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**HOST PLANT SUITABILITY AND A TEST OF THE FEEDING
SPECIALIZATION HYPOTHESIS USING *PAPILIO
CRESPHONTES* (LEPIDOPTERA: PAPILIONIDAE)**

J. Mark Scriber¹ and Robert V. Dowell²

ABSTRACT

The concept that host plant favorites would be used for more rapid and/or efficient growth of the "locally adapted" individuals was tested in a preliminary way using the giant swallowtail butterfly, *Papilio cresphontes*. Populations feeding only on northern prickly ash, *Zanthoxylum americanum* (from Wisconsin), primarily (or exclusively) on hoptree, *Ptelea trifoliata* (in Ohio) and on lime prickly ash, *Z. fagara*, or *Citrus*, (in Florida) were compared on alternate hosts and on their actual local hosts under controlled environmental conditions. While the results with final instar larvae generally support the feeding specialization hypothesis with regard to more rapid and/or more efficient growth on local foodplant favorites, we are hesitant to extrapolate these results to the species as a whole for several reasons discussed herein.

The giant swallowtail butterfly, *Papilio cresphontes* Cramer (Lepidoptera: Papilionidae) is a wide-ranging species, occurring from Minnesota and New England south to the tip of Florida, westward to southern Arizona and California, throughout Mexico into Central America (Tyler 1975, Opler and Krizek 1984, Buetelspacher and Howe 1984). The larvae, called "orangedogs", are occasional minor pests of *Citrus*, but are also reported to feed on a large number of hosts from at least nine plant families (Kimball 1965, Tietz 1972, Crocker and Simpson 1979). Many of these literature records are suspect. However, it is certain that plant species in the Rutaceae are the favorite hosts for *P. cresphontes* and are the most frequently reported (Scriber 1984). In fact, it has yet to be verified that the larvae of *P. cresphontes* can grow and survive on any plants other than those in the Rutaceae family.

Within the Rutaceae there are local population preferences from northern prickly ash *Zanthoxylum americanum*, in Wisconsin (Ebner 1970); hoptree, *Ptelea trifoliata*, in Illinois and Ohio and lime prickly ash, *Zanthoxylum fagara*, torchwood, *Amyris elemifera*, and various *Citrus* spp. in Florida (Opler and Krizek 1984). The Mexican Orange, *Choisya dumosa*, is a native Texas shrub which has also recently been reported as a foodplant for *P. cresphontes* in Dallas, Texas (Crocker and Simpson 1979).

The occurrence of local foodplant favoritism (i.e. ecological monophagy) is common in the tree-feeding species of *Papilio* in North America, and may in fact be the rule rather than the exception in Lepidoptera. Scriber (1975) and Smiley (1978) have suggested that such ecological monophagy might lead to increased biochemical and

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digestive efficiencies. Subsequent reduction of such efficiencies with respect to ancestral or locally non-used (allopatric) foodplants might lead to what could be called "obligate monophagy" (Smiley 1978). The evidence available for evaluation of this concept is meager (see Fox and Morrow 1981, Scriber 1983, 1986).

The objective of this study was to assess the possibility that *P. crespontes* populations are differentially adapted to their local foodplant favorites compared to other plants. Our approach was to collect *P. crespontes* from various geographic locations and carefully bioassay the larval growth performances on their local favorites as well as the allopatric foodplants which are local favorites used by other *P. crespontes* populations.

METHODS

Sources of Larvae

Larvae from eggs obtained from *Citrus* spp. in Broward County, Florida were distributed at eclosion (unfed neonates) to the following foodplants: Lime prickly ash, *Zanthoxylum fagara*; Northern prickly ash, *Zanthoxylum americanum*; sweet orange *Citrus sinensis* Osbeck; and hoptree, *Ptelea trifoliata*. In Wisconsin, larvae were obtained from eggs of a field-captured female in western Dane County and a field-captured female in eastern Iowa County and subsequently were randomly distributed to various rutaceous foodplants, including northern prickly ash and hoptree. In these two populations (and nearly all of Wisconsin) prickly ash is the only host plant available. For this study additional Wisconsin *P. crespontes* were obtained from Richland County where prickly ash, *Z. americanum*, shrubs are the only hosts available. Ohio *P. crespontes* were obtained from Preble County where the local favorite and dominant host plant is hoptree, *Ptelea trifoliata*.

