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ABSENCE OF BEHAVIORAL INDUCTION IN OVIPOSITION PREFERENCE  
OF *PAPILIO GLAUCUS* (LEPIDOPTERA: PAPILIONIDAE)J. Mark Scriber<sup>1</sup>

## ABSTRACT

This study addressed the possible behavioral induction effects of previous exposure to several specific host plants on subsequent host "preference hierarchy" and "specificity" (i.e. how far down the ranking order a female will go) in the most polyphagous swallowtail butterfly in the world, *Papilio glaucus* (Papilionidae). Multi-choice preference bioassays using individual females in revolving arenas were used to assess one of the potentially most significant non-genetic sources of variation: learned (or induced) oviposition preferences. Results of the 4-choice studies using tulip tree (*Liriodendron tulipifera*; Magnoliaceae), black cherry (*Prunus serotina*; Rosaceae), quaking aspen (*Populus tremuloides*; Salicaceae), and hoptree (*Ptelea trifoliata*; Rutaceae), fail to show any significant oviposition preference induction with two-day prior exposure to any of the host species tested. It appears that the eastern tiger swallowtail butterfly, while polyphagous as a species (feeding on more than 9 families of plants), and variable in its population responses to oviposition favorites, has what may be considered a genetic "hard-wiring" at an individual level, with no evidence that preferences change with recent oviposition experience. Older females were not and did not become more random in their choices, and in fact increased in their specificity for tulip tree leaves.

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Preference induction by previous exposure to a particular host plant has been reported for various lepidopterous larvae (Jermy et al. 1968, Hanson 1976, Greenblatt et al. 1978, Barbosa et al. 1979, Wiseman and McMillian 1980) and also for some ovipositing adults (Papaj and Rausher 1983, 1987; Stanton 1984, Traynier 1984, 1986; Papaj 1986). In other insects, prior exposure to one specific resource has been reported to enhance a female's tendency to oviposit on that resource; including Diptera (Jaenike 1982, 1988; Prokopy et al. 1982, Hoffman 1985, Cooley et al. 1986), Coleoptera (Mark 1982, Rausher 1983), and Hymenoptera (Vinson et al. 1977, Vet and vanOpzeeland 1984, Wardle and Borden 1985). Modification of the "specificity" of oviposition responses by previous exposure seems more common than changes in the "rank-order" (or preference hierarchy) for phasmids (Cassidy 1978), flies (Hoffman 1985, Jaenike 1982, 1983; Prokopy et al. 1982), sawflies (Craig et al. 1989), and some butterflies (Rausher 1978, Singer 1983). This study was designed to see to what extent the "specificity" or the host-ranking oviposition "hierarchy" (see Courtney and Kibota 1990) of the polyphagous tiger swallowtail butterfly, *Papilio glaucus* L., would be affected in multi-choice studies by pre-conditioning to several particular hosts.

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In adult phytophagous insects the acceptability of host plants for oviposition is influenced by a balance of various internal and external excitatory factors (Miller and Strickler 1984). However, unlike foraging vertebrates that often successfully adjust their individual feeding behaviors through learning, phytophagous insects are generally assumed to be more "hard-wired". For example, limited host plant breadth in insects may be the result of constrained sensory modalities, genetics, and allelochemical detoxification systems (Dethier 1941, Ehrlich and Raven 1964, Feeny 1991, Caprio and Tabashnik 1992, Nitao 1993). Divergence of insect preferences for certain plants results from physiological, biochemical, and behavioral adaptations to plant availability, acceptability, and suitability, which in turn are generally determined by the interactions of plant nutrients and allelochemicals (Scriber 1984a, Ehrlich and Murphy 1988, Schultz 1988, Berenbaum 1990, Lindroth 1991), the associated community of natural enemies and, (or) competitors (e.g., Strong et al. 1984, Barbosa 1988, Bernays and Graham 1988, Jermy 1984, 1988; Scriber 1992) and various abiotic factors such as microclimate or seasonal thermal unit accumulations affecting latitudinal voltinism and feeding specialization patterns (Scriber and Lederhouse 1992).

