

POPULATION DIFFERENTIATION IN *EUPHYDRYAS EDITHA* BUTTERFLIES: LARVAL ADAPTATION TO DIFFERENT HOSTS

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Adaptation of phytophagous insects to novel larval host plants can involve changes in at least three different suites of characters: those associated with female oviposition behavior, with larval feeding behavior, and with larval digestive physiology (Dethier, 1954, 1970; Bush, 1974; Feeny, 1975). Differences between closely related insect species and between conspecific populations indicate that evolutionary change in oviposition behavior is common (Singer, 1971; Smiley, 1978; Jones and Ives, 1979). Moreover, similar differences in larval growth rates and survivorship when different species or populations are reared on the same host plant indicate that larval adaptation often accompanies changes in oviposition behavior (Smiley, 1978; Futuyma et al., in press). However, few investigations have explicitly attempted to separate the contributions of differences in larval feeding behavior and digestive physiology to observed differences in growth performance. Because both the number and type of characters involved in larval adaptation will presumably influence the probability that a newly-founded insect population will successfully adapt to a novel host before becoming extinct, it seems desirable to characterize the types of changes that occur during adaptation of a population to its host plants. This study was conducted to provide such a characterization for the checkerspot butterfly, *Euphydryas editha*.

In western North America, *E. editha* exists as a series of discrete populations (White and Singer, 1971; Ehrlich et al., 1975). In most populations, females oviposit on only one or perhaps two different plant species in the family Scrophulariaceae or the genus *Plantago* (Plantagina-

ceae), even though other species used by other populations may be available. Although populations differ both in acceptance responses of females to a standard array of host species (Singer, 1971, and pers. comm.) and in electrophoretically detectable patterns of enzyme variation (McKechnie et al., 1975), little is known about variation among populations in characters associated with larval adaptation.

Although populations are normally highly localized and dispersal between them is low (Ehrlich, 1961; Ehrlich et al., 1975), population extinction and refounding by occasional migrants is probably fairly common (Ehrlich et al., 1980). Moreover, because populations specializing on one host species interdigitate geographically with populations specializing on others (White and Singer, 1974), it is likely that the founding of a new population often involves colonization of a novel host. A comparison of populations using different host species may elucidate the types of evolutionary changes that accompany such colonization.

In this study I compare the growth performances of larvae from two *E. editha* populations that use different hosts. Specifically, I ask (1) Do larvae from different populations exhibit differential adaptation to their own host plants, as measured by growth rates and survivorship? and (2) If so, are observed differences due to differences in digestive physiology, feeding behavior, or both?

MATERIALS AND METHODS

Organisms and Field Sites

Adult *Euphydryas editha* females were obtained between 15 and 20 May 1979

from two populations separated by a distance of approximately 120 km. One population, Del Puerto Canyon (DP), is located in Stanislaus County, California. Females at DP oviposit almost exclusively on *Pedicularis densiflora* (Scrophulariaceae) although at least three other potential food plants are present: *Castilleja foliolosa*, *C. affinis*, and *Collinsia bartsiaefolia* (all Scrophulariaceae). Late-instar (post-diapause) larvae also normally feed on *P. densiflora*, though in years of high population density and consequent heavy defoliation they may also feed on *C. foliolosa* and *C. affinis* (White, 1974; White and Singer, 1974; M. Singer, pers. comm.). The Indian Flat (IF) population is located in the western foothills of the Sierras in Mariposa County, California. Females at IF oviposit exclusively on and larvae feed solely on *Collinsia tinctoria* (White and Singer, 1974; pers. observ.). Although *Plantago erecta*, *Penstemon brevifloris*, *Orthocarpus* sp. and *Castilleja* sp., all potential host plants, grow within flight distance of the *C. tinctoria* plants at IF, neither adults nor larvae use these species.

Egg clusters were obtained from captive DP and IF females at Stanford University. Those eggs yielded the larvae that were used in the two experiments described below.