Feeding Experiments

Freshly molted penultimate instar larvae were individually weighed and distributed to 150 x 25 mm petri dishes and maintained on a specific host under standardized rearing conditions (16:8 photo, scoto-phase with a corresponding 23:19-C° thermoperiod, with moistened filter paper in each dish). Plant leaves collected from several trees near the U.W. Arboretum or from our greenhouse were weighed fresh, placed in water-filled floral aquapics® to maintain leaf turgor and subsequently introduced into the petri dishes for standard gravimetric determination of food consumption (Waldbauer 1968). Nutritional indices were calculated based upon the dry weight (biomass) of leaves, feces, and larvae. The mean larval weight during the stadium was estimated by the (initial plus final weight)/2. Indices of larvae performance are reported as in Scriber and Slansky (1981):

RGR, relative growth rate (mg biomass gained per day per mg larval biomass)

$$(RGR = RCR \times AD \times ECD)$$

RCR, relative consumption rate (mg biomass ingested per day per mg larval biomass)

AD, approximate digestibility (also called assimilation efficiency) =

$$\frac{\text{Food infested (mg dry wt)} - \text{Feces (mg dry wt)}}{\text{Food ingested (mg dry wt)}} \times 100\%$$

ECD, efficiency of conversion of digested food (also called net growth efficiency) =

$$\frac{\text{Biomass gained (mg dry wt)}}{\text{Food ingested (mg dry wt)} - \text{Feces (mg dry wt)}} \times 100\%$$

ECI, efficiency of conversion of ingested food (also called gross growth efficiency) =

$$\frac{\text{Biomass gained (mg dry wt)}}{\text{Food ingested (mg dry wt)}} \times 100\%$$

$$\text{ECI} = \text{AD} \times \text{ECD} = (\text{overall efficiency})$$

Plants, larvae, and feces were frozen and freeze-dried for dry weight determinations. Statistical analyses were performed and where the ANOVA indicated significant differences between the means were analyzed by Tukey's test for unequal sample sizes (Winer 1962, Snedecor and Cochran 1967). The very conservative Tukey's test was used because our sample sizes were not as large as we had wished. We therefore believe that all statistically significant differences represent very real biological differences.

RESULTS

Growth of the Florida *Papilio cresphontes*, which uses only Citrus and lime prickly ash as natural host plants, was significantly faster on lime prickly ash, *Zanthoxylum fagara*, than was growth of Ohio *P. cresphontes* on this Florida plant species for both the penultimate and the final instars (Table 1). The Florida population also had a higher efficiency of processing ingested biomass (ECI) than the Ohio larvae. This central American plant species (*Z. fagara*) occurs only in the southern half of Florida and southern tip of Texas (Fig. 1). As such this Ohio butterfly population gets no closer than 1000 kilometers to the plant.

The congeneric northern prickly ash, *Z. americanum*, occurs sporadically from Georgia and Alabama northward to the Great Lakes States and Canada. While all Wisconsin populations and the Ohio populations are sympatric with northern prickly ash and despite the fact that northern prickly ash is the only host plant for *P. cresphontes* in Wisconsin, larval growth and efficiency of these larvae were no better than for Florida larvae (which are totally allopatric with the plant range; Fig. 2 and Table 2). No consistent differences are observed between the growth performances of the penultimate and final instars of Wisconsin, Ohio, and Florida giant swallowtail larvae. While Florida larvae exhibit the highest overall efficiency of processing *Z. americanum* (ECI) in the penultimate instar, they exhibit the lowest efficiency in the final instar (Table 2). The reverse is true for the consumption rates (RCR).

