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Evolutionary Ecology of Sympatric *Catocala* Moths (Lepidoptera: Noctuidae)
I. Experiments on Larval Foodplant Specificity

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Abstract. Larval foodplant specificities are presented for 31 species of Nearctic *Catocala* moths whose larvae feed on trees in the plant families Juglandaceae, Fagaceae, and Salicaceae. Arena tests determined preferences when larvae could choose on which plants to feed, and field rearing experiments determined survival and growth rates in no-choice situations. In arenas, larvae of the Juglandaceae, Fagaceae and Salicaceae feeders ate only foods from their own plant family. Taxonomic divisions within each plant family defined further boundaries to foodplant acceptability. Thus, among the Juglandaceae feeders, 2 species ate walnuts (*Juglans*), 2 ate pecans (section *§Apocarya* of *Carya*), and the remaining 14 ate hickories *sensu strictu* (section *§Eucarya* of *Carya*). All the *Carya* section *§Eucarya* feeders preferred shagbark hickory, *Carya ovata*, and 6 of the 14 species specialized on it. Among the Salicaceae feeders, 1 species ate willows (*Salix*) and 6 ate poplars (*Populus*). Foodplant preferences were not crisply defined in the 5 Fagaceae feeders. Larvae usually selected the favored foodplant as a resting site. Preferences broadened as larvae matured, and the Juglandaceae and Salicaceae feeders preferred young leaves over old leaves. In nearly all cases, survival was highest and growth rates most rapid in the field on the foodplants preferred in arena tests.

INTRODUCTION

The Holarctic noctuid moth genus *Catocala* Schrank contains slightly over 200 species, distributed equally across the Nearctic and Palearctic temperate zones. The genus is most atypical for noctuids in showing great species diversity coupled with highly restricted larval foodplant use — larvae of individual *Catocala* species eat only one or several closely related plant genera, and the recorded foodplant breadth of the genus spans but nine dicotyledonous plant families. Even this liberally estimates foodplant breadth among *Catocala*, as 137 of the 161 species whose life histories are currently known feed only on plants in the families Juglandaceae, Fagaceae, Salicaceae, or Rosaceae. There are large arrays of sympatric, synchronic, closely related species feeding in each of these four plant families, and hence the *Catocala* are well suited for studying the phylogenetic history of foodplant exploitation (note that the reported high species diversity is not in question, since survey collecting for the moths and the species-level taxonomy of the genus have been amply studied: see Hampson, 1912; Barnes & McDunnough, 1918; Forbes, 1954; Sargent, 1976, 1977).

This is the first of three baseline data papers addressing the foodplant-linked ecologies of *Catocala* moths, and covers experiments on larval foodplant specificity of 31 Nearctic *Catocala* species whose larvae feed on Juglandaceae, Fagaceae, Salicaceae, and Rosaceae. The following two articles in this journal issue examine distributions of wild larvae among their foodplants and the oviposition preferences of the female moths; a related paper has covered larval feeding habits within individual foodplant trees (Gall, 1987). The data in these articles help circumscribe the limits of potential foodplant acceptability for the major groups of *Catocala*, and form the backdrop against which questions about foodplant use in ecological and evolutionary time by the same *Catocala* species can be appropriately framed.

Because analysis of the phylogenetic history of *Catocala* foodplant use is made easier by simultaneously comparing results from all these studies, I have extracted parts of what would traditionally comprise the Discussion sections from the three articles in this series, and will be integrating these into a comparative treatise on the subject. Toward that same goal, a separate series of concurrent articles is addressing taxonomic and nomenclatural issues in the genus (see Gall & Hawks, 1990; our taxonomic monograph of all the Nearctic *Catocala* species is also in the late stages of preparation, to be published in a forthcoming "Moths of North America North of Mexico" fascicle).

