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FIELD OBSERVATIONS OF FOODPLANT OVERLAP AMONG SYMPATRIC *CATOCALA* FEEDING ON JUGLANDACEAE

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ABSTRACT. Field collections or observations of eggs, larvae and ovipositing females confirm that *Catocala epione* Drury, *habilis* Grote, *judith* Strecker, *obscura* Strecker, *residua* Grote, *retecta* Grote, and *palaeogama* Guenée feed on shagbark hickory, *Carya* (section Eucarya) *ovata* in Connecticut. *C. obscura* and probably *C. residua* prefer this species over other Eucarya while *C. palaeogama* seems to oviposit randomly on species of this section. No species of *Catocala* appears to prefer a species of Eucarya other than *C.* (*E.*) *ovata*. None of the Eucarya feeders were encountered on section Apocarya or *Juglans*. Since *C. ovata* accounts for well over half of all Juglandaceae in Connecticut, it would be the *de facto* primary foodplant of any *Catocala* species that oviposits randomly on Eucarya. The hypothesis that *Catocala* are extensively partitioning the available Eucarya by species is untenable. Individual trees are frequently used by several *Catocala* species, and there is little evidence of partitioning at that level except that *C. epione* appears to feed largely on small plants.

Catocala subnata Grote oviposits on *Carya* (section Apocarya) *cordiformis* and *Juglans cinerea*. *Catocala neogama* (J. E. Smith) and *C. piatrix* Grote probably feed largely or entirely on *Juglans* in Connecticut. Few comparable assemblages of oligophagous or monophagous congeneric Lepidoptera utilizing a single foodplant occur in the North Temperate Zone.

The moth genus *Catocala* is well known for its extreme sympatric diversity (see Sargent, 1976). In southern New England, three well sampled locations have produced from 35 to 40 species[1] each (Sargent, 1976), and I have taken 39 species in seven years within a kilometer of my home in Hamden, Connecticut, almost entirely at sugar bait. Most of the species are taken every year, and many are taken in large numbers. I estimate that 52 species of *Catocala* have been taken in Connecticut since about 1890. Forty-six of those are present now on a regular basis. At least one that is now common (*C. judith* Strecker) is absent from old area collections, while *C. robinsonii* Grote was established between about 1898 and 1964, but no longer occurs. *C. pretiosa* Lintner has also disappeared.

In addition to sympatry, *Catocala* have been suspected of extensive foodplant overlap. For example, fourteen species of current Connecticut *Catocala* are well known to use Juglandaceae as larval foodplants. Four additional Juglandaceae feeders have been taken in the state. However, the foodplant compilations of Sargent (1976) are based largely on rearings *ex ovis*, and it is not possible to determine precise natural foodplants. The situation with older references is much worse as specific plant names were almost never given. Thus, with two

[1] *C. "amica"* includes two species at all three localities.

species of *Juglans* and five of *Carya* [four Section Eucarya, one Apocarya (Fernald, 1950)] present widely in Connecticut, it seemed possible that fourteen *Catocala* species indeed might be partitioning the Juglandaceae by species to some extent. However, one species of hickory, *Carya ovata*, greatly outnumbers all other combined Juglandaceae in most portions of the state (see localities, below).

With the data presented below, I intend to document the *Catocala* fauna of *Carya ovata* and to provide some indication of the range of foodplant choices of these moths.

METHODS

A variety of methods have been used to document foodplant usage in the field. During the winter of 1978–1979 bark samples of five to ten shags were taken from seven mature *Carya ovata* and two mature *C. glabra* at Roxbury, Litchfield Co., Connecticut, as well as from two to five mature *C. ovata* each from four localities in New Haven County, for a total of 18 *C. ovata* samples, each containing visible *Catocala* eggs.

Bark samples were sleeved on *C. ovata* in April 1979, and larvae were changed to new sleeves as needed in June. A limited supply of sleevable branches necessitated pooling of some samples. A more serious complication was the excessive number of larvae produced. The two most rapidly growing species, *C. palaeogama* and *C. residua* severely depleted food supplies, and this may well have led to high mortality of other species. Table 1 gives the results of this method.

A second method was searching for larvae. On 30 June 1979 I

TABLE 1. *Catocala* reared from eggs collected during the winter of 1978–1979 in Litchfield (Roxbury) and New Haven (all others) Cos., Connecticut. Identifications were mostly from adults, but some were from larvae which were subsequently preserved. All eggs were sleeved on *Carya ovata*.