Ohio populations of *P. cresphontes* primarily use hoptree *Ptelea trifoliata* in the source area (Preble Co., OH) for our experimental larvae (Fig. 3). Growth rates of these Ohio larvae were nearly three times as fast (.215 mg mg⁻¹ d⁻¹) as Wisconsin larvae in the final instar (Table 3). The Ohio efficiencies (ECI and ECD) averaged twice those of Wisconsin larvae in the final instar (eg., ECI = 18.8% versus 8.1% and 8.7% respectively). These patterns were not observed in the penultimate instar, however the digestibility (AD) and consumption rates (RCR) were higher for Ohio than Wisconsin larvae (Table 3). Not enough Florida larvae were available for bioassays on hoptree.

DISCUSSION

Larvae of *P. cresphontes* from Florida, Ohio, and Wisconsin exhibit significant differences in growth rates, consumption rates, and efficiencies of processing three different plant species. For final instars, where the largest amounts of food are consumed, populations in Florida grow faster and more efficiently on the local foodplant, lime prickly ash, than Ohio larvae (Fig. 1). Similarly, populations in

Table 1. — Growth performance of penultimate and final instar *Papilio cresphontes* fed *Zanthoxylum fagara* (lime prickly ash). Data are presented as a mean ± SE.

Instar and Source population	(n)	Instar duration (days)	Growth Rate (RGR)	Consumption Rate (RCR)	Efficiencies			Leaf quality (% water)
					(A.D.)	(E.C.D.)	(E.C.I.)	
Penultimate Instar								
Ohio (Preble Co.)	(5)	6.6±0.2	.130±.010	1.74±.13	24.3±4.4	33.9±4.5	7.5±0.5	69.2±1.4
Florida (Broward Co.)	(4)	6.1±0.1 n.s.	.224±.010 **	2.16±.17 n.s.	43.0±4.5 *	26.0±4.9 n.s.	10.5±0.9 *	70.9±2.3
Final Instar								
Ohio (Preble Co.)	(3)	16.2±1.4	.032±.003	1.89±.12	25.8±2.9	6.7±0.6	1.7±0.1	66.7±1.7
Florida (Broward Co.)	(3)	11.8±1.1 n.s.	.084±.006 **	1.44±.41 n.s.	27.2±3.1 n.s.	30.4±14.3 n.s.	11.8±1.1 *	72.6±1.6

¹Significant differences are indicated (* = P±0.05, ** = P±0.01) ANOVA (Snedecor and Cochran 1967).

Table 2. — Growth performance of penultimate and final instar *Papilio cresphontes* fed *Zanthoxylum americanum* (northern prickly ash).

Instar and Source population	(n)	Instar duration (days)	Growth Rate (RGR)	Consumption Rate (RCR)	Efficiencies			Leaf (% water)
					(A.D.)	(E.C.D.)	(E.C.I.)	
Penultimate Instar								
WI (Dane Co.)	(8)	4.7±0.2 bc	.277±.011 bc	1.49±.06 a	36.0±2.2	53.6±4.2	18.7±0.6 c	71.1±0.9
(Iowa Co.)	(8)	4.1±0.2 ab	.321±.012 a	1.35±.07 ab	38.8±2.1	63.0±3.8	24.0±3.8 ab	70.8±0.7
(Richland Co.)	(5)	3.9±0.5 a	.307±.016 ab	1.34±.15 ab	46.2±3.3	56.2±5.3	23.9±2.5 ab	72.5±0.9
OH (Preble Co.)	(6)	5.0±0.2 c	.248±.017 c	1.30±.11 ab	42.3±5.4	51.8±9.9	19.3±0.9 c	74.0±0.5
FL (Broward Co.)	(9)	4.3±0.2 ab	.293±.005 abc	1.14±.05 b	39.7±1.3	66.3±3.6	26.0±0.8 a	77.8±0.1
L.S.D.¹		(0.7)	(.049)	(.34)	(n.s.)	(n.s.)	(4.4)	
Final Instar								
WI (Dane Co.)	(3)	8.5±1.0 ab	.128±.042	1.06±.28	34.1±5.5 ab	34.2±2.4 b	11.4±1.2 ab	66.8±1.4
(Iowa Co.)	(3)	8.1±0.5 ab	.135±.012	1.04±.08	29.4±3.3 b	45.4±5.1 a	13.0±0.4 a	69.9±1.2
(Richland Co.)	(3)	8.5±0.5 ab	.107±.020	1.18±.17	45.4±2.6 a	20.0±0.8 c	9.0±0.4 bc	63.9±1.4
OH (Preble Co.)	(4)	7.0±0.0 b	.160±.005	1.27±.05	41.7±0.9 ab	30.4±1.7 b	12.6±0.4 a	73.2±0.9
FL (Broward Co.)	(6)	10.5±0.6 a	.100±.009	1.67±.26	41.4±2.7 ab	15.2±1.2 c	6.3±0.7 c	74.4±4.1
L.S.D.¹		(2.8)	(n.s.)	(n.s.)	(14.3)	(10.4)	(3.4)	