MATERIALS AND METHODS

A Biological Profile of *Catocala*

All *Catocala* are univoltine, with adults flying in mid to late summer and hibernal diapause as eggs. The adults have cryptic forewings which conceal boldly patterned hindwings; the interactions of the adults with avian predators have been the topic of many previous studies by Sargent and his coworkers (e.g., Sargent, 1976, 1977; Schlenoff, 1985). Eggs are laid singly or in clumps under exfoliating bark, or in crevices on tree trunks and branches. In northeastern North America, most species commence feeding as larvae during May. Egg hatch can be synchronous or highly staggered, but is constant within any given *Catocala* species, the degree of staggering being closely linked to the foliating schedules of the different larval foodplants (Schweitzer, 1982; Schweitzer and Gall, in preparation).

The larvae are semiloopers, usually with highly cryptic morphologies that match the twigs and bark which serve as resting sites during the daytime. Larvae generally feed at night. Prior to this research, the wild larvae had been presumed to be mildly oligophagous among related plant genera within single plant families. Foodplant breakdowns for the 108 Nearctic species which I currently plan to recognize in the forthcoming taxonomic monograph are as follows: Fagacaeae, 26; Juglandaceae, 25; Salicaceae, 23; Rosaceae, 15; Leguminoseae, 7; Ericaceae, 4; Myricaceae, 4; Tiliaceae, 1; not yet recorded, 3 (which with virtually no question will prove to be 1 Fagaceae, 1 Juglandaceae, and 1 Salicaceae).

Foodplant Arena Protocol

The technique employed here was the "foodplant arena," in which both potentially suitable and presumably unsuitable foods are offered to larvae, which then must make a choice for feeding (see Gall, 1987). Small branches from young (2-5 cm dbh) foodplant trees are collected late each afternoon, ca. 1-3 weeks after bud burst in spring. Near dusk (the time at which *Catocala* larvae become active and begin feeding), pieces of leaves of different plant species are clipped from their petioles and taped by one edge to a paper strip (food choice items being ordered at random along the strip), and the strip coiled and placed flush against the wall of a small glass jar. Several young larvae are then introduced to the bottom of the jar (variation in foodplant preference among individual larvae of the same *Catocala* species is not pronounced, and the total amount of leaf material in each choice item is more than the maximum that the several larvae can potentially consume; Gall, 1987). Strips are removed the following morning, and larval resting locations and the amount of different food items consumed are used to calculate preference.

Two types of control foods were offered in each arena. Type I controls were plant species from a *Catocala* foodplant group other than the group being examined: red/scrub oak or lombardy poplar for the Juglandaceae-feeding *Catocala*; shagbark/pignut hickory or lombardy poplar for the Fagaceae-feeding *Catocala*; and red/scrub oak or shagbark/pignut hickory for the Salicaceae-feeding *Catocala*. Type II controls were "entirely inedible" plant species — ones not closely related to present foodplants of any *Catocala*. The Type II control in arenas was typically plantain (*Plantago major* L.).

For each arena test, the area of food consumed per choice item was expressed as a percentage of the total area consumed, preserving relative between-choice differences while assigning unit weight to each arena test. For first instars, the amounts eaten were measured using a dissecting microscope fitted with an ocular grid. For partially grown larvae, a clear plastic ruled sheet was used.

Intervening Factors in Foodplant Arenas

Problems typically confronting foodplant preference studies include, among others: (1) the geometry of how to present food choices; (2) how to minimize the effects of geo- and phototaxis; and (3) how to insure that larvae are aware of and/or have "tested" all available food items as they are beginning to feed. For many lepidopteran larvae, these present serious methodological obstacles, and, in general, the more polyphagous and/or sedentary a species one tests, the more significant these obstacles are likely to be. A brief summary of these variables as they relate to *Catocala* is relevant.

