

PREDICTING HOST RANGE EVOLUTION: COLONIZATION OF
CORONILLA VARIA BY *COLIAS PHILODICE*
(LEPIDOPTERA: PIERIDAE)

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Abstract.—Extensive sympatry is currently arising between the common sulfur butterfly, *Colias philodice* Latreille (Lepidoptera: Pieridae) and a potential leguminous host plant, *Coronilla varia* (L.). In laboratory trials, larval survivorship and growth were higher on the primary host, *Medicago sativa* (L.), than on the nonhost *C. varia*. However, because females reared from *C. varia* were on average more fecund than females reared from *M. sativa*, fitness on *C. varia* (approximately as survivorship times fecundity) was commensurate with fitness on *M. sativa*. Thus, it is predicted that selection would favor oviposition on *C. varia*, if such behavior were to arise. In addition, significant among-family variation exists for several measures of larval performance on both *C. varia* and *M. sativa*, indicating that *C. philodice* can potentially respond to selection for increased performance on each species. Moreover, larval performance was significantly positively correlated across these species, suggesting that selection for increased performance on each species will facilitate, not constrain, evolution of increased performance on the other. It is concluded that behavioral rather than physiological barriers currently account for the absence of *C. philodice* from *C. varia* and that, if such barriers are overcome, *C. philodice* will expand its host plant range to include *C. varia*.

Received January 17, 1989. Accepted December 15, 1989.

The evolution of host plant range is of both theoretical and economic importance, since present associations between insect herbivores and their host plants are largely attributable to past host shifts and host range expansions. Although the evolutionary lability of host plant range among herbivorous insects has long been recognized (Dethier, 1954; Ehrlich and Raven, 1964), the study of host range evolution among herbivorous insects remains essentially a post hoc science. However, as argued by Gould (1978, 1983), this need not be the case.

For herbivorous insects with relatively immobile larvae, such as many Lepidoptera, colonization of a potential host plant may be precluded by the failure of females to recognize the potential host as a suitable oviposition site. However, if at least some females accept the potential host for oviposition, and if such variation is heritable, then the course of local host range evolution might reasonably be anticipated from knowledge of (1) the initial relative fitness of the herbivore on potential and existing

hosts, (2) the degree of within-population genetic variation in fitness on potential and existing hosts, and (3) the degree and sign of genetic correlation in fitness between potential and existing hosts.

Selection should favor host range expansion if initial fitness on the potential host is commensurate with fitness on existing hosts, particularly if fitness is limited by the rate at which suitable oviposition sites are encountered (Levins and MacArthur, 1969; Jaenike, 1978; Courtney, 1984). If, on the other hand, fitness differs substantially between potential and existing hosts, then selection should generally act to decrease preference for, or to increase fitness on, the poorer host (Futuyma, 1983a; see also Castillo-Chavez et al., 1988). If preference for the better host evolves more rapidly than performance on the poorer host, then the poorer host (whether potential or existing) should be eliminated from the herbivore's host plant range.

Genetic correlations in performance across hosts may strongly influence the rate at which performance on any single host evolves (Antonovics, 1976; Lande, 1980; Via and Lande, 1985). In particular, if performance is negatively correlated across hosts, then selection for increased perfor-

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mance on the poorer host may be constrained by the associated "cost" of reduced performance on the more suitable host (Rausher, 1983). Such circumstances are likely to inhibit the expansion of host plant range. On the other hand, if performance is positively correlated across diets, then selection for increased fitness on either host will result in increased fitness on both, and expansion of the herbivore's host plant range is more likely.