¹Significant differences (P = 0.05) between the means are indicated by letters (Tukey's test for unequal sample sizes; Winer 1962, Snedecor and Cochran 1967).

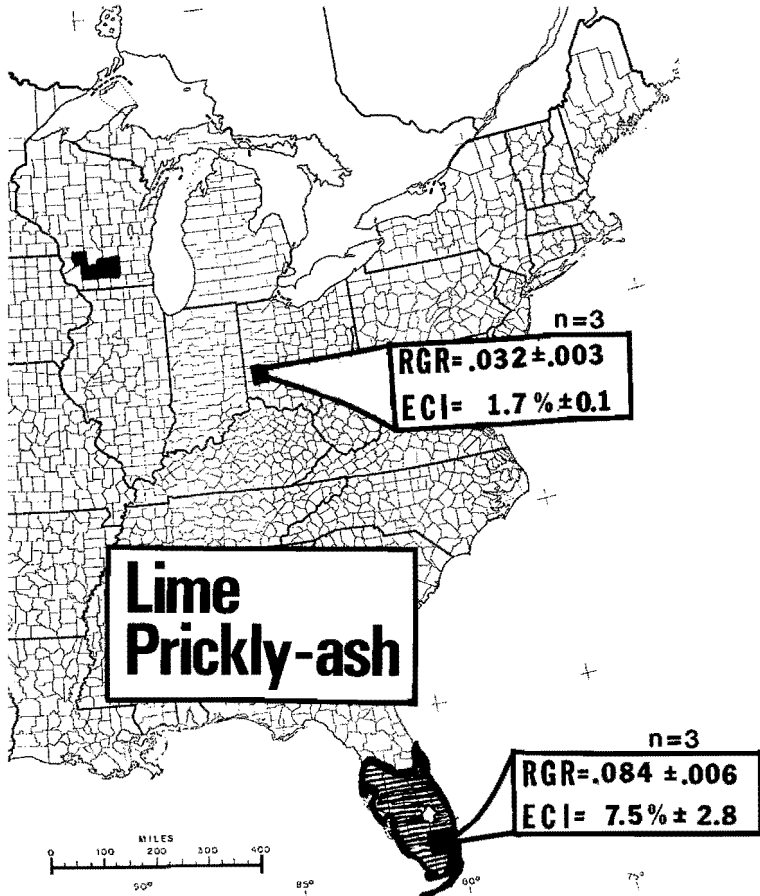


Figure 1. Performance of final instar *P. crespontes* larvae (data are presented as a mean \pm se) as a function of geographic source and range (shaded area) of the test plant, lime prickly ash (*Zanthoxylum fagara*).

Ohio grow faster and more efficiently on their local favorite, hoptree compared to Wisconsin populations that prefer northern prickly ash (Fig. 3). Larvae of both Ohio and Wisconsin populations grow faster and more efficiently than Florida larvae on the northern prickly ash *Z. americanum* (Fig. 2).