Experiment 1

This experiment measured the growth rates and laboratory survivorship of newly-hatched larvae from each population on *Collinsia tinctoria* and on *Pedicularis densiflora*. The experiment thus had a two-way factorial design, with host plant and population of origin as the main effects. Each replicate consisted of 20 larvae, obtained from the same egg cluster, placed on one host plant. Because it was difficult to obtain more than one egg cluster from the same female and because most clusters had fewer than 40 eggs, each replicate represented larval offspring of a single female. Consequently, the variation among replicates in all statistical analyses is due to both variation among individual

host plants and to variation among full-sib families. (Males deposit a mating plug after copulation, which normally prevents subsequent matings [Labine, 1964]. The eggs from any female are thus in all likelihood full sibs.)

In the *C. tinctoria* treatments, the 20 newly-hatched larvae in a replicate were placed onto a potted *C. tinctoria* plant. The plants had been potted at the IF site and transported to Stanford prior to the experiment. A Coleman lantern chimney, covered with fine-mesh cheesecloth, was placed over each plant.

Intact, living plants could not be used in the *P. densiflora* treatments because this species is a root parasite and could not be transplanted successfully. Instead, larvae were grown on leaves collected from the DP site and stored at approximately 5 C with petioles inserted in water-filled water pics (Scriber, 1977; Rausher, 1981) until used. Leaves were used less than two days after being collected. At the beginning of the experiment three *P. densiflora* leaves were placed in a water pic, which was then sunk into a soil-filled plastic pot. The leaves projected vertically from the pic. The 20 newly-hatched larvae in a replicate were then placed onto the leaves of one pot. A Coleman lantern chimney was placed over the leaves in each pot and the top opening was covered with cheesecloth. Twice daily the pics were refilled with water and the tips of the petioles were cut to facilitate water uptake by the leaves.

All replicate pots were placed on the same day in a growth chamber maintained at a photoperiod of 16L:8D and a temperature regime of 32 C Day: 10 C Night. After four days the larvae were removed and weighed. Relative biomass gain was calculated as the ratio $\Delta W/W_i$, where ΔW is change in larval biomass during the experiment and W_i is initial larval biomass (Scriber, 1977). Initial biomass was determined for each replicate from a sample of larvae from the same egg cluster and weighed at the time the experiment was begun. Survivorship was calculated as the fraction of the initial 20 larvae that were alive after four days.

Experiment 2

Differences between populations in larval growth rate may be due to either or both of two causes: (1) larvae from the two populations may differ in the ability to process host tissue physiologically, i.e., they may differ in digestive efficiency; or (2) they may differ in their propensity to consume host tissue, which is often reflected in differences in consumption rates (Slansky and Feeny, 1977; Blau et al., 1978). This experiment examined whether the two populations differed in either of these characters. Ability to process host tissue was estimated by two measures of larval growth efficiency. One of these measures was standard gross growth efficiency (*ECI*), which is calculated as

$$ECI = \Delta W/I = G/I, \quad (1)$$

where ΔW is larval biomass, G is change in larval biomass, and I is biomass of foliage ingested (Waldbauer, 1968; Scriber, 1977).

A second measure of growth efficiency, β , was derived using a modification of the technique employed by Blau et al. (1978) and Rausher (1981). For each host \times population combination a regression relating relative growth rate ($RGR = \Delta W/W_i$, W_i = initial larval biomass) to relative consumption rate ($RCR = I/W_i$), is obtained by varying experimentally the amount of leaf material that is consumed by different larvae. The slopes of the regression are then compared by standard statistical methodology for linear models (Searle, 1971). The actual statistical model is

$$RGR = \beta \times RCR + \alpha. \quad (2)$$

The two measures are not equivalent. As described in the appendix, *ECI* incorporates weight loss due to basal metabolism, whereas β does not. Moreover, if weight loss due to metabolic activity associated with consumption, digestion, absorption and storage of food is small compared to the amount of food digested and absorbed, as is often assumed (Waldbauer, 1968), then β is approximately

equivalent to the Approximate Digestibility (*AD*) coefficient of Waldbauer. If this assumption is not correct, then β is intermediate between *ECI* and *AD* (see Appendix).

To estimate the regression of *RGR* on *RCR*, larvae in each treatment were assigned randomly to one of three feeding regimes: (1) No food. Larvae were starved for two days. (2) Half food. Larvae were offered host leaves for seven hours a day for two days. The remainder of the time larvae did not have access to foliage. (3) Full food. Larvae were offered host leaves continuously for two days. These three feeding regimes generated a wide range of values of *RCR* against which the corresponding values of *RGR* were regressed.