Throughout the eastern and midwestern United States, extensive sympatry is currently arising between the common sulfur butterfly, *Colias philodice* Latreille (Lepidoptera: Pieridae) and a recently introduced potential host plant, *Coronilla varia* L. (Fabaceae). In southeastern Michigan, *C. varia* often occurs in the same habitat as *Medicago sativa*, the primary host plant of *C. philodice*. The absence of *C. philodice* from *C. varia* in nature is apparently due to pre-alighting discrimination by ovipositing females (Karowe, 1988). The aim of this study is to determine whether physiological barriers to colonization also exist, and to use this information to anticipate the likely course of host range evolution should females initiate oviposition on *C. varia*. Accordingly, I ask:

1. How does present performance of *C. philodice* on *C. varia* compare to that on *M. sativa*?
2. Can selection potentially act to improve performance on *M. sativa* and/or *C. varia*, i.e., does *C. philodice* exhibit heritable variation for performance on either species?
3. Will evolution of increased performance on one host facilitate or constrain evolution of increased performance on the other, i.e., is fitness on *C. varia* correlated, either positively or negatively, with fitness on *M. sativa*?

To answer these questions, I measured the performance of *C. philodice* larvae on *M. sativa* and *C. varia* during two successive generations, determined whether the sampled population contained genetic variation for larval performance on these plant species, and determined the nature of correlations in performance across plant species.

MATERIALS AND METHODS

Study Organisms

Over approximately the last 200 years, *Colias philodice* has incorporated numerous introduced legumes into its host plant range (Klots, 1951; Tabashnik, 1983; Scott, 1986). In Michigan, *C. philodice* feeds primarily on the introduced European species *M. sativa* L. (alfalfa) and *Trifolium pratense* L. (red clover), and uses *Melilotus alba* L. (white sweet clover) as a secondary host (personal observation).

Coronilla varia L. (crown vetch) represents a potential host plant for *C. philodice*. At present, *C. philodice* is not known to occur on *C. varia*, though females do visit this species for nectar (Karowe, 1988). Introduced into the eastern United States in 1890 (Henson, 1963), *C. varia* is a considerably more recent addition to the North American flora than are *M. sativa*, *T. pratense*, and *M. alba*. Due to its attractiveness as groundcover and forage (Reynolds et al., 1969; Burns et al., 1969, 1972), and its ability to escape cultivation, *C. varia* is becoming increasingly abundant throughout much of the eastern and midwestern United States. By 1974, nearly 30,000 acres of *C. varia* had been planted along highway slopes in Pennsylvania alone (Wheeler, 1974). Moreover, with continued naturalization, sympatry between *C. varia* and *C. philodice* is likely to increase since the typical habitats of *C. varia*, *M. sativa*, *T. pratense*, and *M. alba* (roadsides, waste places, and other disturbed areas) are very similar (Fernald, 1950).

Parental Performance

To obtain a parental generation consisting of individuals whose relative performance on *M. sativa* and *C. varia* was known, 17 *C. philodice* females were caught in southern Montmorency County, Michigan, in July 1985 and their offspring were reared to pupation on each plant species. Both *M. sativa* and *C. varia* grow in this habitat, but larvae occur only on *M. sativa*.

On each plant species, neonate larvae from all 17 females were allowed to mix, and were then divided randomly among ten 10-cm plastic Petri dishes. Larvae were reared in an environmental chamber under a 16:8 L:D

cycle and a corresponding 29:19°C temperature cycle. Larvae were provided fresh food every second day or more often if necessary. Within 2 hr after it pupated, each larva was marked with a unique number. Ten pupae from each diet were sacrificed to establish a wet weight/dry weight ratio used to estimate the dry weight of all remaining pupae. The performance of 43 larvae fed *M. sativa* and 92 fed *C. varia* was measured in terms of egg-to-pupa development time and pupal weight. Two-way analysis of variance was performed with host and sex as main effects.

To facilitate mating between fast- and slow-growing individuals within each diet, all pupae were refrigerated at approximately 6°C within 24 hr after pupation. Twenty-four hours after the last larva pupated, all pupae were returned to the environmental chamber to resume development. The resulting adults eclosed synchronously and appeared normal.