In all instars, *Catocala* larvae are extremely active — within moments of introducing them to a foodplant arena, they typically traverse the entire perimeter of the jar. When placed in arenas during the daytime, the larvae eventually settle down after a few minutes, on or near a food item, and rest. When introduced at dusk, this initial period of rapid movement also includes mandibular contact and/or momentary chewing on leaves encountered. Again, after a period of usually less than five minutes, the larvae have passed several times around the arena, and start to settle and feed (rather than rest). The distribution of larvae in arenas remains largely stable from that settling period on through the next morning, when arenas are disassembled.

Most *Catocala* larvae are positively phototactic to some degree. I have always found mature larvae to be somewhat less active during the day than first instars (see Wojtusiak, 1979, for diel locomotor actograms of *Catocala fraxini* L. larvae of varying ages). Starting arena tests at dusk or night, in dark rooms, largely eliminated problems with phototaxis (all laboratory preference tests were con ducted under uncontrolled, but essentially natural photoperiod). Note that *Catocala* larvae become active and commence feeding at true dusk even in fully lit rooms with no windows.

In initial trials, the geometry of how foods were presented had no discernible effect on larval foodplant preference. To test this, leaves were presented hanging, as above, or flat on the bottom of the arena. Foodplant preferences were the same in three such paired tests (n=4 arenas per test) for the Salicaceae-feeding *Catocala cara* Guenee, and the Juglandaceae-feeding *Catocala neogama* Smith and *Catocala retecta* Grote ($p>.25$ for each by ANOVA). Foods were presented hanging in all subsequent trials.

Field Rearing Procedures

To assay survival and development rates on foodplants in the field, I confined larvae to large rearing exclosures ("sleeves") on branches of different foodplants. Sleeves were made of either lightweight muslin or fine nylon netting, and varied in size depending upon the number and age of larvae confined in them. Equal numbers of newly hatched, unfed larvae were placed in sleeves on suitable foodplants, the genetic background of larvae for each rearing experiment being controlled by splitting the progeny of a single female among the sleeves. Environmental differences were controlled, insofar as possible, by selecting sleeving sites at which all foodplants for an experiment were growing in immediate proximity. Larval instar was used as the growth index, and was assayed by using both head capsule width and the instar-specific morphological patterns of *Catocala* larvae. Each instar was further subdivided into an early and late stage, which was assayed using body size.

The primary research site for larval rearing was West Rock Park, three miles west of the Yale University campus. This is an open-canopied, xeric to mesic igneous trap-rock ridgetop habitat (Gall, 1987). West Rock is near the northern limit for many elements of more southerly biota and in addition contains the usual fauna and flora of southern New England broadleaf forests. The canopy is dominated by oak, hickory, and ash, with a sparse understory of rosaceous, ericaceous, and other shrubs.

It should be noted that when sleeve rearings were initiated in 1980, I began measuring development rate as the number of days elapsed from first sleeving until pupation. In 1980, and especially 1981, the essentially total defoliation of the West Rock study sites by the introduced pest gypsy moth (*Lymantria dispar* L.) terminated most sleeve experiments before the *Catocala* larvae could successfully pupate, and re-sleeving was impossible. Hence, the measure of development rate was soon switched to larval instar at the time of sleeve census.

Catocala and Foodplant Species Studied

Arena and rearing tests were carried out for 19 Juglandaceae-feeding *Catocala* species: *angusi* Guenee, *dejecta* Strecker, *flebilis* Grote, *epione* Drury, *habilis* Grote, *insolabilis* Guenee, *judith* Strecker, *lacrymosa* Guenee, *luctuosa* Hulst, *nebulosa* Edwards, *neogama*, *obscura* Strecker, *palaeogama* Guenee, *piatrix* Grote, *residua* Strecker, *retecta* Grote, *subnata* Grote, *ulalume* Strecker, and *vidua* Smith. Hickories (*Carya* Nutt.) and walnuts (*Juglans* L.) are the foodplants of these *Catocala*. Because the generic abbreviation ("*C.*") is the same for both *Catocala* and *Carya*, by convention I drop the abbreviation when referring to the moths, and retain it for the foodplants. Among the four hickories offered in arena tests were three *Carya* from section *§Eucarya* DC.: shagbark hickory, *Carya ovata* (Mill.) K. Koch; pignut hickory, *Carya glabra* (Mill.) Sweet; and mockernut hickory, *Carya tomentosa* Nutt. The fourth was a *Carya* from section *§Apocarya* DC.: bitternut hickory, *Carya cordiformis* (Wang.) K. Koch. Two species of *Juglans* were offered to larvae in arena tests: black walnut, *Juglans nigra* L.; and butternut, *J. cinerea* L.