While these results with final instars lend support to the feeding specialization hypothesis and suggest that biochemical adaptation has occurred with local specialization, the same patterns are not observed in all cases with larvae in their penultimate instar. While Florida larvae grow significantly faster and more efficiently on *Z. fagara* in the penultimate instar (Table 1), Ohio larvae in their penultimate instar grow no faster on their favored *Ptelea trifoliata* (Table 2), and Wisconsin popula-

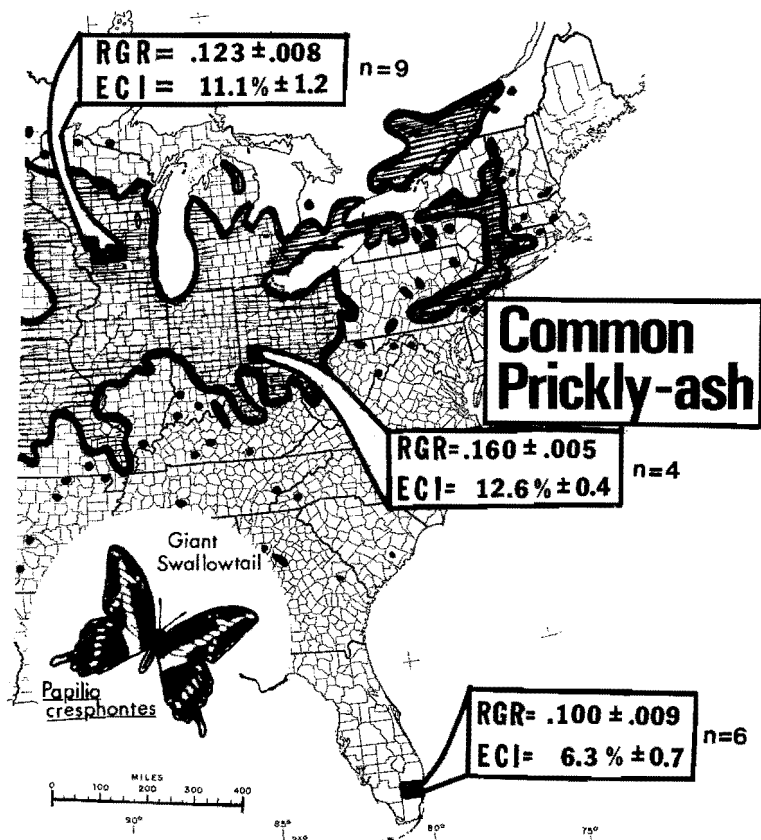


Figure 2. Performance of final instar *P. cressphontes* on northern prickly ash, *Z. americanum* as a function of insect population and plant range (shaded).

tions do not grow significantly faster nor more efficiently than Florida larvae on their favorite host *Z. americanum* (Table 3).

Variable leaf nutritional quality can be very important in determining the larval growth rates and efficiencies (Scriber and Slansky 1981). Different growth performance on different plant species is not unexpected, but there are also significant differences in nutritional quality within a plant species. For example, some leaf quality variability (as indexed by leaf water content) may have been involved in the differential growth performances to some extent in these studies, especially with northern prickly ash where 8–10% differences in leaf water content were detected. These differences may have been largely responsible for the good performance of the Florida populations on northern prickly ash (Table 2).

Another important aspect of local adaptation (not addressed in this study) is the critical first instar survival differences among geographic populations or host races (Diehl and Bush 1984, Futuyma and Moreno 1988). Whether these differences in survival may be related to behavioral (antixenosis) or toxicological (antibiosis) mechanisms, they are of fundamental importance to the ecological success of the