The amount of leaf tissue consumed by a larva during the experiment was determined by standard gravimetric techniques (Waldbauer, 1968; Scriber, 1977). Each leaf offered to a larva was cut longitudinally along the midrib. One half was weighed, frozen, then later freeze-dried and reweighed to determine proportion dry matter. The second half of the leaf was weighed and placed in a plastic cup with a larva. After 24 h (7 h in the half food regime) the leaf was removed and frozen. Later it was freeze-dried and reweighed to determine the dry weight uneaten. By subtracting this value from the calculated dry weight of the leaf when initially offered to the larva, the dry weight eaten was obtained.

In this experiment third-instar larvae were used. The larvae had been reared from hatching on the host species on which they were tested. Relative growth rate was determined by standard gravimetric methods. At the beginning of the experiment each larva was weighed. In addition, several larvae that had been reared under the same conditions as the experimental larvae were chosen randomly and sacrificed to determine proportion dry matter, with which the initial dry weight of each experimental larva was calculated. At the end of two days the experimental larvae were frozen. They were later freeze-dried and reweighed to determine final dry

weight. For each larva, *RGR* and *ECI* were then calculated as described above.

Statistical Analyses

All comparisons of larval survivorship, growth rates, and feeding efficiencies employed analyses of variance or covariance. In most cases, statistical procedures of the Statistical Analysis System were used (Barr et al., 1979). Because in most analyses the data were unbalanced, Type IV sums of squares, which are appropriate for tests with unbalanced data, were used in tests of significance of main effects and interactions. In some analyses, nested random effects are included. In these cases the procedure for unbalanced, nested designs outlined by Sokal and Rohlf (1969) was used. Analyses of survivorship were performed on $\log(\arcsin \sqrt{l_x})$ transformed data, where l_x is the proportion of a cohort remaining alive at the end of the experiment. Logarithms were used because interaction effects on survivorship are more likely to be multiplicative than additive.

RESULTS

Experiment 1

First-instar larvae from each population grew faster on their normal host species than did larvae from the population that normally does not use that species. That is, DP larvae exhibited a significantly larger growth rate on *Pedicularis densiflora* than did IF larvae, while the reverse was true for larvae reared on *Collinsia tinctoria* (Table 1). There was a highly significant added variance component due to replicates within treatments. Although this added variance could be due to either variation among host plant individuals or variation among butterfly families, the separate contribution of each of these factors could not be assessed in this experiment. The host \times population interaction effect was also highly significant. From the pattern of growth rates in Table 1, it is evident that this interaction effect indicates that larvae from each population grow relatively faster on their own host than do larvae from the other population.

TABLE 1. Comparison of relative growth rate (RGR) for first-instar *E. editha* larvae from different populations fed *C. tinctoria* and *P. densiflora*. Figures in parentheses are standard errors of the mean. Values are in units of mg/mg/48 h.

Host	Population	
	DP	IF
<i>P. densiflora</i>	4.82 ($\pm .15$)	3.65 ($\pm .12$)
<i>C. tinctoria</i>	10.53 ($\pm .46$)	16.44 ($\pm .50$)

Source	<i>d.f.</i>	<i>F</i>	<i>P</i>
Population	1	4.51	<.05
Host	1	72.79	<.001
Host \times population	1	10.93	<.005
Replicates	25	23.26	<.001
Error	406	—	

Both main effects were also highly significant. Growth rates were higher on *C. tinctoria* than on *P. densiflora* for larvae from each population, suggesting that *C. tinctoria* is a better substrate for larval growth regardless of any local larval adaptation. The main effect of population is difficult to interpret, since the values of relative growth rate for DP lie between those for IF larvae.

Survivorship of first-instar larvae showed a pattern similar to that exhibited by growth rate: on *P. densiflora*, survivorship was higher for DP larvae, while on *C. tinctoria* it was higher for IF larvae (Table 2). Analysis of variance demonstrated that these differences were significant, although there was no detectable main effect for either host species or population of origin (Table 2).

Experiment 2

Relative growth rates, consumption rates and gross growth efficiencies were calculated for third-instar larvae fed *ad libitum* (feeding regime full food). Growth rates exhibited the same pattern as that shown by first-instar larvae: on *P. densiflora*, DP larvae grew faster than IF larvae, while the reverse was true for larvae fed *C. tinctoria* (Table 3). These differences were significant, as indicated by the host \times population interaction effect in the analysis of variance. There was no appar-

TABLE 2. Comparison of survivorship of first-instar *E. editha* larvae from different populations fed *C. tinctoria* and *P. densiflora*.