Upon eclosing, parental generation adults were sexed, marked with the same number they bore as pupae, and placed in one of two mating cages (described in Karowe, 1988). Each cage contained all adults from one rearing diet. Cages were inspected every 30 min for mating pairs (successful copulations last more than one hour). Seventeen mating pairs were obtained from larvae reared on *M. sativa*, and 20 pairs from larvae reared on *C. varia*. Attempts to obtain half-sib families were unsuccessful. When the pair separated, the female was placed in an oviposition chamber (described in Karowe, 1988) containing fresh *M. sativa*. All mated females were provided fresh *M. sativa* every second day, at which time all eggs laid during the previous 48 hr were counted. Females were fed thrice daily to satiation on a 10% solution of honey in water, and were allowed to continue laying eggs throughout their lifetimes (6–14 days).

To determine whether increased larval performance led to increased adult performance, lifetime fecundity of *C. philodice* was regressed against female egg-to-pupa growth rate (which, since it includes both development time and pupal weight, was considered the best single measure of larval performance). Analysis of covariance was used to determine whether regression slopes or intercepts differed between diets.

Offspring Performance

Performance was measured for the offspring of 12 mated pairs from *M. sativa* and 12 (for survivorship) or 11 (for all other measures) from *C. varia*. Parental pairs from each diet were chosen to provide as wide a range as possible of paternal, maternal, and mid-parent growth rates.

Survivorship.—Fifty newly hatched offspring from each set of parents were divided into two groups of 25 and placed into plastic Petri dishes containing fresh leaves of either *M. sativa* or *C. varia*. Larval density was 25 per dish during the first instar and 5 per dish thereafter. Survivorship of larvae on each diet was monitored at 2-day intervals until they had reached the fourth (penultimate) instar. Previous rearings indicated that less than 5% of larval mortality occurs after the third instar (Karowe, 1988). Larvae were provided fresh food every second day or more often if necessary. Student's *t* test (Sokal and Rohlf, 1981) was used to determine whether percent survivorship through the third instar differed between diets.

Nutritional Ecology of Fifth Instar Larvae.—Quantitative nutritional indices (Waldbauer, 1968) were calculated for 10 offspring from each set of parents: five offspring fed *M. sativa* and five fed *C. varia*. The offspring of one parental pair from *C. varia* were lost during the fourth instar and are not included.

Within 2 hr of molting to the fifth instar, each test larva was weighed and placed individually into a 5.5-cm plastic Petri dish containing a weighed amount of the same plant species on which it had been reared. The initial dry weight of each test larva was estimated from a wet weight/dry weight ratio established by weighing, freezing, and drying to constant weight at 70°C 10 newly molted non-test fifth instar larvae from each rearing diet. Test larvae were provided fresh leaves every second day or more often if necessary.

For each larva, relative consumption rate (RCR), approximate digestibility (AD), efficiency of conversion of digested food (ECD), efficiency of conversion of ingested food (ECI), and relative growth rate (RGR), were calculated as defined by Waldbauer (1968):

$$\text{RCR} = \frac{\text{weight of food ingested}}{\text{average larval weight} \times \text{instar duration}}$$

$$\text{AD} = \frac{\text{weight of food ingested} - \text{weight of frass}}{\text{weight of food ingested}}$$

$$\text{ECD} = \frac{\text{larval weight gained}}{\text{weight of food ingested} - \text{weight of frass}}$$

$$\text{RGR} = \frac{\text{larval weight gained}}{\text{average larval weight} \times \text{instar duration}}$$

where average larval weight = (weight at onset of the fifth instar + weight at pupation)/2. Egg-to-pupa development time and egg-to-pupa growth rate (pupal weight/egg-to-pupa development time) were also calculated for each test larva. All calculations were made on a dry weight basis.

Two-way analysis of variance with host and family as main effects was used to determine whether egg-to-pupa developmental time, pupal weight, and fifth instar RCR, AD, ECD, and RGR differed significantly between offspring larvae fed *M. sativa* and *C. varia*, or among offspring from different families fed either plant species. Heritability in the broad sense for each measure of larval performance was inferred from the significance of the family main effect in the corresponding analysis of variance.

