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THE ROLE OF NECTAR SOURCE DISTRIBUTION IN HABITAT USE AND OVIPOSITION BY THE TIGER SWALLOWTAIL BUTTERFLY

DAVID W. GROSSMUELLER AND ROBERT C. LEDERHOUSE[1]
Department of Zoology and Physiology, Rutgers University,
Newark, New Jersey 07102

ABSTRACT. In northern New Jersey, larval hosts of the polyphagous butterfly *Papilio glaucus* L. are widely distributed but nectar plants are clumped. Females were rarely captured in an area rich in preferred hosts during the spring generation, when the area lacked concentrations of nectar plants. During summer, second generation females fed and oviposited in the study area while thistles bloomed. The locations of hosts receiving eggs correlated significantly with locations of nectar plants. Such an ovipositional pattern, although probably not maladaptive for larvae, appears to be unrelated to improved larval growth or survival.

Additional key words: Papilionidae, *Papilio glaucus*, adult resources, activity centers.

The distribution of individuals of a butterfly population generally reflects the distribution of their resources. Sources of adult or larval nutrition, or areas facilitating mating or roosting, may all occur in the same habitat as in the Jasper Ridge colonies of *Euphydryas editha* (Ehrlich 1965). In this case the population was local and sedentary (Gilbert & Singer 1973). More commonly, different requirements are met in different habitats. Other populations of *E. editha* were much less localized due to the dispersed distribution of nectar sources (Gilbert & Singer 1973) or local defoliation of larval host plants (Murphy & White 1984). In central Sweden, *Leptidea sinapis* females regularly moved from a woodland nectar foraging habitat to a meadow oviposition habitat (Wiklund 1977). Some habitats that appear to be rich in larval resources may be rarely used (Singer 1971, Cromartie 1975, Chew 1977, Rausher 1979). Areas of otherwise suitable habitat may not be used if they lack a limited resource such as adult nectar plants (Murphy 1983).

In any one habitat, butterflies often do not oviposit on all of their potential larval hosts (Singer 1971, Wiklund 1975, Smiley 1978), nor use all of the habitats in which preferred hosts grow (Singer 1972, Cromartie 1975). Selective oviposition has been interpreted to favor better larval growth or survival (Ehrlich & Raven 1964, Wiklund 1975, Holdren & Ehrlich 1982). Although this has been clearly demonstrated in some cases (Rausher 1980, Rausher & Papaj 1983, Williams 1983), in other cases, no advantage for the larvae has been shown (Chew 1977, Rausher 1979, Courtney 1981, 1982). Certain hosts may favor high

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[1] Present address: Department of Entomology, Michigan State University, East Lansing, Michigan 48824.

oviposition rates, and higher larval mortality is offset by the greater number of eggs (Rausher 1979, Courtney 1982). If hosts are widely distributed and of similar overall quality, selective oviposition may represent the response of females to other factors such as restricted adult resources (Murphy et al. 1984). This suggests that in many cases the distribution of eggs is a compromise between larval and adult needs.

The tiger swallowtail, *Papilio glaucus* L., is the most polyphagous of the over 500 species of Papilionidae (Scriber 1973), using hosts from over 14 plant families (Tietz 1972). Northern New Jersey is near the limit of bivoltine populations of *P. glaucus* (Hagen & Lederhouse 1985), and in this area, *P. glaucus* females show a strong preference for tuliptree, *Liriodendron tulipifera* L. (Grossmueller & Lederhouse 1987), although several other suitable hosts are abundant (Grossmueller 1984). In northern New Jersey, they also oviposit on the W and S sides of trees within 3 m of the ground (Grossmueller & Lederhouse 1985). Such selective oviposition greatly increases the probability of completing two generations during normal and cooler than normal years. Potential larval hosts are abundant in this area, and *P. glaucus* populations never reach densities high enough to deplete their larval food supply. Our question in the present report was whether the temporal and spatial distribution of adult resources affect which habitats and individual hosts are selected for oviposition.