Locality and tree	*Catocala* produced			
	palaeogama	*residua*	*retecta*	*obscura*
Carya ovata				
Roxbury, tree B	6	3	1	0
C	21	13	0	0
D	?	2	0	0
E	13	6	0	0
Roxbury, trees A, F, G	35	14	4	2
Lake Gaillard, 2 trees	20	0	0	0
New Haven-Hamden, 9 trees	7	0	2	0
Carya glabra				
Roxbury, 2 trees	6	0	0	0

TABLE 2. Collections of *Catocala* larvae in Connecticut and southern New Jersey. Designations under N refer to number of trees, except letters specify an individual tree. A range of dates indicates two or more checks of that tree. Larvae were reared until large enough to identify.

Tree species	N	Approx. diameter	Locality	Date	Catocala
J. nigra	>15	8–20 cm	Batsto, N.J.	10 July '73	*maestosa* (≥1), *neogama* (≥2)
J. nigra	2	8 cm	Batsto, N.J.	1 June '80	*neogama* (1, mature)
J. nigra	3	10–15 cm	New Haven, Ct.	1–15 June '78	*neogama* (>10)
J. nigra	3	10–15 cm	New Haven, Ct.	1–8 June '79	*neogama* (5–10), *piatrix* (1)
J. nigra	3	10–15 cm	New Haven, Ct.	May–June '80	*neogama* (21)
J. cinerea	2	20 cm	New Haven, Ct.	1–15 June '78	*neogama* (>5)
J. cinerea	2	20 cm	New Haven, Ct.	1–8 June '79	*neogama* (5)
J. cinerea	1	20 cm	New Haven, Ct.	May–June '80	*neogama* (3)
J. cinerea	4	10–20 cm	N. Ashford, Ct.	9 June '79	*neogama* (1)
J. cinerea	4	10–20 cm	N. Ashford, Ct.	30 June '79	*neogama* (1)
C. pallida	3	8 cm	Greenbank, N.J.	1 June '80	*vidua* (3)
C. tomentosa	5	<6 cm	Elmer, N.J.	20 May '79	*epione* (3)
C. ovalis	3	10 cm	West Rock, Ct.	20–30* May '80	*palaeogama* (1)
C. glabra	1	8 cm	West Rock, Ct.	20–30* May '80	none
C. ovata	A	8 cm	West Rock, Ct.	25 May '80	*palaeogama* (2), *epione* (1), *retecta* (2)
	B	8 cm	West Rock, Ct.	30 May '80	*palaeogama* (2)
	C	10 cm	West Rock, Ct.	26 May '80	*palaeogama* (9), *epione* (5), *retecta* (1)
	D	8 cm	West Rock, Ct.	26 May '80	*palaeogama* (1), *residua* (2)
C. ovata	E	15 cm	West Rock, Ct.	26 May '80	*residua* (2)
C. ovata	F	8 cm	West Rock, Ct.	20–30* May '80	none
C. ovata	>15	>25 cm	N. Ashford, Ct.	30 June '79	*habilis* (6), *residua* (1)
C. ovata	1	8 cm	New Haven, Ct.	1–10 June* '80	*habilis* (3)

* Checked two or more times during this time period.

TABLE 3. Summary of *Catocala* ovipositions and number of trees (*Carya, Juglans*) checked in New Haven County, Connecticut (during 1979 and 1980). Numbers in parentheses refer to same night repeats of previously checked trees (see text).

Tree species	N observations	*Catocala* species						
		neogama	*subnata*	*palaeogama*	*residua*	*obscura*	*judith*	*retecta*
C. ovata	179 (12)	0	0	42	15	22	1	3
C. glabra	35 (3)	0	0	4	1	0	0	0
C. ovalis	5	0	0	1	0	0	0	0
C. tomentosa	13	0	0	3	0	0	0	0
C. cordiformis	36 (19)	0	5	0	0	0	0	0
J. cinerea	19 (10)	1	1	0	0	0	0	0

searched for larvae under shags of mature *C. ovata* near North Ashford, Connecticut. No other *Carya* species was encountered, but four *Juglans cinerea* were checked. By this date most larvae had probably pupated. During May 1980 young larvae were collected from foliage and branches of small hickories on West Rock, New Haven, Connecticut. Branches were beaten after being inspected visually. Most larvae were found by inspection. Larvae were also taken on *Juglans* in various years on the trunk, at the base of large limbs, or in debris at the base of the trees. None were found on small branches or leaves. Numbers of trees searched and larvae found are given in Table 2.

A third method was searching for ovipositing females at night when they are easily found on tree trunks. Initial attempts at this method in 1979 were somewhat haphazard, but systematic searches were implemented that year and in 1980 with exact numbers of trees searched being recorded (Table 3).

