AD		ECD		BEGWT	
	PA	PU	PA	PU	PA	PU	PA	PU	PA	PU	PA	PU
2	1.60 (.18)	.94 (.13)	.36 (.05)	.33 (.05)	.17 (.06)	.28 (.08)	.63 (.05)	.77 (.04)	.35 (.08)	.41 (.11)	1.11 (.09)	1.27 (.09)
3	1.71 (.14)	1.31 (.11)	.31 (.06)	.38 (.05)	.17 (.03)	.29 (.03)	.66 (.05)	.76 (.02)	.33 (.06)	.39 (.04)	.77 (.05)	1.02 (.06)
5	1.63 (.15)	1.04 (.12)	.37 (.06)	.31 (.06)	.23 (.03)	.24 (.07)	.61 (.04)	.84 (.03)	.42 (.05)	.32 (.09)	1.12 (.09)	1.38 (.11)
7	1.79 (.13)	1.37 (.13)	.27 (.05)	.33 (.06)	.14 (.03)	.20 (.06)	.66 (.05)	.82 (.03)	.28 (.07)	.28 (.07)	.83 (.09)	.85 (.09)
8	1.80 (.15)	1.16 (.13)	.35 (.05)	.35 (.07)	.18 (.02)	.26 (.09)	.63 (.04)	.76 (.04)	.35 (.04)	.50 (.26)	.90 (.05)	1.20 (.07)
13	1.70 (.14)	1.53 (.07)	.42 (.04)	.50 (.03)	.27 (.03)	.33 (.01)	.58 (.03)	.79 (.02)	.55 (.09)	.42 (.02)	.82 (.08)	1.00 (.05)
14	1.68 (.18)	1.06 (.17)	.25 (.05)	.28 (.07)	.20 (.05)	.41 (.14)	.55 (.11)	.73 (.06)	.17 (.09)	.68 (.23)	.72 (.04)	1.05 (.10)
23	1.53 (.10)	.85 (.15)	.34 (.05)	.20 (.05)	.22 (.02)	-.09 (.29)	.50 (.29)	.80 (.05)	.48 (.10)	.00 (.30)	1.11 (.10)	1.34 (.09)
24	1.43 (.18)	1.01 (.17)	.35 (.05)	.29 (.06)	.22 (.04)	.26 (.03)	.60 (.04)	.84 (.04)	.44 (.09)	.34 (.05)	1.13 (.08)	1.29 (.10)
25	1.75 (.14)	1.17 (.19)	.41 (.04)	.35 (.05)	.24 (.20)	.35 (.05)	.57 (.04)	.75 (.03)	.19 (.07)	.48 (.07)	1.13 (.08)	1.35 (.11)
26	1.18 (.18)	1.05 (.16)	.26 (.06)	.23 (.07)	.08 (.05)	.48 (.30)	.66 (.05)	.80 (.02)	.19 (.07)	.54 (.30)	1.30 (.08)	1.07 (.07)
107	1.68 (.16)	1.27 (.15)	.37 (.04)	.38 (.05)	.21 (.02)	.13 (.15)	.60 (.04)	.91 (.11)	.41 (.07)	.29 (.08)	1.19 (.10)	1.42 (.08)
Mean	1.67 (.04)	1.16 (.04)	.34 (.01)	.33 (.02)	.20 (.01)	.26 (.04)	.61 (.02)	.80 (.01)	.38 (.02)	.38 (.05)	1.01 (.03)	1.19 (.03)

genetic variation that gives rise to negative correlations. It is thus possible that negative correlations exist but were not detected for fecundity. However, all three traits for which there was any evidence of genetic variation (i.e., pupal weight, development time, and survivorship) exhibited high positive genetic correlations. Such differences arise because individuals and families deviate from mean performance in the same direction on the two hosts, whereas negative genetic correlations can arise only if individuals and families deviate from the mean in opposite directions on the two hosts. Because the analyses in this study were based on full-sib families, it is possible that much of the main effect between-family variation, and hence much of the estimated positive genetic correlation, in pupal weight, development time and survival could be due to maternal effects. Even if this were the case, however, it remains true that none of the characters analyzed provide any positive indication for the existence within populations of negative correlations of the type sought.