Wiklund (1981) suggested that ovipositing female butterflies exhibit a "preferential-hierarchy" in which the specificity of individuals (how far down the ranking the female will go in a multi-choice arena) for sub-optimal hosts, may vary depending on environmental, induced, or genetically based behaviors. This "preference-hierarchy" model (see also reviews in Courtney and Kibota 1990, Thompson and Pellmyr 1991), predicts that a female will consistently lay more eggs on highly preferred host plant species and fewer eggs on plants that are less preferred when simultaneously offered several choices. Some individuals will be more specific than others, not accepting some of the lower-ranked host species (see Fig. 1). Less specific females may be considered generalists; however, most studies with butterflies to date have been done with relatively specialized (oligophagous) species (Wiklund 1975, Chew 1977, Rausher 1978, Tabashnik et al. 1981, Courtney 1982, Feeny et al. 1983, Stanton and Cook 1983, Singer 1986, Damman and Feeny 1988, Thompson 1988a, 1988b, 1988c; Lederhouse et al. 1992). Feeding on 9 plant families, *Papilio glaucus* is the most polyphagous of all 560+ species of swallowtail butterflies (Scriber 1984b). Such polyphagous species may provide unique insights into the evolution of host preference behavior of ovipositing females. However, only the *P. glaucus* group (6 species) in North America and the *P. scamander* group in South America are reported to feed on more than 4 families of plants (Scriber et al. 1991b, 1991c).

The degree to which female butterflies will accept lower-ranked host plants in addition to or instead of their preferred host is affected by a variety of internal and external factors that are ecologically influenced and evolutionarily derived. For example, older females (Gossard and Jones 1977) or females with a large number of accumulated eggs (Jones 1977, Fitt 1986) may be less specific in their oviposition preferences. The length of time since last oviposition (e.g., due to the distance between hosts) can also influence female specificity (Singer 1983). Perhaps the most intriguing of all internal factors is the effect of adult learning on oviposition behavior. The interaction of learning in the insect with various sensory cues such as color, shape, size or chemistry of leaves has been the subject of numerous studies (see review by Papaj and Prokopy 1989).

This study describes preliminary attempts to assess the behavior of adult tiger swallowtail butterflies, *Papilio glaucus* to multi-choice oviposition opportunities on host plants of varying suitability for larvae. It specifically addresses the possible effects of previous exposure (learning) on subsequent host ranking and specificity. A relatively high level of polyphagy suggests

## “Hierarchy - Threshold” model of Oviposition Preferences

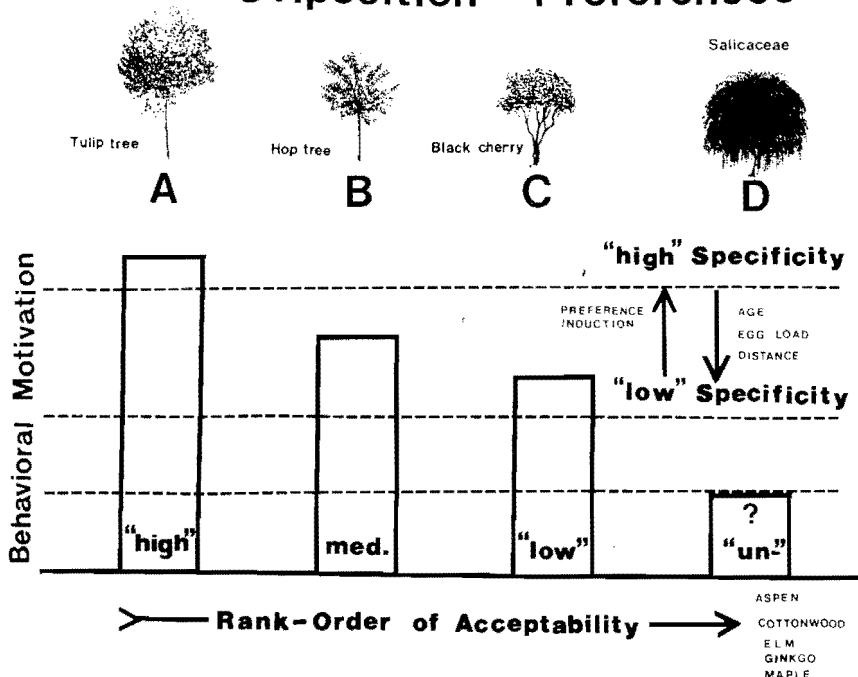


Figure 1. A general "hierarchy-threshold" model of host preferences (see Wiklund 1981, Courtney and Kibota 1990) as adapted to *Papilio glaucus* in these studies with 4 host plant families. High specificity would be when a female oviposits only on plant "A"; and low specificity would be when a female oviposits on plants A, B, and C, but some remain nearly unacceptable (D). Specificity may be greater for individual females that have experienced a preference induction (see arrow) or lowered (see arrow) due to other variables (e.g. age).