Arena tests were also conducted with 12 other *Catocala* species. Included were 7 Salicaceae feeders: *amatrix* Hubner, *cara*, *concumbens* Walker, *meskei* Grote, *parta* Guenee, *relicta* Walker, and *unijuga* Walker. Food choices offered to these species included: black willow, *Salix nigra* Marsh.; pussy willow, *S. discolor* Muhl.; cottonwood, *Populus deltoides* Bartr.; quaking aspen, *P. tremuloides* Michx.; bigtooth aspen, *P. grandidentata* Michx.; and lombardy poplar, *P. nigra* var. *italica* Muench. Preferences were also determined for 5 oak-feeding *Catocala*: *amica* Hubner, *coccinata* Grote, *ilia* Cramer, *lineella* Grote, and *micronympha* Guenee. Foods offered in the red oak subgenus (*Erythrobalanus* Spach) included: red oak, *Quercus borealis* Michx.; scarlet oak, *Q. coccinea* Muench.; and scrub oak, *Q. ilicifolia* Wangenh. Foods offered in the white oak subgenus (*Lepidobalanus* Endl.) included: white oak, *Q. alba* L.; chestnut oak, *Q. prinus* L.; and post oak, *Q. stellata* Wangenh.

Statistical Procedures

Data analysis was done on either an IBM 3083 mainframe or an IBM/PS2 Model 70 microcomputer, using SAS Version 5.16 and SAS/PC Version 6.03, respectively (SAS Institute Inc., 1985a, 1985b). The GLM procedure was used for analysis of variance, with a posteriori comparisons of means done by Tukey's HSD (results using Tukey tests were comparable statistically to those from Bonferroni and Duncan multiple-range tests, and each returned the same biological conclusions). Percentage data were arcsine square root transformed prior to analysis. Most nonparametric analyses used the NPAR1WAY and FREQ procedures, but in instances where expected cell sizes were five or less, and the number of cells was also small, Fisher's exact tests and/or exact binomial probabilities were calculated. For these, I used my own analysis of frequency routines programmed in REXX and FORTRAN following the methods of Sokal & Rohlf (1981).

RESULTS

Arena Tests: First Instars

1. GENERAL PATTERNS

Reactions of larvae to Type I and Type II controls were quite different. That the larvae of all *Catocala* species readily discriminated between potentially suitable and unsuitable foods is shown by the minuscule amounts of Type II controls eaten; similarly, that larvae identified their own foodplant group correctly is shown by the low amounts of Type I controls eaten (Figures 1-3).

Table 1 shows the (Spearman rank) correlations between amounts of food eaten and larval resting sites in arenas. While these resting sites tended to be on the same leaves at which larval feeding occurred, it was apparent from the outset of this research that resting site was an insensitive index of preference. The correlations for the Juglandaceae

Table 1. Mean correlation between resting positions on foods in arenas and amounts of same foods eaten by first instar Catocala larvae. R = Spearman rank correlation coefficient. N = total number of arenas. Correlations calculated for each arena, then pooled by species.