Nevertheless the observed divergence between sites in fecundity suggests that such negative genetic correlations may exist for this fitness component. Beetles collected from *I. pandurata* at the DF site have a higher fecundity on that host than beetles collected from *I. purpurea* at the WW site, whereas the opposite is true for beetles from the two sites when reared on *I. purpurea*. This pattern is expected if genotypes with high fecundity on one host necessarily have low fecundity on the other and if different genotypes are favored by selection at the two sites. Under such divergent selection one would also expect genetic variation to be reduced within sites. Unless selection on fecundity were very strong and migration very low, however, within-site genetic variation in fecundity would not be completely eliminated (Christiansen and Feldman, 1975), especially not in the 30 or fewer generations the DF populations is estimated to have existed. Nevertheless, selection might reduce variability

TABLE 7. Multivariate Analysis of Variance for indices of growth performance in Experiment 2. The test statistic is Wilke's lambda criterion (λ). Initial larval weight was used as a covariate.

Source (effect)	Effect used as error	d.f.	λ	P
Initial weight (1)	9	1	.864	<.001
Host (2)	6	1	NC*	—
Family (3)	7	11	.115	NS
Day (4)	6 + 7 pooled	2	NC*	—
Host \times family (5)	8 + 9 pooled	11	.847	NS
Host \times day (6)	8 + 9 pooled	2	.857	<.001
Family \times day (7)	8 + 9 pooled	22	.569	<.001
Host \times family \times day (8)	9	22	.668	NS
Error (9)	—	321	—	—

* These values of λ were not calculable because the Host \times Day sums of squares and cross-products matrix was singular.

sufficiently that detection of it would be difficult using the sample size employed in this study, especially if migration between sites with different host plants is low. Failure to detect genetic variation in fecundity within habitats, even though it exists between habitats, is thus consistent with expectations under divergent selection if fecundity on *I. purpurea* is negatively correlated genetically with fecundity on *I. pandurata*.

An alternative explanation for the crossing pattern of variation evident in Figure 1 is that the DF and WW populations differ at two loci, each of which affects fecundity on one host but not on the other (see Table 8). If the DF population is fixed for A_1 and B_2 , while A_2 and B_1 are fixed at the WW site, a crossing pattern similar to that in Figure 1 would be observed and there would be no genetic variation within sites; yet this type of variation does not involve loci characterized by the crossing type of genotype \times host interaction thought necessary for sympatric speciation.

TABLE 8. Hypothetical genotypic values of fecundity for a two-locus system in which each locus influences fecundity of larvae grown on one host but not larvae grown on a second host.

Genotype	Fecundity on <i>I. pandurata</i>	Fecundity on <i>I. purpurea</i>
A_1- , B_1-	$\mu + \sigma_1$	$\mu + \sigma_2$
A_2A_2 , B_1-	μ	$\mu + \sigma_2$
A_1- , B_2B_2	$\mu + \sigma_1$	μ
A_2A_2 , B_2B_2	μ	μ

Unfortunately it is not possible to distinguish conclusively between these two explanations. The critical data needed for