that *P. glaucus* females may be non-discriminating in their oviposition choices (i.e., generalized individuals), or, alternatively, different individuals of different populations may vary considerably the host plants on which they have specialized, resulting in a "composite" generalist species with local feeding specialization (Scriber and Feeny 1979, Fox and Morrow 1981). We have previously shown that almost every individual from populations of *P. glaucus* from Florida to Michigan strongly prefer tulip tree, *Liriodendron tulipifera* (Magnoliaceae) over black cherry, *Prunus serotina* (Rosaceae), and quaking aspen, *Populus tremuloides* (Salicaceae) in laboratory 3-choice arenas (Scriber et al. 1991a). The following 4-choice studies also include hoptree, *Ptelea trifoliata* (Rutaceae), which has been reported as a local favorite for certain populations (Scriber 1972). Quaking aspen was included in the following study even

though the Georgia butterfly population does not encounter this plant species. Previous studies (Scriber et al. 1991a, Bossart and Scriber 1993) have shown low levels of aspen and cottonwood (Salicaceae) oviposition acceptability for populations as far south as Florida, even though these Salicaceae family plants are toxic to essentially every larva tested (Scriber et al. 1991b).

## MATERIALS AND METHODS

Female *Papilio glaucus* butterflies for oviposition studies were obtained from one population in the southeastern United States (Clarke Co., Georgia) and shipped overnight to our laboratory at Michigan State University. Georgia butterflies have no genetic introgression from *P. canadensis* (Hagen et al. 1991), and were available in sufficient numbers for this study. These females were classified into four age categories based on wing wear, fed 20% honey water solution daily until death, and placed individually into clear round plastic containers (10 cm high, 25 cm diameter) with leaves of various host plant species draped along the side of the container (Fig. 2) at equally-spaced distances for the 4-choice preference induction studies. Plastic containers, with plant leaves in water-filled vials and with one butterfly each, were stacked on rotating platforms aligned in front of a bank of 100-W incandescent bulbs on a 4-h on/off cycle. The revolution of the containers was adjusted so that each of the leaves passed in front of the light 10 times per hour. Since the butterflies flutter and bounce along the inside of the round dishes at the side facing the lights, the multi-choice arena provided a continuous sequence of leaves to each female each revolution (six minutes). The order of the leaves was randomized each time they were replaced. The treatments consisted of a direct 4-choice test ( $n = 50$  females), while four other groups (8 females each) were presented a no-choice arena with one of the four host plant species for 2 days prior to the test. This was designed to assess the influence, if any, of previous experience in oviposition preference.

Eggs were removed from each container daily and counted until the female died. This ranged from 2 to 9 days. The few stray eggs placed on the plastic or paper towel bottom lining were excluded from the analyses unless they were obviously immediately adjacent ( $\leq 5$  mm) to the edge of a leaf. Strays generally represented less than 1% of the total eggs collected. Only females that laid 10 or more eggs are included in the tables and analyses. Leaves in containers were replaced at 2 to 3-day intervals, or at 24 h if they had eggs. Leaves were collected fresh from trees in Ingham Co., Michigan.

A series of multi-choice oviposition studies were conducted using quaking aspen as a "non-host" in combination with the tulip tree, black cherry, hoptree or white ash (3-choice, 4-choice and 5-choice). In addition, tulip tree and hoptree were used in combination with other non-hosts; sugar maple and cottonwood (4-choice) or with elm and ginkgo added (6-choice). The same procedures were used in these as in the 4-choice induction studies, however additional females of *P. glaucus* from this Georgia population were used.