All analyses were performed using the Michigan Interactive Data Analysis System of the University of Michigan.

Correlations between Parental and Offspring Performance on the Same Host

To determine whether superior parents from each plant species give rise to superior offspring on the same species, correlation coefficients were calculated between mid-parent egg-to-pupa growth rate (which includes both pupal weight and development time) on each species and the family means of all measures of offspring performance on the same species.

Correlations between Measures of Performance across Hosts

The potential consequence(s) of selection for increased larval performance on each plant species vis-à-vis performance on the

alternative species were evaluated in two distinct ways. First, the degree and sign of correlation between mid-parent egg-to-pupa growth rate on each plant species and the family mean of each measure of offspring performance on the alternative species were determined. Second, the degree and sign of correlation between family means for each measure of offspring performance on one species and the same measure among full-sibs on the alternative species were determined.

RESULTS

Relative Suitability of M. sativa and C. varia as Larval Hosts

C. philodice larvae performed better on *M. sativa* than on *C. varia* during both generations. Survivorship through the third instar was significantly higher on *M. sativa* than on *C. varia* [84 vs. 68%; $T(44) = 3.29$, $P = 0.002$]. Egg-to-pupa development was significantly faster and pupal weight was significantly higher on *M. sativa* than on *C. varia* both for parents (Table 1a and b) and offspring (means given in Table 2; significance of host main effect presented in Table 3). Relative growth rate (RGR) during the fifth instar was significantly higher on *M. sativa* than on *C. varia*, due primarily to a significantly higher relative consumption rate (RCR). Neither approximate digestibility (AD) nor the efficiency of conversion of digested food (ECD) differed significantly between diets.

Fecundity on M. sativa and C. varia

Lifetime fecundity of *C. philodice* females was significantly positively correlated with egg-to-pupa growth rate on *M. sativa* and

TABLE 1. Larval performance for male and female *C. philodice* during the parental generation on each host. Means (\pm SD) are presented in Table 1a. Two-way analysis of variance is presented in Table 1b.

Species	Egg-to-pupa development time (days)		Pupal weight (mg dry)	
	Males (N)	Females (N)	Males (N)	Females (N)
<i>M. sativa</i>	12.95 (24) ± 0.89	13.84 (19) ± 1.01	52.01 (24) ± 3.37	49.36 (19) ± 12.03
<i>C. varia</i>	17.77 (46) ± 1.84	18.52 (46) ± 1.99	44.04 (46) ± 6.42	45.89 (46) ± 6.05

TABLE 1b.

Source	SS	df	MS	F	P
Egg-to-pupa development time (days)					
Host	659.84	1	659.84	124.34	<0.001
Sex	21.34	1	21.34	7.63	<0.001
Interaction (Host \times Sex)	0.14	1	0.14	0.05	NS
Error	366.68	131	2.80		
Pupal weight (mg dry)					
Host	1,017.57	1	1,017.57	20.94	<0.001
Sex	6.12	1	6.12	0.13	NS
Interaction (Host \times Sex)	147.54	1	147.54	3.04	0.084
Error	6,445.89	131	49.21		

nearly significantly positively correlated with egg-to-pupa growth rate on *C. varia* (Fig. 1). Because the regression was only nearly significant for females from *C. varia*, the results of analysis of covariance must be interpreted with caution. Such analysis reveals that regression intercepts differ significantly between diets [$F(1) = 5.36$, $P = 0.027$] but slopes do not [$F(1) = 0.28$, $P > 0.5$]. Thus, at any specific egg-to-pupa growth rate, a female reared on *C. varia* is expected to lay, on average, more eggs than a female reared on *M. sativa*. Moreover, this difference is sufficient that, despite their lower average growth rate ($\bar{x} = 2.51$ vs. 3.60 mg/day), females reared on *C. varia* are expected to lay on average 14% more eggs ($\bar{x} = 235$ vs. 204) than females reared on *M. sativa*.