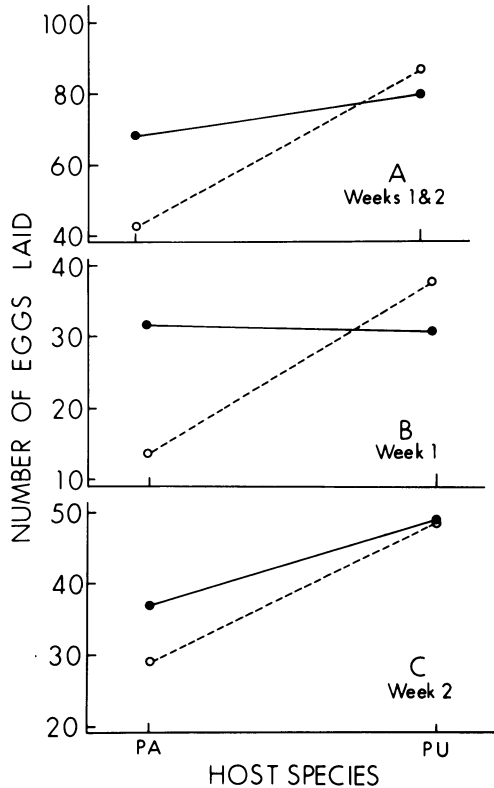


FIG. 1. Pattern of site \times host interaction for fecundity. Symbols: PA—*I. pandurata*; PU—*I. purpurea*; solid lines—Duke Field site; broken line—Wilbur Way site. A. Overall fecundity during first two weeks of reproductive activity. B. Fecundity during first week of reproductive activity. C. Fecundity during second week of reproductive activity.

doing so are the amount of migration that occurs between sites having different host species present, since the correctness of the second, alternate explanation depends crucially on very low migration between sites. Only if populations at the two study sites are highly isolated and small, so that genetic drift would have an opportunity to fix either A_2 or B_2 , would the crossing pattern in Figure 1 have a non-trivial probability of arising by the second mechanism proposed (Crow and Kimura, 1970). Otherwise, with even a small amount of migration, selection averaged over the beetle metapopulation would be expected to fix alleles like A_1 and B_1 (Table 8) that confer maximal fecundity of individuals feeding on either host, leaving only variation of the type producing negative correlations across hosts (Lerner, 1950; Falconer, 1960; Antonovics, 1976).

Little is known quantitatively about migration by *D. guttata*. Relatively rapid colonization of new host patches (Rausher, pers. observ.) does suggest that movement between sites is not rare and that populations are not completely isolated. If this conclusion is substantiated by further experimentation, the alternative explanation for the crossing pattern in Figure 1 will be unlikely and that pattern will be best explained by divergent selection acting on a trait that is negatively correlated across hosts due to pleiotropy. Taken with Gould's (1979) detection of such negative correlations in the mite *Tetranychus urticae*, these results would then indicate that in two species examined in detail genetically, negative correlations between fitnesses on different hosts are present. Since in neither case is the organism examined thought to be atypical of phytophagous arthropods, these results would indicate that a condition believed necessary for sympatric speciation commonly exists in natural populations of these animals. The existence of geographical biotypes locally adapted to different host species in both natural populations (Rausher, 1981; Tabashnik, 1981; Scriber, 1983) and pop-

ulations of agricultural pests (Rausher, 1983b) is consistent with this conclusion, though it is also consistent with explanations involving variation of the type shown in Table 8.

Implications of Positive Correlations

The results of this study suggest that while negative genetic correlations across hosts exist for some fitness components, positive correlations are more common. Three fitness components examined exhibited positive correlations, while for only one was there any evidence of a negative correlation due to pleiotropy. Gould (1979) similarly reports that while selection for adaptation by *Tetranychus urticae* mites to cucumbers caused a decrease in adaptation to lima beans, the original host, it also increased the mites' ability to survive and reproduce on novel host plants that were not involved in the actual selection experiments. This cross-adaptation indicates that positive as well as negative correlations in fitness across hosts exist in these mites.

The existence of positive correlations of this type do not diminish the potential importance of negative correlations for sympatric divergence and speciation. Positive correlations do not interfere with these processes and only one fitness component need exhibit negative correlations for divergence and speciation to occur. However, the existence of positive correlations does suggest that selection for adaptation to one host plant in nature may commonly confer some degree of preadaptation to using currently unused host species. Such preadaptation would in turn facilitate both host range expansion and shifts to novel hosts, either sympatrically or allopatrically, as discussed by Futuyma (1983b).

SUMMARY

Although models of host race formation and sympatric speciation in phytophagous insects assume that genotypes that have high viability and/or fecundity on one host species have low viability and/or fecundity on others, this assump-

tion has seldom been tested explicitly. This report describes experiments designed to determine whether such negative genetic correlations in performance on different hosts exist in the tortoise beetle *Deloyala guttata*. No evidence for such negative correlations was found within the populations examined. Between-population variation in fecundity is suggestive of but does not conclusively demonstrate the existence of such trade-offs.

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