MATERIALS AND METHODS

The study area was located in Flanders, Morris Co., New Jersey, and consisted of a 5300 m^2 extension of a larger field (Grossmueller & Lederhouse 1985). It was surrounded on three sides by woods, and had progressed to late old-field succession. Potential hosts such as tuliptree, wild black cherry (*Prunus serotina* Ehrh.), and white ash (*Fraxinus americana* L.) were abundantly scattered throughout the open field, around the edges and in the surrounding woods. The only major source of nectar in or around the study site was bull thistle, *Cirsium vulgare* L., which was in bloom from mid-July through August. The locations of all flowering bull thistles and of all potential hosts within the study site were mapped. The site was divided into 23 plots (10 m × 20 m) to facilitate relocating marked hosts (Grossmueller 1984).

Adult *P. glaucus* were captured and marked from 1 May until 15 September each year of the study. Date, time of day, atmospheric conditions, age, sex, and behavior at time of capture were recorded. No butterflies were removed from the study site. Eggs were sampled four times per week during June through August 1980–82. The upper surface of all potential host leaves at heights of 5 m or less were examined for each host along a 310 m long, 2 m wide transect through the study area. Additional sampling of taller hosts was described in Grossmueller

TABLE 1. Behavior of *Papilio glaucus* adults immediately before capture within the study area.

Brood	Sex	n	Percentage		
			Puddling	Flying	Nectaring
1980-1	Male	43	83.7	9.3	7.0
	Female	4	—	25.0	75.0
1980-2	Male	35	—	11.4	88.6
	Female	42	—	7.1	92.9
1981-1	Male	21	85.7	9.5	4.8
	Female	1	—	—	100.0
1981-2	Male	3	100.0	—	—
	Female	6	—	16.7	83.3

and Lederhouse (1985), but relatively few eggs were laid above 3 m. Because 88.2% of the eggs found within the study area were on tuliptree (Grossmueller 1984), only the relation between the location of tuliptrees on which females oviposited and the location of flowering thistles was analyzed.

RESULTS

Although the study site was selected for its abundance of potential *P. glaucus* larval hosts, only 5 eggs (4.6% of the yearly total) were found in it during the first generation of 1980. Tiger swallowtails were frequently encountered in the area, and 47 were captured and marked. However, 43 (91.5%) of these were males, nearly all of which had been puddling along a swimming pool at the edge of the study area (Table 1). Puddling males form conspicuous groups on moist soil where they ingest sodium, amino acids, and possibly other nutrients (Arms et al. 1974, Berger & Lederhouse 1985).

During the second generation of 1980, 103 eggs were found within the study area. Tiger swallowtails were somewhat more abundant; 77 were captured and marked. The major differences were that only 45.5% of the captures were males, and 90.9% of all captures were nectaring on bull thistle (Table 1). A significantly greater proportion of males captured during the second generation were nectaring (χ^2, $P < 0.001$). However, the distribution of captured females did not differ by behavior between the two broods. The number of eggs discovered each generation was distributed differently from the total number of *P. glaucus* captures by brood (χ^2, 2×2 contingency table, $P < 0.001$) but did not differ from the distribution of female captures ($P > 0.50$).

The use of the study site during the first generation of 1981 was similar to that brood in 1980. Of the 22 *P. glaucus* that were captured, 95.5% were male, and 85.7% of the males had been puddling when captured. Only one egg was found during this brood. During June 1981, the State of New Jersey sprayed the entire Flanders area with a formulation of *Bacillus thuringiensis* to kill gypsy moth caterpillars. Tiger swallowtail caterpillars are easily killed by this insecticide (Grossmueller unpubl. results). Only nine captures were made during the second generation of 1981, and only six eggs were found. However, two-thirds of the captures were females, which was consistent with the previous year. The population level of tiger swallowtails continued to be very low throughout 1982. No eggs were found during the first generation of 1982, but nine were found at the site during the second generation.

Despite differences in overall population size, the pattern of study site use was similar from year to year. Although host trees were of similar availability and quality throughout oviposition periods, females were attracted to and oviposited within the study area mainly when thistles were in bloom. Males were attracted to the area to puddle during first broods, and to feed on nectar when thistles were blooming.