Host	Population		
	DP	IF	
<i>P. densiflora</i>	0.88 (\pm .07)	0.65 (\pm .10)	
<i>C. tinctoria</i>	0.69 (\pm .08)	0.81 (\pm .08)	
Source	<i>df</i>	<i>F</i>	<i>P</i>
Host	1	0.00	NS
Population	1	0.01	NS
Host \times population	1	4.53	<.05
Error	24	—	

ent effect of population on growth rate, though the main effect of host species was significant. As was found for first-instar larvae, *C. tinctoria* is apparently a better substrate for larval growth than is *P. densiflora*.

Relative consumption rates do not differ for larvae from the two populations (Table 4). Although on each host DP larvae consumed foliage faster than did IF larvae, this effect was not quite statistically significant ($P = .1$). However, both populations consumed *P. densiflora* foliage at a higher rate than they consumed *C. tinctoria* foliage, indicating a behavioral compensation for the apparently low quality of *P. densiflora* foliage.

Gross growth efficiencies exhibited a pattern similar to that seen in larval growth

TABLE 3. Comparison of relative growth rate of third-instar *E. editha* larvae from different populations fed ad libitum on *C. tinctoria* and *P. densiflora*. Values are in units of mg/mg/48 h.

Host	Population		
	DP	IF	
<i>P. densiflora</i>	0.74 (\pm .12)	0.41 (\pm .15)	
<i>C. tinctoria</i>	0.69 (\pm .28)	1.34 (\pm .11)	
Source	<i>df</i>	<i>F</i>	<i>P</i>
Host	1	5.94	<.025
Population	1	0.19	NS
Host \times population	1	7.44	<.025
Error	27	—	

TABLE 4. Comparison of relative consumption rates of third instar *E. editha* larvae fed ad libitum on *C. tinctoria* and *P. densiflora*. Values are in units of mg/mg/48 h.

Host	Population		
	DP	IF	
<i>P. densiflora</i>	3.11 (\pm .43)	2.14 (\pm .42)	
<i>C. tinctoria</i>	1.79 (\pm .38)	1.49 (\pm .16)	
Source	<i>df</i>	<i>F</i>	<i>P</i>
Host	1	6.92	<.025
Population	1	2.90	=.10
Host \times population	1	0.80	NS
Error	27	—	

rates: on *P. densiflora*, *ECI* was higher for DP larvae than for IF larvae, while the opposite was true for larvae on *C. tinctoria* (Table 5). There was also a significant main effect of population on *ECI*, though again, this effect is difficult to interpret because both values for DP larvae lie between the values for IF larvae. However, for both populations, *ECI* was higher on *C. tinctoria* than on *P. densiflora*, another indication that *C. tinctoria* is a higher-quality host plant.

Regressions of relative growth rate on relative consumption rate are shown separately for the two plants in Figure 1. Among all four host \times population treatments there was a significant heterogeneity of regression slopes or values (Table 6). Partitioning of this heterogeneity into independent contrasts revealed that β dif-

TABLE 5. Comparison of gross growth efficiencies (*ECI*) of third-instar *E. editha* larvae fed ad libitum on *C. tinctoria* and *P. densiflora*.

Host	Population		
	DP	IF	
<i>P. densiflora</i>	0.27 (\pm .06)	0.16 (\pm .05)	
<i>C. tinctoria</i>	0.36 (\pm .15)	0.96 (\pm .12)	
Source	<i>df</i>	<i>F</i>	<i>P</i>
Host	1	16.16	<.001
Population	1	5.05	<.05
Host \times population	1	10.07	<.005
Error	27	—	