Tree trunks were searched after dark with lights, and when possible, moths were captured. Only females seen probing bark crevices with the tips of their abdomens were recorded as ovipositing. Interestingly, startled females sometimes returned to such activity almost immediately. Very few females were encountered that were not clearly ovipositing. The most effective procedure was to have one person, armed with a net and cyanide jar, search using a headlamp, while a second person would operate a more powerful hand-held lantern and record data.

Some trees were checked more than once as indicated in Table 3. Such checks were always more than forty-five minutes apart, and moths were removed each time; therefore, I treat these as independent observations. All Juglandaceae over about 5 cm in diameter that were encountered were checked.

Localities

All localities at which searches for ovipositing females were conducted are in New Haven County, Connecticut. The majority of observations were on Nelson Rd., Southbury, or on West Rock Ridge, New Haven. Other observations were from Brooksvale Park, Hamden and various areas in Cheshire and Wallingford. Except on West Rock, all trees were mature, almost always with trunk diameters of 25 cm or more. Some were greater than 70 cm in diameter. Most of the trees were at the edges of extensive mixed mesic forests.

West Rock Ridge is a hotter and drier habitat than the others with thin acid soils overlying trap rock. The hickories there are stunted, though numerous. Very few have diameters of 20 cm or greater. The canopy is more open than at the other forested sites. This is the only one of the localities where *C. ovata* accounted for less than half of all Juglandaceae searched, and the only one where *Carya ovalis* was seen.

At Brooksvale Park, Hamden the area checked contained 13 *C. ovata*, 1 *C. glabra*, 2 *C. tomentosa* and 1 *J. cinerea*. The Southbury area contained 36 *C. ovata*, 9 *C. glabra*, 6 *C. cordiformis* and 3 *J. cinerea*. At West Rock 22 *C. ovata*, 16 *C. glabra*, 5 *C. ovalis*, 6 *C. tomentosa* and 1 *J. cinerea* were checked. The Wallingford area contained 10 *C. ovata*, 1 *C. glabra*, 1 *C. tomentosa*, 4 *J. cinerea*, and the Cheshire locality had 8 *C. ovata* and 1 *J. cinerea*. Most of these areas were checked on more than one occasion, and some trees were sometimes overlooked.

The few larval data from New Jersey are from the vicinity of villages in the Pine Barrens region, ca. 200 kilometers southwest of the Connecticut sample areas.

RESULTS

Egg and larval samples. These data (Tables 1 and 2) permit several conclusions: 1) at least *Catocala epione, habilis, obscura, residua, retecta* and *palaeogama* utilize *Carya ovata* as an important foodplant in Connecticut; 2) *C. neogama* is restricted, or nearly so, to *Juglans* in this region; 3) those species regularly utilizing *Carya* were not encountered on *Juglans*; 4) little can be deduced regarding utilization of other *Carya* spp., but *C. palaeogama* at least uses species other than *C. ovata* in Connecticut and *C. epione* does so in New Jersey.

It was not uncommon for several species to occur together on individual trees. *C. epione* seems to utilize primarily small plants (based on observations herein, and those of H. D. Baggett, L. F. Gall, T. D. Sargent, all pers. comm.), but the other *Carya* feeders must often all occur together.

One unsolved enigma is the absence of *C. habilis*, a common species, from oviposition observations (below) and bark samples. L. F. Gall (pers. comm.) has also failed to record it. Perhaps it oviposits very late at night or high in the trees. Larvae are common on *Carya ovata* (Table 2; L. F. Gall, pers. comm.).

Analysis of oviposition data. The data in Tables 2 and 3 convincingly demonstrate that *C. palaeogama, C. residua, C. obscura* and *C. retecta* regularly utilize *Carya ovata* for oviposition. *C. judith* is also added to the list of *C. ovata* feeders.

Chi-square goodness of fit tests were performed with oviposition data for those *Catocala* species for which ten or more observations are available. These analyses show that oviposition is non-random among all Juglandaceae for *C. palaeogama* ($P < .001$), *residua* ($P < .01$), and *C. obscura* ($P < .001$). *C. palaeogama* apparently oviposits randomly on any Eucarya ($P > .20$), while *C. obscura* prefers *C. ovata* over the other (pooled) Eucarya ($P < .05$). I suspect that *C. residua* also prefers *C. ovata* over other Eucarya in this region, but current data do not demonstrate such a preference ($P > .10$), probably due to the small sample size. The preferences of *C. palaeogama* ($P < .001$) and *C. obscura* ($P < .05$) for Eucarya over Apocarya and *Juglans* combined are significant.