On each plant species, female egg-to-pupa growth rate was significantly positively correlated with the number of eggs laid per day [$r(16) = 0.55$, $P = 0.022$ on *M. sativa*; $r(19) = 0.59$, $P = 0.007$ on *C. varia*] but not with adult longevity [$r(16) = 0.23$, $P > 0.3$ on *M. sativa*; $r(19) = -0.14$, $P > 0.5$ on *C. varia*].

Genetic Variation in Larval Performance

Among offspring larvae, survivorship ranged from 48 to 100% on *M. sativa* and from 32 to 96% on *C. varia*, and differed significantly among families on each diet ($X^2(11) = 86.0$, $P < 0.001$ on *M. sativa* and $X^2(10) = 62.1$, $P < 0.001$ on *C. varia*). The extent to which among-family variation in

TABLE 2. Mean values for measures of egg-to-pupa and fifth instar performance of *C. philodice* offspring larvae fed *M. sativa* or *C. varia*. Two-way analysis of variance is presented in Table 3.

Species	N	Egg-to-pupa development time (days)	Pupal weight (mg)	RGR	RCR	AD	ECD
<i>M. sativa</i>	115	14.50 ± 1.26	57.18 ± 8.39	0.425 ± 0.071	1.719 ± 0.291	0.581 ± 0.049	0.435 ± 0.075
<i>C. varia</i>	115	16.17 ± 1.10	49.32 ± 9.07	0.401 ± 0.071	1.612 ± 0.258	0.581 ± 0.052	0.431 ± 0.058

TABLE 3. Two-way analysis of variance for measures of performance for *C. philodice* larvae from 23 full-sib families reared on *M. sativa* and *C. varia*.

Source	SS	df	MS	F	P
Egg-to-pupa development time (days)					
Family	164.14	22	7.46	2.57	0.018
Host	157.68	1	157.68	54.42	<0.001
Interaction (Family × Host)	63.75	22	2.90	6.16	<0.001
Error	83.80	184	0.47		
Pupal weight (mg)					
Family	364,463.7	22	16,566.5	2.52	<0.001
Host	366,694.3	1	366,694.3	55.83	<0.001
Interaction (Family × Host)	155,168.5	22	7,053.1	1.07	NS
Error	1,169,120.4	184	6,568.1		
RCR					
Family	3.18	22	0.14	2.09	0.005
Host	0.63	1	0.63	9.09	0.003
Interaction (Family × Host)	1.49	22	0.068	0.98	NS
Error	12.32	184	0.069		
AD					
Family	0.0353	22	0.0016	0.65	NS
Host	0.0001	1	0.0001	0.02	NS
Interaction (Family × Host)	0.0621	22	0.0028	1.14	NS
Error	0.4402	184	0.0025		
ECD					
Family	0.0822	22	0.0037	0.47	NS
Host	0.0002	1	0.0002	0.03	NS
Interaction (Family × Host)	0.1726	22	0.0078	2.12	0.004
Error	0.6576	184	0.0037		
RGR					
Family	0.2531	22	0.0115	1.77	0.018
Host	0.0381	1	0.0381	5.86	0.025
Interaction (Family × Host)	0.1430	22	0.0065	1.58	0.055
Error	0.7357	184	0.0041		

survivorship reflects genetic differences remains unclear, however, since all larvae from a given family shared a common environment during the first instar. Significant among-family variation was observed for egg-to-pupa development time, pupal weight, and fifth instar RCR and RGR (Family main effect, Table 3). Fifth instar RCR and ECD also exhibited a significant Host × Family interaction, and RGR exhibited a nearly significant Host × Family interaction, indicating that families differ in their relative responses to the two hosts.