## RESULTS

The average population preference profile of 27 Georgia (Clarke Co.) females (which produced more than 10 eggs) in four-choice tests was 46.6% on tulip tree, 30.5% on hoptree, 20.0% on black cherry and only 2.9% on quaking aspen. The female butterflies that were exposed to one of four hosts as an

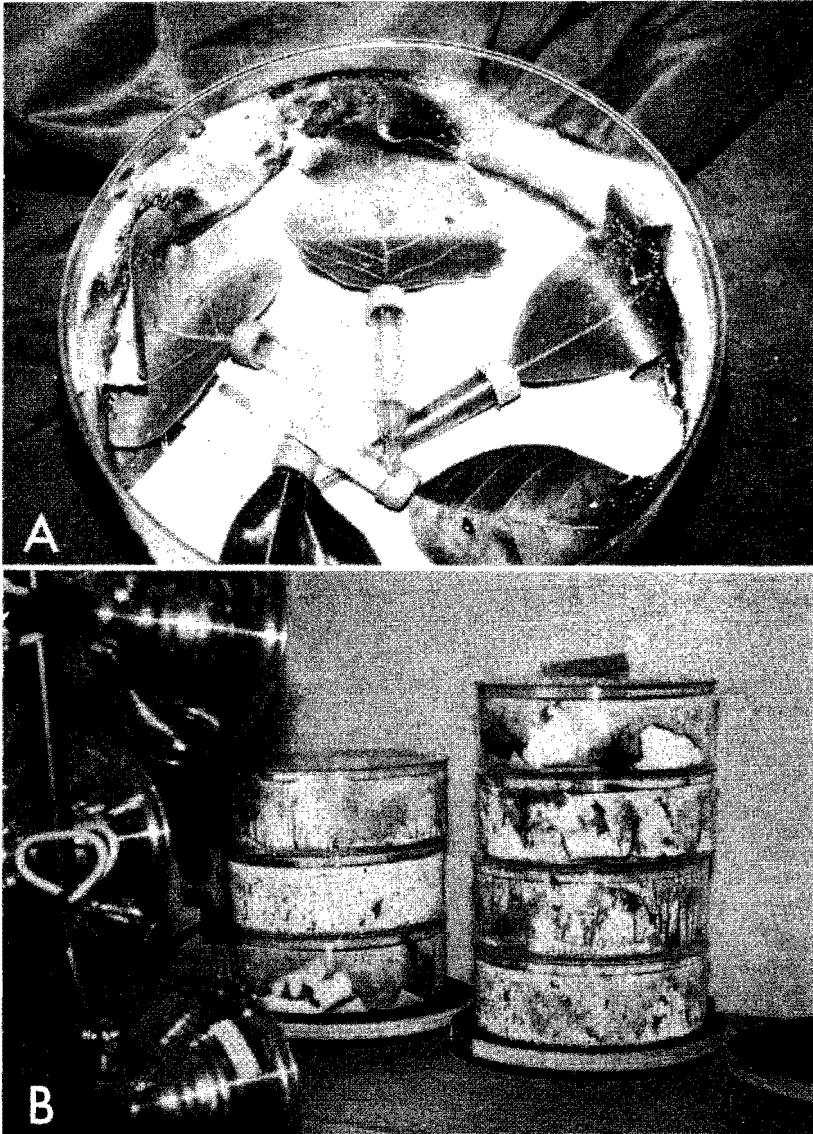


Figure 2. (a) Plastic box with leaves draped on the side, used for multi-choice oviposition studies. With this round container placed on a rotating platform (b), the leaves "pass by" between the female butterfly and the outside light source 10 times per hour. Females bounce along the side facing the light and have repeated opportunities to oviposit on each leaf for 1-to 1-1/2 minute intervals.

Table 1. Overall average oviposition preference profiles (4-choice test) for a *P. glaucus* population from Georgia (Clarke Co.) compared to groups exposed to four different plants for 2 days prior to testing. Data are presented as the percentage of total eggs by host (mean  $\pm$  SE). The lower portion of the table represents mean percentage of eggs produced in the first day only.