Data for *C. subnata* are not adequate for analysis, but it is presumably limited to Apocarya and possibly *Juglans*. *Juglans cinerea* is the only previously reported host (Sargent, 1976). In 1981 L. F. Gall and I attempted to rear the progeny of three different female *C. subnata*. Hatchlings accepted *Carya* (Apocarya) *cordiformis*, and adults were obtained using this plant. *C.* (*A.*) *illinoiensis* was also readily accepted, but the plants available were too small to allow for an attempt at rearing larvae on this species. In no-choice situations, some larvae would accept both species of *Juglans*, but no larvae matured in sleeves on these. When cuttings were used, no larvae completed the first instar. My larvae would not accept any species of Eucarya. In 1981 I observed two more *C. subnata* ovipositing on *C. cordiformis* and L. F. Gall also observed several. Aside from *C. subnata*, no species of Connecticut *Catocala* seems to prefer a species of *Carya* other than *C. ovata*.

DISCUSSION

The above observations document that not less than seven species of *Catocala* utilize *Carya ovata* in Connecticut. These are *C. epione, C. habilis, C. judith, C. obscura, C. residua, C. retecta* and *C. palaeogama*. I have also reared adults of all of these *ex ovis* on *C. ovata*. *Catocala serena* Edwards adults rest on this tree in Connecticut and

have been observed ovipositing on it in Michigan (Nielsen, 1978). Sargent (1976) and myself have reared *C. dejecta* Strecker on *Carya ovata*, and in some of the moth's localities other hickories are nearly absent. *Juglans cinerea* is also an acceptable foodplant for at least the first three instars (pers. obs.). *C. dejecta* is very rare in New Haven County where oviposition observations were made. Two other *Carya* feeders, *C. vidua* (J. E. Smith) and *C. flebilis* Grote, occur in Connecticut at present. Their local foodplants are unknown. Thus, it is quite possible that 11 species of *Catocala* use *Carya ovata* in Connecticut and, as discussed previously, some of these species prefer this plant. However, even random oviposition on any Eucarya individual would result in *C. ovata* being *de facto* the principal foodplant in most of the state (see localities above). Thus, the hypothesis that these *Catocala* extensively partition the Eucarya by species is untenable.

There is at present no evidence that they are extensively partitioning *C. ovata* by individual trees, except for *C. epione*, although more data are desirable. The four trees on which multiple (>2) ovipositions were observed always had more than one species present. At Southbury on 2 September 1980 one tree had three *C. palaeogama*, one *C. judith* and one *C. obscura* ovipositing on it, while an adjacent tree had two *C. palaeogama*, two *C. obscura* and one *C. retecta*. Observations of *C. residua* and *C. palaeogama* ovipositing together have been frequent, and at least three species have been obtained from some larval collections and bark samples (Tables 1, 2). Doubtless, had observations of individual trees been carried out over the entire *Catocala* season at Southbury (the early *C. judith* was largely missed), many trees would have had recorded ovipositions by five or more species.

Although the observations reported here show that several species of *Catocala* larvae frequently occur together on *Carya ovata*, there are insufficient data to determine whether other forms of niche splitting are used. With seven or more species potentially occurring on the same tree and with all of these feeding exclusively on foliage and most having similar egg hatching dates (manuscript in prep.), such niche splitting would have to be rather fine. Sargent (1976) has pointed out that some similar species grow at different rates as larvae, and I have similar data (unpublished). Eucarya foliage appears rather synchronously in early spring, and additional foliation after early May is rare. Therefore, late maturing species (e.g. *C. habilis, obscura*) might compete with the early species if food became limiting. Effective avoidance of competition for food, if such occurs, would probably have to involve utilization of different portions of the tree. As I note

elsewhere (Schweitzer, 1982) there is some evidence for differences in resting behaviors (see also Sargent, 1976).

Casual observation suggests that *Catocala* larvae are held at relatively low numbers (relative to leaf availability) by some as yet unknown factor, probably predators and/or parasitoids. One can consult most ecology texts (e.g. Ricklefs, 1973, pp. 510, 522–523) and find that the "principle of competitive exclusion" applies only with regard to limiting resources. Sargent (1976, 1977) suggests foodplant availability may not be an important factor in *Catocala* evolution. The data in this paper support that contention at least to the extent that competition has not forced the Eucarya feeders to specialize on different species or to avoid frequent co-occurrence on individual trees.

Nevertheless, I am not aware of any well documented comparable sympatric assemblages of congeneric (or even of closely allied genera), largely synchronic, monophagous or oligophagous macro-Lepidoptera on a single foodplant species in the North Temperate Zone. However, at least eight species of *Zale* (Noctuidae : Catocalinae) are sharing two species of pines in much of southern New Jersey. There may well be a comparable assemblage of *Catocala* on Apocarya in the southeastern United States. Comparable assemblages of polyphagous congeners may well occur on some trees. *Lithophane* would be a likely candidate genus, with *Quercus* spp. and *Betula* spp. being likely hosts.

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