Correlations across Generations on the Same Host

Among parents and offspring fed *M. sativa*, mid-parent egg-to-pupa growth rate was significantly positively correlated with offspring survivorship [$r(11) = 0.65, P = 0.023$]

and RGR [$r(11) = 0.68, P = 0.016$], and significantly negatively correlated with offspring egg-to-pupa development time [$r(11) = -0.78, P = 0.003$] (note that in this case a negative correlation indicates a positive correlation in performance). Thus, parents that perform relatively well on *M. sativa* give rise to offspring that also perform relatively well on *M. sativa*.

Among parents and offspring fed *C. varia*, mid-parent egg-to-pupa growth rate was not significantly correlated with any measure of offspring performance.

Correlations between Measures of Performance across Hosts

Mid-parent egg-to-pupa growth rate on *M. sativa* was significantly positively correlated with offspring egg-to-pupa growth rate on *C. varia* [$r(11) = 0.59, P = 0.045$].

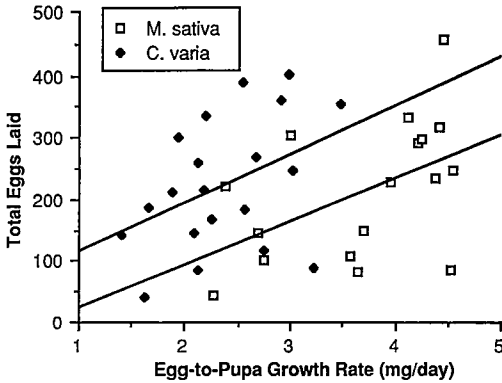


FIG. 1. Regressions of fecundity against egg-to-pupa growth rate for *C. philodice* females reared on *M. sativa* and *C. varia*. Regression equations are *M. sativa*: $y = 701x - 45$, $r = 0.49$, $P = 0.045$; *C. varia*: $y = 788x + 37$, $r = 0.41$, $P = 0.070$. Slopes do not differ significantly between diets. Intercepts differ significantly between diets ($F = 5.36$, $P = 0.027$).

Similarly, mid-parent egg-to-pupa growth rate on *C. varia* was significantly positively correlated with offspring egg-to-pupa growth rate [$r(10) = 0.65$, $P = 0.029$] and fifth instar RGR [$r(10) = 0.73$, $P = 0.010$] on *M. sativa*. Thus, parents that perform relatively well on either plant species give rise to offspring that perform relatively well on the alternative species.

Moreover, among full-sibs, egg-to-pupa growth rate was significantly positively correlated across diets [$r(22) = 0.46$, $P = 0.027$].

In no case was mid-parent egg-to-pupa growth rate on either diet significantly negatively correlated with any measure of larval performance on the alternative diet, nor was any measure of performance significantly negatively correlated between full-sibs reared on the two diets.

DISCUSSION

The results of this study provide three lines of evidence which together suggest that the absence of *C. philodice* from *C. varia* in nature is due to the failure of *C. philodice* females to oviposit on *C. varia* rather than to larval physiological inability to utilize this potential host, and that, if oviposition on *C. varia* occurs, selection will favor expansion of *C. philodice*'s host plant range to include *C. varia*.

First, initial fitness of *C. philodice* on *C. varia* appears to be commensurate with fit-