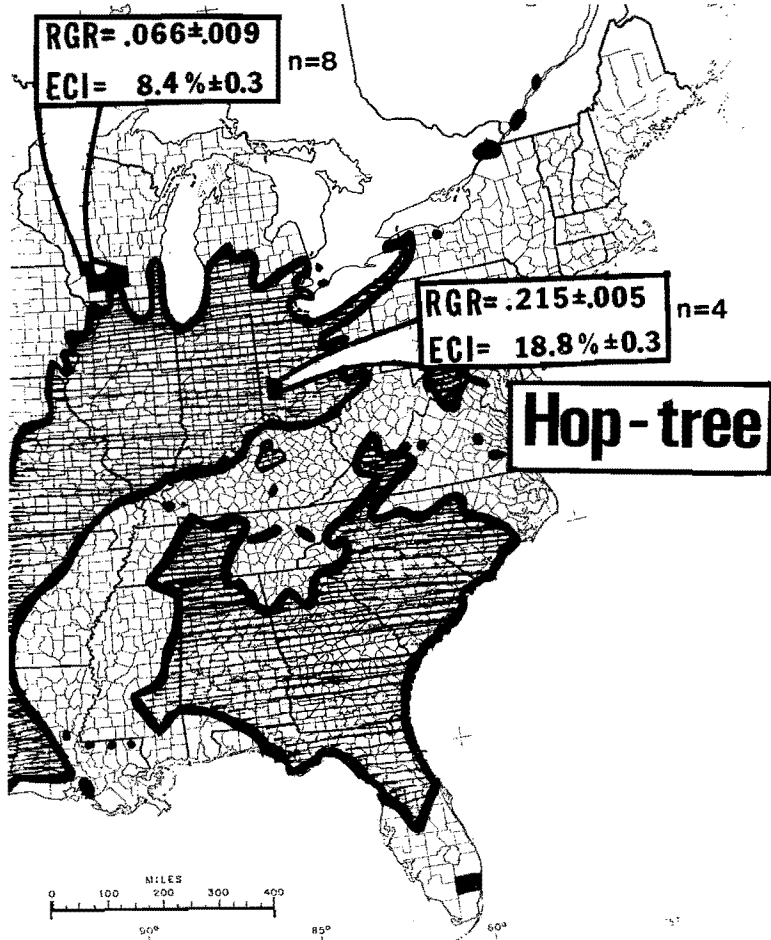


Figure 3. Performance of final instar *P. cresspontes* larvae on noptree (*Ptelea trifoliata*) as a function of the plant range (shaded).

population. The differences in growth performance detected at the penultimate and final instars for surviving larvae may be of minimal significance compared to the differential survival of the initial cohort of larvae in their neonate stages. However, these later instars are around longer and other defenses appear to be useful (Fig. 4a, 4b).

For example, cryptic resting larvae on the side of the stem (Fig. 4a) could avoid early bird detection and predation (Hirose et al. 1980), whereas osmeterial glands (Fig. 4b) may be effective at deterring foraging ants or wasps as has been shown on related *Papilio* in North America and Japan (Hirose and Tagaki 1980, Damman 1986). In addition, the resting spot for the larger larvae is on the inside of the thorny

Table 3.—Growth performance of penultimate and final instar *Papilio cresphontes* fed *Ptelea trifoliata* (hoptree).

Instar and Source population	(n)	Instar duration (days)	Growth Rate (RGR)	Consumption Rate (RCR)	Efficiencies			Leaf (% water)
					(A.D.)	(E.C.D.)	(E.C.I.)	
Penultimate Instar								
WI (Dane Co.)	(9)	4.6±0.2 b	.282±.020	1.29±.04 ab	42.8±1.0 b	51.7±4.3 a	21.9±1.6	71.6±0.4
(Iowa Co.)	(8)	4.3±0.1 ab	.303±.009	1.21±.04 b	47.4±2.0 b	54.0±3.2 a	25.3±1.0	71.6±0.4
OH (Preble Co.)	(3)	3.8±0.2 a	.312±.030	1.46±.05 a	65.6±3.9 a	32.8±2.7 b	21.3±1.3	72.9±0.4
L.S.D. ¹		(0.7)	(n.s.)	(.180)	(7.6)	(16.8)	(n.s.)	
Final Instar								
WI (Dane Co.)	(3)	12.3±1.0 b	.057±.007 b	0.71±.11 b	55.2±4.0	14.9±1.3 b	8.1±0.3 b	69.3±1.2
(Iowa Co.)	(5)	9.9±1.6 ab	.075±.012 b	0.87±.08 ab	52.8±3.1	17.1±3.0 b	8.7±1.1 b	68.3±1.1
OH (Preble Co.)	(4)	6.3±0.1 a	.215±.005 a	1.14±.01 a	49.6±3.1	38.4±2.9 a	18.8±0.3 a	72.3±0.5
L.S.D. ¹		(5.20)	(.040)	(.31)	(n.s.)	(11.5)	(3.3)	