4-choice with no prior exposure	Number of females (n)	Magnoliaceae (tulip tree)	Rutaceae (hoptree)	Rosaceae (black cherry)	Salicaceae (quaking aspen)
	(27)	46.6 $\pm$ 4.9	30.5 $\pm$ 4.0	20.0 $\pm$ 2.9	2.9 $\pm$ 0.7
Total Egg Distribution:					
Tulip tree induction*	(3)	61.0 $\pm$ 14.9	16.6 $\pm$ 7.4	13.5 $\pm$ 5.1	9.0 $\pm$ 4.1
Hoptree induction*	(5)	51.0 $\pm$ 9.1	25.6 $\pm$ 5.3	19.6 $\pm$ 5.0	3.8 $\pm$ 1.4
Black cherry induction*	(5)	66.8 $\pm$ 9.0	20.0 $\pm$ 5.2	11.3 $\pm$ 4.1	2.0 $\pm$ 1.5
Quaking aspen induction*	(3)	43.6 $\pm$ 3.4	29.4 $\pm$ 3.3	22.3 $\pm$ 5.0	4.7 $\pm$ 0.8
First Day Egg Distribution:					
Tulip tree*	(3)	76.5 $\pm$ 19.8	10.8 $\pm$ 9.0	2.9 $\pm$ 2.9	9.8 $\pm$ 8.0
Hoptree*	(5)	59.9 $\pm$ 8.5	12.8 $\pm$ 3.4	25.4 $\pm$ 6.5	1.8 $\pm$ 1.8
Black cherry*	(5)	72.2 $\pm$ 12.3	10.9 $\pm$ 6.9	12.4 $\pm$ 7.7	4.4 $\pm$ 3.9
Quaking aspen*	(3)	48.8 $\pm$ 4.2	31.3 $\pm$ 4.4	18.2 $\pm$ 7.6	1.7 $\pm$ 1.7

\*Females were previously placed in a box with 4 leaves of the same plant (no-choice) for 2 days before given the 4-choice option. In no case was the average preference in 4-choice of females significantly different than the reference group at the top of the table ( $n = 28$ ;  $t$ -tests  $p = 0.10$ ; Snedecor and Cochran 1967).

induction treatment subsequently produced overall 4-choice egg distribution profiles that were not significantly different (Table 1, Fig. 3). This suggests for *P. glaucus* that overall egg distribution does not follow the most recent host plant the female is exposed to, at least in these laboratory multi-choice arenas.

Females ( $n=18$ ) that preferred tulip tree from this Georgia population generally preferred it every day, as was the case with hoptree ( $n=6$  females) and black cherry ( $n=3$  females). All females basically avoided quaking aspen, both in the baseline control population ( $n=27$ ) and in all of the induction treatment attempts (Table 2). In the total 4-choice responses from the various preference induction treatments, it was observed that 15 of 16 females exhibited a total oviposition preference for tulip tree (a weak hoptree preference observed by a single female). Thus while there exists some variation in the preference for tulip tree, hoptree or cherry in the base population ( $n=27$  females), there were essentially no such variable preferences evident in any of the induction treatments, nor were there induction effects.

The age of the females (as indicated by wing-wear and abdominal girth; see Lederhouse and Scriber 1987) was not a major variable in the overall total preference profiles of this Georgia population (Table 2). It is interesting, however, that the oldest females were not less specific in host plant choice. In fact, the older females laid a significantly greater proportion of their eggs on tulip tree leaves (with fewer on hoptree and black cherry), and these older females did not accept aspen any more readily than younger females (Table 2).

As a population, older appearing females (at the initiation of the experiments) preferred tulip tree for the highest average proportion of their eggs. It is important to note that individual females did vary in their oviposition