Species	r	n	Species	r	n
habilis	0.77	4	amatrix	0.95	4
judith	0.75	8	cara	0.72	5
obscura	0.83	9	concumbens	0.55	6
residua	0.83	8	meskei	0.54	3
			parta	0.56	8
epione	0.65	11	relicta	0.65	14
palaeogama	0.70	11	unijuga	0.65	5
retecta	0.64	10			
vidua	0.64	7	amica	0.59	3
			coccinata	0.86	8
subnata	0.96	11	ilia	0.42	6
			lineella	0.76	4
neogama	0.70	4	micronympha	0.62	5

feeders are greater than those for either the Salicaceae or Fagaceae feeders (p<.01 in each case, by Mann-Whitney U-tests using data from individual arenas). The low correlations for several oak feeders are in part due to small sample sizes, which are in turn due to the habits of those larvae to rest away from the food choices (on arena walls, and so forth). This clearly reflects real biological differences in preferred natural resting sites (e.g., off the trees, as in *ilia*). The lower correlations for the Salicaceae feeders are not traceable to lower sample sizes as with the oak feeders. Again, some of these Salicaceae feeders doubtless tend to rest off their foodplants, but their native larval biologies remain less thoroughly investigated.

2. JUGLANDACEAE-FEEDING *CATOCALA*

Figure 1 shows foodplant preferences for 18 Juglandaceae-feeding *Catocala* species (data are from a total of 134 arenas, involving larval broods from 45 different female moths).

Only *neogama* and *piatrix* preferred *Juglans* over all other foods, each eating black walnut (*J. nigra*) and butternut (J. *cinerea*) nearly equally. Unfed, newly hatched larvae of five *neogama* broods refused to feed on either *Carya ovata* or *Carya cordiformis*, even when no other food was offered. Although *piatrix* larvae ate more *Juglans* than *Carya*, they clearly tolerated hickories better than did larvae of *neogama*.

Larvae of *subnata* and *nebulosa* preferred bitternut hickory, *Carya cordiformis*. Their distantly second-ranking food choice next to *C. cordiformis* was *Juglans nigra*. Unfed first instars of three *subnata* and two *nebulosa* broods refused to eat any *Carya*, and barely nibbled on *Juglans nigra* when only it was offered as food; larvae of each species also