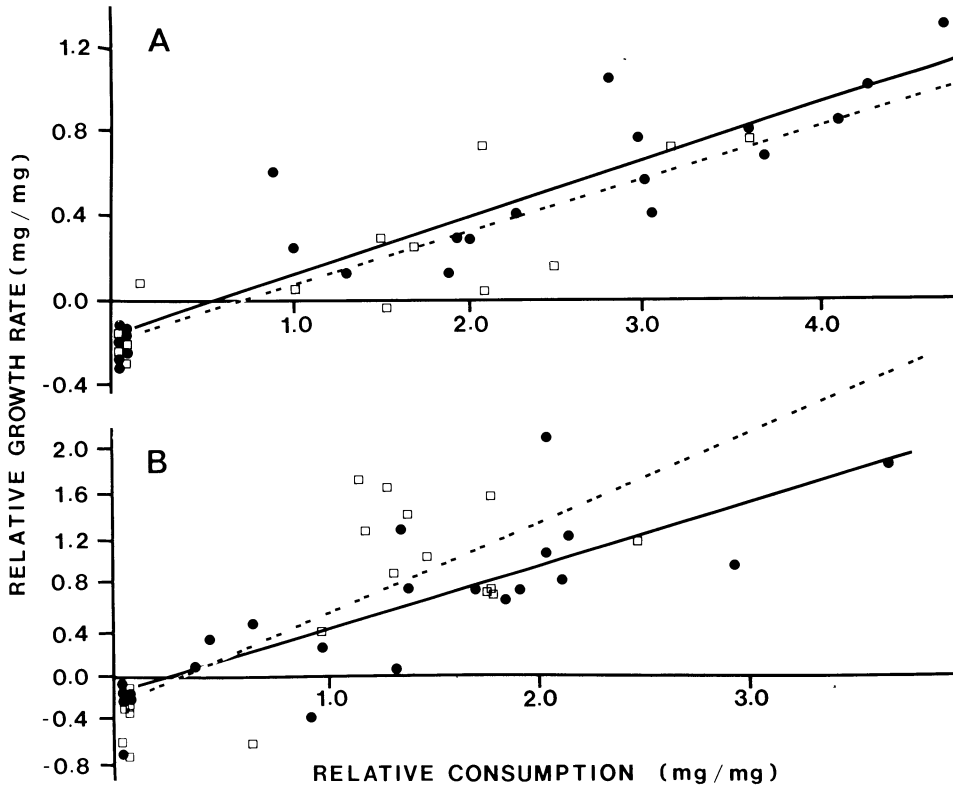


FIG. 1. Relationship between relative growth rate and relative consumption rate for third-instar larvae from different populations. Circles and solid lines: DP larvae; Squares and broken lines: IF larvae; A. Larvae fed *P. densiflora*. For IF larvae, $RGR = 0.250 \times RCR - 0.196$, $r = 0.816$, $N = 15$; For DP larvae, $RGR = 0.275 \times RCR - 0.179$, $r = 0.921$, $N = 23$. B. Larvae fed *C. tinctoria*. For IF larvae, $RGR = 0.819 \times RCR - 0.292$, $r = 0.799$, $N = 22$; For DP larvae, $RGR = 0.583 \times RCR - 0.204$, $r = 0.848$, $N = 25$.

ferred significantly between food plants ("Between Hosts" in Table 6), but that within a particular food plant there was no significant difference between butterfly populations ("Between Populations" in Table 6). This experiment, therefore, did not detect any differences between butterfly populations in efficiency as measured by β , though both populations appear to be more efficient at converting *C. tinctoria* leaf tissue into larval biomass than at converting *P. densiflora* tissue.

DISCUSSION

Population Differentiation in Larval Growth Performance

Growth performance on each host species differs for the two populations

of *Euphydryas editha* examined in this study. Larvae from each population grow faster and have lower early-instar mortality when reared on their own primary host than do larvae from the other population when reared on the same host. These dif-

TABLE 6. Comparison of β 's for third-instar *E. editha* larvae.

Source	df.	F	P
Slopes (β 's)	3	12.02	<.0001
Between hosts	1	34.19	<.0001
Between populations fed <i>C. tinctoria</i>	1	3.86	NS
Between populations fed <i>P. densiflora</i>	1	0.08	NS
Error	77	—	

ferences have presumably resulted from selection to increase survival and growth rate on the host species most commonly used by each population. The types of selection pressures acting on *E. editha* to favor rapid growth are discussed by Ehrlich et al. (1975).