4-Choice Oviposition Preferences

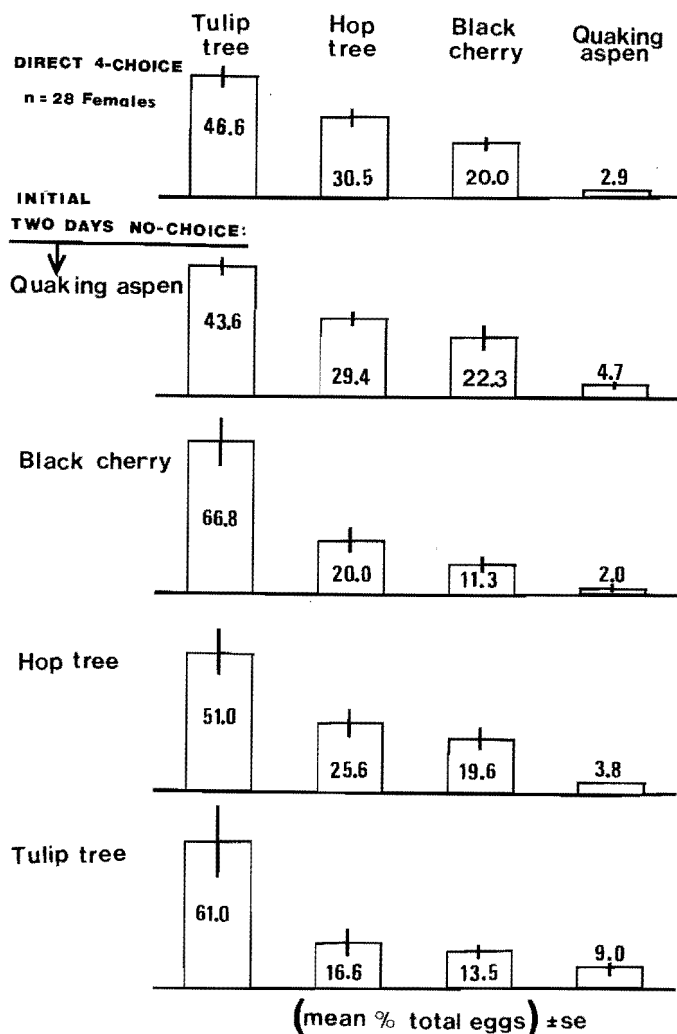


Figure 3. Observed average 4-choice oviposition response pattern of 27 field-captured (Georgia) female butterflies (top) compared to the 4-choice response patterns of their contemporaries (females from the same population) subsequent to 2 days of exposure in no-choice induction arenas for each of the 4 hosts. Data are presented as the mean percentage ( $\pm$ SE) of the total eggs laid on each host.



Table 2. Four-choice oviposition preference profiles of *P. glaucus* females of different age classes<sup>1</sup> (for females laying more than 10 eggs)<sup>2</sup>

Age Class Category	(n)	Tulip Tree (%)	Hop Tree (%)	Black Cherry (%)	Quaking Aspen (%)	Mean Total Eggs	Number of days alive in the lab
1.0 (new)	(5)	34.4 ± 8.6 a	40.3 ± 13.7 b	22.3 ± 5.7 ab	2.9 ± 1.6 a	57 ± 17 a	5.2 ± 0.8 a
2.0 (slightly worn)	(15)	37.8 ± 5.3 a	34.3 ± 4.6 ab	25.2 ± 4.1 b	2.7 ± 0.7 a	87 ± 13 a	4.2 ± 0.4 a
3.0 (worn)	(7)	74.2 ± 6.9 b	15.3 ± 3.9 a	7.2 ± 2.6 a	3.3 ± 1.9 a	51 ± 8 a	4.9 ± 0.9 a
4.0 (old)	(0)	—	—	—	—	—	—
Totals	(27)	46.6 ± 4.9	30.5 ± 4.0	20.0 ± 2.9	2.9 ± 0.7	72 ± 9	4.6 ± 0.3

<sup>1</sup>The age (wear) class categories for adult female butterflies go from 1 (near perfect/fresh) to well worn (with broken wing edges, slender abdomen, and most scales on wings gone; see Lederhouse and Scriber 1987 for discussion).

<sup>2</sup>Significant differences between the means for 3 age classes are indicated by different letters via Tukey's test for unequal sample sizes ( $p = 0.05$ ; Winer 1962, Snedecor & Cochran 1967).

preference responses for total eggs. However, it was observed that the daily preferences (for females producing at least 80 total eggs, with at least 8 eggs per day, for at least 4 days) did not change very much for any of the 6 females in these 4-choice oviposition studies (Table 3). In fact, the mean percent of total eggs produced for each host is very similar to the mean of the daily percents (Table 3). Quaking aspen was ranked last for every day of every female (except the last day of female #8652).

## DISCUSSION

In no treatment was there induction of oviposition preferences in 4-choice laboratory arenas after 2 days of previous exposure to either quaking aspen, black cherry, hoptree, or tulip tree in no-choice situations. The overall population ranking hierarchy pattern of 4-choice oviposition preferences was similar for all 4 induction treatments to the direct 4-choice reference group study (i.e. those not exposed in a 2-day induction treatment) using females from the same Georgia population. While tulip tree selection was numerically greater for butterflies with tulip tree (and black cherry) exposure, it was not significant (even at  $p = 0.10$  level) for total eggs (or for the first day's eggs; Table 1) in 4-choice studies. Since eggs in these studies were not collected on an hourly basis, it was not possible to determine if a short-term behavioral preference induction may have actually occurred in the first minutes of the 4-choice arena, and was subsequently erased or swamped by the full day (and subsequent days) of 4-choice exposure. Nonetheless, there is no evidence to suggest that either daily or the overall totals for oviposition by *P. glaucus* populations is influenced in rank-ordering or specificity by previous exposure to any of the host choices (Fig. 3).