ness on *M. sativa*. Survivorship through the third instar on *C. varia* is high, and females reared from this plant are expected to be, on average, slightly more fecund than females reared from *M. sativa*. Despite their lower average egg-to-pupa growth rate, females from *C. varia* are expected to lay on average more eggs than females from *M. sativa*. When approximated as larval survivorship times fecundity of survivors, fitness is expected to be only slightly lower on *C. varia* than on *M. sativa* ($68\% \times 235 = 160$ eggs per hatched female on *C. varia* vs. $84\% \times 204 = 171$ eggs per hatched female on *M. sativa*). Of course, this is a rough estimate only, since relative fitness in nature will be influenced by abiotic and biotic factors not addressed in this study (Gilbert and Singer, 1975; Vinson, 1976; Price et al., 1980, 1986; Feeny et al., 1985; Lawton, 1986; Bernays and Graham, 1988). For instance, larval mortality due to weather (e.g., drowning) is likely to be lower on *M. sativa*, since larval development is approximately 10–26% faster on this host (Tables 1a, 2). In contrast, mortality due to predation and parasitism is likely to be higher on *M. sativa* since, in the population studied, potential predators and parasitoids (spiders, ants, reduviids, pentatomids, and braconid and ichneumonid wasps) were common on *M. sativa* but absent from *C. varia* (personal observation). Moreover, larval mortality on *M. sativa* may be periodically severe, due to harvesting and pesticide application. It therefore seems likely that fitness on *C. varia* in nature would not be substantially less than, and may even exceed, fitness on *M. sativa*.

Even if initial fitness were lower on *C. varia*, selection may favor oviposition on this host if fecundity of *C. philodice* in nature is limited by the rate at which acceptable oviposition sites are encountered rather than by the rate at which eggs are matured, and if females can search simultaneously for *M. sativa* and *C. varia*. There is reason to believe that these conditions may be met. A *C. philodice* female is capable of laying over 200 eggs per day (Karowe, 1988), suggesting that fecundity is not limited by egg maturation rate. *M. sativa* and *C. varia* often grow intermingled along roadsides and in other disturbed areas (Karowe, 1988), sug-

gesting that, in at least some habitats, females can search simultaneously for both species.

Second, *C. philodice* populations contain substantial genetic variation for egg-to-pupa development time, pupal weight, and fifth instar RGR and RCR on *C. varia*, and therefore may potentially respond to selection for increased physiological ability to utilize this potential host. It seems likely that increased larval performance would arise primarily in response to selection for increased RCR. Moreover, the significant positive correlation between egg-to-pupa growth rate and total egg production suggests that selection for increased larval performance on *C. varia* will result also in increased potential fecundity.

Third, larval performance is positively correlated across hosts, both within and between generations in this study. The existence of substantial genetic variation for performance on *M. sativa* suggests that selection for increased performance on this host will continue (the fact that such variation exists on *M. sativa* may indicate that insufficient time has elapsed for selection to eliminate variation in these characters or that, on this host, evolution of increased performance is constrained by factors not yet identified). Nonetheless, the observation that performance is positively correlated across hosts suggests that future selection for increased performance on *M. sativa* will facilitate, not constrain, evolution of increased performance on *C. varia*.

Oviposition on C. varia in Nature

The observation that *C. philodice* does not presently occur on *C. varia*, despite a substantial physiological capacity to use this species, is consistent with the hypothesis that evolution of host plant range is generally constrained by behavioral rather than physiological barriers (Futuyma, 1983b; Mitter and Futuyma, 1983; Rausher, 1983; Jaenike, 1985; Futuyma and Philippi, 1987). The absence of *C. varia* from the host plant range of *C. philodice* appears to be due primarily to the failure of *C. philodice* females to oviposit on *C. varia*. Although it is impossible to predict such an event with certainty, four lines of evidence suggest that *C. philodice* will eventually oviposit in nature

on *C. varia*. First, oviposition behavior of *C. philodice* is highly labile: nearly 60% of *C. philodice*'s current host plants are not native to North America (Fernald, 1950; Gleason and Cronquist, 1963; Allen and Allen, 1981; Scott, 1986). Second, colonization of *C. varia* appears to be particularly facile for species, such as *C. philodice*, that presently feed on *M. sativa*. Nearly 50% of herbivorous insect species that have colonized *C. varia* in Pennsylvania are primary herbivores of alfalfa (Pimentel and Wheeler, 1973; Wheeler, 1974). Third, *C. eurytheme*, which has a host plant range nearly identical to that of *C. philodice* (Klots, 1951; Scott, 1986) and which was long considered to be the same species (Hovanitz, 1949), has recently colonized *C. varia* (Wheeler, 1974). Fourth, when given a choice between *M. sativa*, *C. varia*, and *M. alba* in small laboratory cages (which essentially allowed expression only of postlighting discrimination), *C. philodice* females lay approximately 10% of their eggs on *C. varia* (Karowe, 1988); this suggests that the absence of *C. philodice* from *C. varia* is due primarily to prelighting discrimination by ovipositing females.