Since blooming thistles attracted females to the area during the second generation, the influence of thistle location on the particular host plants chosen for oviposition was investigated. Using the large sample from the second brood of 1980, numbers of eggs, flowering thistles, and tuliptree hosts were determined for each of the 23 plots. There was no relation between number of thistles and number of tuliptrees in the plots ($n = 23$, $r = 0.12$, $P > 0.50$). Surprisingly, number of eggs was not correlated significantly with number of host trees ($r = 0.11$, $P > 0.50$). Since eggs must be on a host tree, we excluded plots without hosts from analysis of the relation between eggs and thistles. The number of eggs was correlated significantly with number of thistles for plots with at least one host ($n = 17$, $r = 0.55$, $P < 0.05$).

A modified nearest-neighbor analysis was used to compare the mean distance of each egg ($n = 108$) to the nearest thistle. The nearest-neighbor value was 0.27, which indicates a significant clumped spatial association between eggs and thistles. The value for all host trees was 0.76, which indicates a random distribution.

DISCUSSION

In the area surrounding the study site, tiger swallowtails are probably not limited by availability of suitable larval hosts. In northern New Jersey, many previously cultivated fields have undergone succession as residential communities have largely replaced agriculture. Many of the host species are early colonizers of abandoned fields, resulting in young stands of tuliptree or white ash. Even at high population levels, *P. glaucus* uses only a small portion of available hosts. For example, in the second brood of 1980, there were 108 eggs oviposited on tuliptrees within the study area. However, there were approximately 50,800 tuliptree leaves that were suitable in condition and location for larval development (Grossmueller 1984). Thus, females can afford to ignore entire areas of host plants in favor of areas containing nectar sources.

In contrast, adult nutrition sources are more restricted. Male tiger swallowtails often form large aggregations at puddling sites (Arms et al. 1974). A puddling site was the prime focus of *P. glaucus* activity during the first broods at our study site. In a study of *P. glaucus* behavior in upstate New York, Berger (1986) found much higher frequencies of occurrence near nectar sources than at locations with abundant host plants but devoid of nectar plants. Our impression is that most of the naturalized nectar plants used during both generations in New Jersey tend to be clumped. Native hosts such as basswood (*Tilia americana* L.) and various briars (*Rubus* spp.) are similarly clumped. When larval hosts are widely distributed and adult resources are localized, female activity and oviposition are greatest near the adult resources (Murphy 1983, Murphy et al. 1984).

Tiger swallowtails are capable of considerable movement in a short time (Lederhouse 1982a). Movements in excess of 5 km between captures are not uncommon for marked males, with one detected displacement of over 2 km in 1 h (Lederhouse unpubl. results). Although females could move from host patches to nectar patches and back again, they appear not to move as much as males (Lederhouse 1982a). Since many nectar plant concentrations may be included in suitable ovipositional habitat, such movement may be unnecessary.

Oviposition in areas of increased male activity is often reduced due to male harassment (Shapiro 1970, Lederhouse 1982b). In *Euphydryas chalcedona*, courtship by nectar-feeding males may reduce the number of eggs laid in the immediate vicinity of nectar plants (Williams 1983). However, disturbed females move only short distances to resume oviposition, producing the overall relation of egg location to nectar plant location (Murphy et al. 1984). Whether this pattern is detected (Murphy et al. 1984) or not (Williams 1983) is a function of what scale is used. When harassment does occur, females may balance problems of interference against costs of extra flight to and away from nectar plants.

In our study, the number of males within the study area was similar for the two generations of 1980. Therefore, lack of females and eggs at the site during the first brood was probably not due to avoidance of males. Furthermore, the presence of abundant nectar plants during the second generation attracted females to the area. The difference in number of females within the study area between the two generations largely accounted for the difference in number of eggs discovered. During the second generation, proximity to a thistle or thistle patch increased the probability that a preferred host would have eggs on it.

Thus, nectar availability controls the local distribution of tiger swallowtail larvae in northern New Jersey.

Results from this study and others (Rausher 1979, Courtney 1982, Murphy 1983, Murphy et al. 1984) support the contention that the distribution of eggs in many butterfly species is a compromise between larval and adult needs. The relative importance of various components in this trade-off will determine the nature of the observed ovipositional pattern.

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