We are in the process of determining how oviposition preference ranking profiles for hosts change geographically and taxonomically with different *Papilio* species. Determining the relative stability of oviposition preferences through evolutionary time requires a careful knowledge of the various non-genetic environmental modifiers of behavior, including learning and preference induction. While we must continue to assess different hosts and host arrays for the polyphagous *P. glaucus*, our preliminary behavioral studies suggest genetic "hard-wiring" of oviposition preferences may already be evident in the consistency of individual responses (Boake 1989). There appears to be minimal influence of previous host plant exposure to the overall pattern of egg laying in multi-choice lab studies where females most probably are discriminating on the basis of tarsal chemoreceptors (Roessingh et al. 1991). It is possible that other sensory modalities may come into play under natural conditions. For example, visual learning of leaf shape or color (or tree size) may occur, or volatile host chemical imprinting may exist (Rauscher 1978).

In addition to the apparent lack of inducibility of host plant oviposition preferences for individual females, it is also suggestive of genetic "hard-wiring" that individual *P. glaucus* females are quite consistent in their pattern of preference hierarchy from day to day (Table 3) in multi-choice arenas. Quaking aspen was recognized as a "non-host" by every female in the 4-choice studies, both in the overall (total eggs; Fig. 3) and in daily ranking consistency (Table 3) as a very distant last place. This last place ranking was true of all age classes of females (Table 2), which signifies that these Georgia females do not become less discriminating of poor hosts with age.

It is interesting that, in spite of the relatively consistent, and non-inducible, preference profiles exhibited by *P. glaucus* females in these studies, there are still a few percent of the total eggs placed on "non-host" leaves (i.e.,

Table 3. Four-choice daily repeatability studies of oviposition preference of individual *Papilio glaucus* females (TT = tulip tree, HT = hoptree, BC = black cherry, QA = quaking aspen).

Female */ (total eggs)	Day	Number of Eggs and % of Total				Percent of Eggs (Daily)			
		TT	HT	BC	QA	TT	HT	BC	QA
8694 (GA) (n = 185)	1	11	6	2	2	52	29	10	9
	2	13	5	11	2	42	16	36	6
	3	10	27	10	5	19	52	19	10
	4	25	12	10	5	48	23	19	10
	5	13	6	9	1	45	21	31	3
mean		38.9%	30.3%	22.7%	8.1%	41.3±5.8	28.1±6.3	22.9±4.6	7.7±1.2
8700 (GA) (n = 90)	1	3	19	12	0	9	56	35	0
	2	1	6	6	0	8	46	46	0
	3	0	5	5	0	0	50	50	0
	4	0	4	29	0	0	12	88	0
	mean		4.4%	37.8%	57.8%	0.0%	4.1±2.4	41.1±9.9	54.9±11.5
8710 (GA) (n = 86)	1	11	6	6	1	46	25	25	4
	2	14	3	2	1	70	15	10	5
	3	4	0	4	0	50	0	50	0
	4	5	2	5	0	42	17	41	0
	5	6	2	11	0	32	10	58	0
mean		46.5%	15.1%	36.0%	2.3%	47.8±6.3	13.4±4.1	36.9±8.7	1.8±1.1
8712 (GA) (n = 170)	1	18	29	19	1	27	43	28	2
	2	6	6	4	0	37	38	25	0
	3	8	12	14	1	23	34	40	3
	4	6	10	15	1	19	31	47	3
	5	1	5	11	1	6	28	61	5
mean		24.1%	36.5%	37.1%	2.4%	22.3±5.2	34.8±2.7	40.3±6.5	2.6±0.9
8653 (GA) (n = 168)	1	35	29	9	4	45	38	12	5
	2	9	3	2	1	60	20	13	7
	3	3	6	4	0	23	46	31	0
	4	17	13	5	4	44	33	13	10
	5	3	5	4	0	25	42	33	0
mean		42.7%	35.7%	15.9%	5.7%	39.4±6.9	35.8±4.5	20.4±4.8	4.4±2.0
8652 (GA) (n = 131)	1	21	11	16	0	44	23	33	0
	2	19	8	12	1	48	20	30	2
	3	4	13	13	4	12	38	38	12
	4	6	0	1	2	67	0	11	22
mean		38.2%	24.4%	32.1%	5.3%	42.4±11.4	20.3±7.9	28.2±5.9	9.1±5.0