Because genetic variation in growth rates was not measured in this study, some caution must be used in making evolutionary inferences about observed phenotypic differences between the two *E. editha* populations. Nevertheless, larval growth was measured under identical laboratory conditions for the two populations and on individuals of several families. Any non-genetic differences between populations must therefore be ascribed to some sort of maternal effect. Although in many animals maternal effects can influence growth rates, such an influence normally occurs through an effect on size of individuals at birth; this effect is in turn usually due to variation in the amount of materials channelled into eggs or embryos (Falconer, 1960; Bakker, 1961; Wellington, 1976; Travis, 1980). It is difficult to imagine how such an effect could produce the population \times host interactions observed for growth rates, since if a greater size at birth allows faster growth on one host it should do so on others. It thus seems reasonable to conclude that the observed phenotypic differences in growth performance reflect underlying genetic differences between the two populations.

Causes of Differences in Growth Rates

The pattern of growth rates and survivorship revealed by this study is one of local specialization: larvae from each population grow and survive better on their own host than larvae from the other population do on that host. Differences in consumption rates between populations do not produce this pattern of specialization, since no significant interaction effect for consumption rates was detected. Although main effect differences between populations approached significance (Table 4), these differences would not produce the pattern of specialization seen in growth

rates and survival. It thus appears that this pattern is due primarily to differences in the ability of the two populations to process tissue from the two hosts.

This conclusion is substantiated by measured differences in growth efficiencies. Gross growth efficiency (*ECI*) on *C. tinctoria* was higher for IF larvae than for DP larvae, while the reverse was true for larvae grown on *P. densiflora*. By contrast, values of β exhibited no differences between populations. To the extent that β measures approximate digestibility (see Methods), the populations do not differ in ability to digest and absorb foliage of the two hosts. However, because *ECI* differs from β in that it includes biomass losses due to basal metabolism, whereas β does not, the difference in results obtained from these two measures of efficiency suggest that the two populations differ in basal metabolic rate on the two hosts. Specifically, these results are consistent with the interpretation that basal metabolism of IF larvae growing on *P. densiflora* is elevated above that of DP larvae on that plant, while the reverse is true for larvae on *C. tinctoria*. The causes for such differences are not presently known, though they may include elevated metabolic activity (e.g., production of broad-spectrum detoxification enzymes; Brattsten et al., 1977, Brattsten, 1979) associated with detoxification of secondary substances to which larvae are not adapted. The failure of such elevated activity to detoxify novel secondary substances completely could account for the higher mortality rates of first-instar larvae on hosts not normally used.

Although the observed pattern of specialization in growth rates does not appear to be due to a similar pattern of specialization in consumption rates, results of this study suggest that larval feeding behavior of the two *E. editha* populations may have diverged. Larvae of many species of insects are known to compensate behaviorally for poor host nutritive quality by increasing consumption rates (Slansky and Feeny, 1977, and references therein). This type of behavioral compensation is also exhibited by each population

of *E. editha* in this study: as measured by both *RCR* and *ECI*, *C. tinctoria* foliage is a better substrate for larval growth than is *P. densiflora* foliage, and larvae from both populations exhibit a higher feeding rate on *P. densiflora*. Though not quite statistically significant, the difference in mean *RCR* between the two populations is in the same direction as the behavioral response within populations. DP larvae, which normally feed on the lower-quality *P. densiflora*, have a higher mean consumption rate on each host than do IF larvae. This population difference, if real, may thus reflect local adaptation of feeding rate to the quality of the primary host.

In *Euphydryas editha*, local adaptation to host plants appears to involve evolutionary change in at least two, and perhaps three, of the suites of characters suggested by Bush (1974) to be involved in colonization of novel host species. Differences between IF and DP populations indicate that female oviposition preferences (Singer, 1971), larval digestive physiology, and perhaps larval feeding behavior have undergone evolutionary change in at least one of these populations. Nevertheless, differences in these characters are not of an "all-or-none" magnitude, either permitting or preventing survival on a particular host. For example, although mortality of IF larvae on *P. densiflora* during the first instar was higher than that of DP larvae, mortality after the first instar was negligible. Many IF larvae were reared to the obligate diapause that occurs after the third instar. It seems probable that most of these larvae would have survived the post-diapause larval period to reproduce as adults had rearing been continued.