Fitness Trade-offs across Host Species

More broadly, this result also suggests that trade-offs in fitness on different host species, which is a necessary condition for many models of sympatric speciation (e.g., Felsenstein, 1981; Tavormina, 1982), may not be common (Futuyma and Mayer, 1980; Templeton, 1981; Mitter and Futuyma, 1983; but see Bush, 1975; Bush and Diehl, 1982; Diehl and Bush, 1984 for an alternative opinion). While several studies have demonstrated trade-offs in fitness parameters across hosts (Gould, 1979; Rausher, 1984; Futuyma and Philippi, 1987), a greater number of studies has demonstrated fitness to be positively correlated across hosts (Gould, 1979, 1983; Rausher, 1984; Via, 1984a, 1984b; Hare and Kennedy, 1986; Futuyma and Philippi, 1987; James et al., 1988; this study).

In particular, the hypothesis that fitness trade-offs commonly arise from differences in host chemistry is not supported by this study. *Medicago sativa* and *C. varia* differ

markedly in secondary chemistry (Harbourne et al., 1971), yet performance of *C. philodice* is positively correlated across these two species. Indeed, given that major herbivore detoxification systems (e.g., mixed function oxidases) are active against a broad spectrum of secondary compounds (e.g., Brattsen, 1979), and that metabolic costs of detoxification may be small (Scriber, 1981), there is little reason to assume a priori that adaptation to one secondary compound will necessarily constrain adaptation to another. To the contrary, selection for ability to detoxify particular plant secondary compounds can result in the ability to detoxify chemically unrelated compounds from taxonomically unrelated species (e.g., Gould, 1983).

SUMMARY AND CONCLUSIONS

By demonstrating that *C. philodice* larvae are physiologically poised to utilize the potential host *C. varia*, this study supports the hypothesis that the primary barriers to host range expansion among herbivorous insects are behavioral rather than physiological (Futuyma, 1983*b*; Mitter and Futuyma, 1983; Rausher, 1983; Jaenike, 1985; Futuyma and Philippi, 1987). This conclusion is also supported by the only other study, to my knowledge, which addressed genetic variation in performance on a host and a nonhost. James et al. (1988) demonstrated that performance of the monophagous *Drosophila quinaria* on its host, *Symplocarpus foetidus*, was positively genetically correlated with performance on a nonhost, *Agaricus bisporus*.

The present study also adds to the growing realization that within-population genetic variation in components of host use is common (e.g., Gould, 1983; Futuyma and Peterson, 1985; Via, 1986; Futuyma and Philippi, 1987; Fry, 1988; Feder et al., 1988; James et al., 1988; McPheron et al., 1988; Singer et al., 1988; Thompson, 1988; Smith, 1988; Mitter et al., 1979), and provides the first evidence of heritable variation in nutritional indices (RCR and RGR) within a sexually reproducing insect herbivore population.

Finally, this study illustrates how information about genetic variation for performance on a potential host species, together

with information about genetic correlations in performance between that potential host and the primary host, can be used to anticipate the course of host range evolution among herbivorous insects.

ACKNOWLEDGMENTS

I am grateful to M. Dicke, J. Fry, J. Jaenike, M. Martin, D. Papaj, B. Rathcke, W. Wagner, and three anonymous reviewers for their helpful comments on earlier versions of this manuscript. This research was supported in part by a Rackham School of Graduate Studies Block Grant, a Kennedy Foundation Grant through the University of Michigan Biological Station, and NSF Grant BSR-8421268 to M. Martin.

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