\*Only females producing at least 80 eggs with at least 8 eggs/day for at least 4 days were included. GA = Georgia source.

quaking aspen). This was also noted in 3-choice studies with tulip tree, black cherry and quaking aspen (Scriber et al. 1991a). It was observed in 5-choice studies (with white ash added to the 4-choice induction array) that nearly the same low percentage of eggs were still placed on quaking aspen (5.5%; Fig. 4). Two additional variations of non-host plant species using sugar maple and cottonwood with hoptree and tulip tree (4-choice), and sugar maple, cottonwood, slippery elm, and ginkgo with hoptree and tulip tree (6-choice). Again, in both studies, only a consistently small percentage of the total eggs were placed on non-hosts (Fig. 4). The ecological or evolutionary advantage of such behavior by *Papilio glaucus* is not entirely clear since the neonate larvae resulting from these eggs on non-host plants cannot survive (Scriber 1988) nor can they likely survive the walk to another host plant species. The evolution-

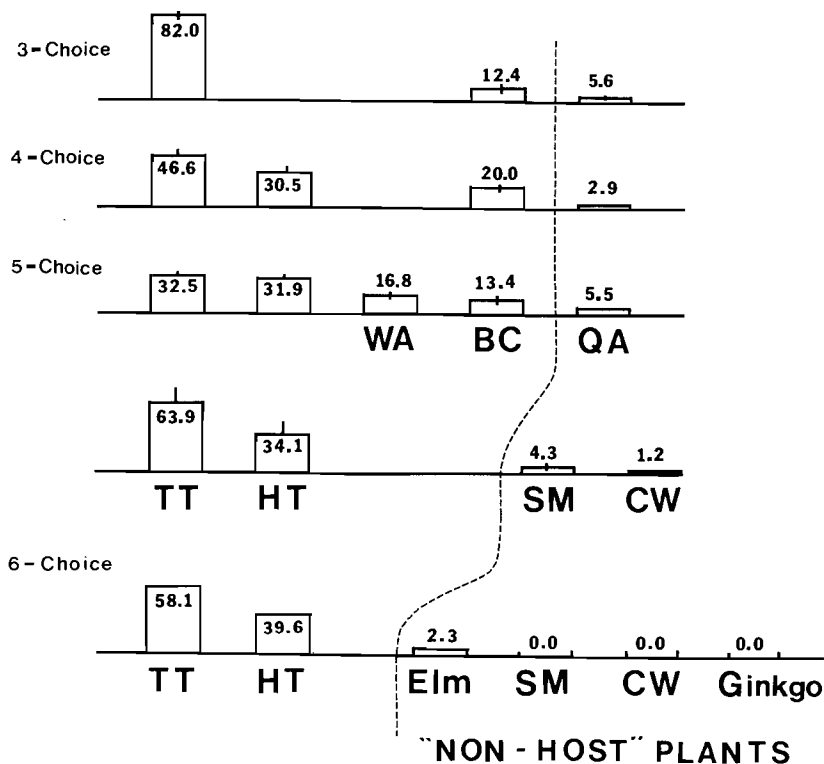


Figure 4. Multiple-choice variations in oviposition preference profiles in studies with *P. glaucus* from Georgia. The 4-choice induction study already described is indicated near the top and includes, from the left side; tulip tree, hoptree, black cherry, and quaking aspen. The 3-choice study above it lacks hoptree and the 5-choice study below it has white ash (*Fraxinus americana*) added to the standard 4-choice array. The bottom two response profiles represent two hosts (tulip tree and hoptree) compared with "on-hosts" of *P. glaucus* (SM = sugar maple, *Acer saccharum*; CW = cottonwood, *Populus deltoides*; Elm = slippery elm *Ulmus rubra*; and *Ginkgo biloba*).

ary variation in *Papilio* detoxication enzyme systems for allelochemicals in natural systems may not be broad nor labile enough for taking advantage of many oviposition mistakes (Nitao 1993, but cf. Feeny, 1991). Behavioral plasticity and learning behavior may play large roles in insect host plant shifts, even if the host plant specialization does not involve physiological (detoxication) traits (cf. Rausher 1992) and even if the trade-off in selecting one host over another is not genetically based (Jaenike and Papaj 1992).

## ACKNOWLEDGMENTS

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