Successful foundation by *E. editha* of a new population on a novel host, which must be a common event (see Introduction), may thus not require simultaneous mutation at two or more loci as has been postulated by Bush (1974) for *Rhagoletis* fruit flies. Instead, the hosts used by different *E. editha* populations may be sufficiently similar in chemical, physical, and nutritional properties that adaptation to one host ensures at least partial adaptation

to others. Such partial adaptation to one host could permit a newly founded population to persist while selection gradually altered oviposition behavior, larval feeding behavior, larval digestive physiology, and other characters to states most appropriate for using the new host.

SUMMARY

Evidence from laboratory rearing experiments on two populations of the checkerspot butterfly *Euphydryas editha* that use different host species indicate that the populations differ in characteristics associated with adaptation of larvae to growth on their food plants. Larvae from each population grow relatively faster and survive better when grown on their own primary host species than do larvae from the other population when grown on the same species. This pattern of specialization is not caused by differences in feeding behavior, but appears to be due to differences in digestive physiology.

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APPENDIX

A biological interpretation of the efficiency measures ECI and β can be given based on the following simple physiological growth model adapted from Waldbauer (1968): let F be the biomass of feces produced, M be the biomass lost due to respiration in a resting larva (basal metabolism), C be the additional biomass lost due to metabolic activity associated with consumption, digestion, absorption and storage of ingested food, and I be the biomass of food ingested. A mass balance equation relating these four variables to change in larval biomass, $G = \Delta W$, is then given by

$$G = I - F - C - M. \quad (A1)$$

Gross growth efficiency, defined as biomass gain divided by biomass of ingested food, is then

$$ECI = G/I = (I - F - C - M)/I. \quad (A2)$$

This measure of efficiency thus incorporates M , the biomass loss due to basal metabolism during the period of the experiment (Waldbauer, 1968).

By contrast, β does not incorporate M . Since β is a regression coefficient, it represents the change in larval biomass gain caused by an incremental change in amount of foliage consumed during the experi-

ment. The change in larval biomass gain is simply $= (\Delta I - \Delta F - \Delta C)/\Delta I$ (A4b)

$$\Delta G = \Delta I - \Delta F - \Delta C, \quad (\text{A3})$$

since basal metabolism is presumed not to be affected by amount of food consumed and therefore $M = 0$ (Waldbauer, 1968). The change in foliage consumed is ΔI . Since β measures the regression coefficient of relative growth rate vs. relative consumption rate,

$$\beta = \frac{\Delta RGR/\Delta RCR = \Delta(G/W_i)/\Delta(I/W_i)}{= \Delta G/\Delta I} \quad (\text{A4a})$$

or, if the change is measured from zero,

$$\beta = (I - F - C)/I. \quad (\text{A5})$$

If C is small compared to $I - F$, as is often assumed (Waldbauer, 1968), then

$$\beta \cong (I - F)/I, \quad (\text{A6})$$

which is equivalent to Approximate Digestibility (AD) of Waldbauer (1968). If C is not small, then β is intermediate between AD and ECI .

ANNOUNCEMENT

COMPUTERS IN BIOLOGY. THE SECOND ANNUAL SHORT COURSE SERIES AT NOTRE DAME—AUGUST 15–21, 1982.

A series of four one-week shortcourses on Computers In Biology will be offered concurrently in the Biology Department of The University of Notre Dame. All instruction will be by biology professors with expertise in computing. Designed for faculty, postdoctorals, and advanced graduate students, the courses and instructors are: 1) Computers In Bioeducation, Theodore J. Crovello; 2) Microprocessor Applications In Physiology And Behavior, Harald E. Esch; 3) Computerized Data Analysis In Biological Research, Ronald A. Hellenthal; and 4) Introduction To Computer Simulation, Stephen R. Carpenter. The courses can accommodate participants with or without a computer background. Enrollment is limited to assure personalized instruction. Courses will begin with a social mixer on Sunday evening 15 August 1982 and end on Saturday morning 21 August. Most days will include lectures and actual experience in the use of computers. Available computing facilities range from an IBM 370/168 computer to a variety of mini and microcomputers.

Tuition is \$400, payable by June 1, 1982. Modern, air conditioned, dormitory rooms will be available on the Notre Dame campus. For more information, contact Professor Theodore J. Crovello, Biocomputing Shortcourses Coordinator, Department of Biology, The University of Notre Dame, Notre Dame, Indiana 46556. Phone: 219/239-7496.