¹Significant differences between the means (P = 0.05) are indicated by different letters (Tukey's test for unequal sample sizes: Snedecor and Cochran 1967, Winer 1962). (n.s. = nonsignificant differences via F-test, ANOVA)



Figure 4a-b. a-Final instar *P. cresphontes* resting cryptically on a stem of northern prickly ash, *Zanthoxylum americanum*. b-Final instar "snake-like" osmeterial defensive response of *P. cresphontes* larva to slight agitation. This has been shown for other *Papilio* to be a defensive behavior to ants, wasps, birds or other predators (see text).

thick stems (Figs. 4a, 4b) down and away from the danger of browsing cattle (and possibly deer) which were believed responsible for the pruned outer foliage on many of these hoptree bushes and lower branches in Wisconsin. The use of taller trees of prickly ash would avoid the mammalian grazing damage (i.e., larvae consumed with leaves). However, it has been shown that taller trees of *Zanthoxylum* have nutritionally poorer leaves upon which the *Papilio* growth is slower and mortality is higher (Watanabe 1982). Female *P. xuthus* L. butterflies in Japan prefer these shorter *Zanthoxylum* trees for oviposition (Watanabe 1982), as the *P. cresphontes* in Wisconsin also seem to do. Eggs and larvae of *P. xuthus* on *Zanthoxylum* in Japan in early stages were attacked primarily by smaller predators such as ants, spiders, bugs, and orthopteroids in contrast to birds and *Polistes* wasps that attack larger larvae (Watanabe 1981).

Additional studies would be needed to determine whether the differences in larval growth performance among the different *P. cresphontes* populations have a genetic basis. The phytochemical cues for oviposition and the allelochemical factors making the Rutaceae the primary host family of this insect are certainly of tremendous ecological (Dethier 1941, 1954) and evolutionary significance for the Papilionidae (Hancock 1983, Miller 1987). The specific chemical cues used by *P. cresphontes* for oviposition and enhancement of larval feeding may not be unlike those for Japanese Rutaceae feeders (Nishida 1977, Ichinosé and Honda 1978). However, chemical similarities in Rutaceae hosts with the Umbelliferae, Lauraceae, Aristolochiaceae, Magnoliaceae, and Asteraceae (see Feeny et al. 1983) make the role of particular allelochemicals (and their interactions) in host selection and the ecology of different *Papilio* uncertain at best.

This study reflects significant biological differences in larval performance among different individual larvae on the same host plants under controlled conditions. However we still lack the extensive geographic replication and intensive (intrapopulation) analysis to detect the extent of genetically based adaptations. We are therefore hesitant to extrapolate the results from any particular host plant or any particular population to the *P. cresphontes* species on the whole. Similarly, we have illustrated that the relative differences in the roles of growth are in some cases instar-dependent. A more rigorous test of the feeding specialization hypothesis must include not only controls for host plant nutritional quality, but should also include a representative sample of genotypes from the entire range of the species of interest. Our studies with the sympatric *Papilio glaucus* group are more extensive and intensive to date, and we have detected several different levels of behavioral biochemical and genetic differences in the adaptation of local populations to favored host plants (Scriber 1986, Scriber et al. 1989, 1990). Yet no single species can be used when evaluating a general ecological concept such as the feeding specialization hypothesis. A comparative approach using different taxa is essential, and thus additional data from other insect/plant systems such as this study are still needed.

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