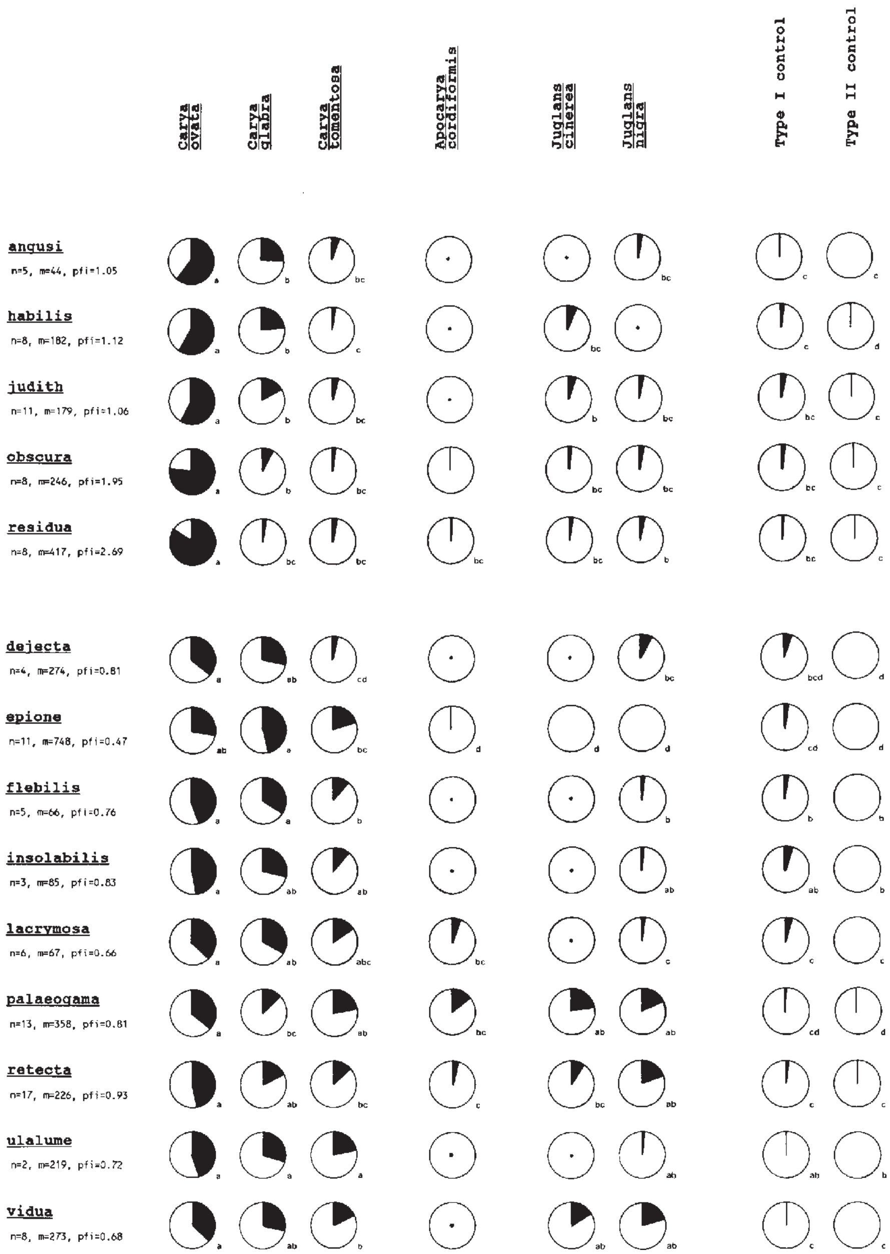
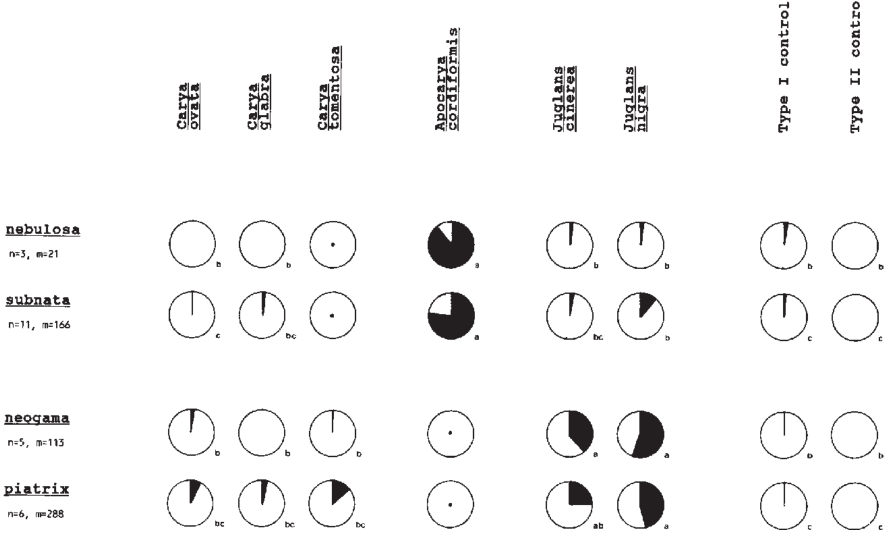


Fig. 1. Foodplant arena results with previously unfed first instar larvae of Juglandaceae-feeding Catocala. Areas of pies proportional to amounts (percent) of food eaten; dot in center = food not offered. Pies having the same subscripted letters are not significantly different at the 0.05 level (Tukey HSD tests). N = total number of arena tests. M = mean amount of food eaten per arena in square mm. PFI = preferred foodplant index, here measuring preference of C. ovata relative to other Carya foodplants (see text for elaboration; the greater the PFI the greater the preference).

Figure 1 continued



accepted pecan, *Carya illinoiensis* (Wang.) K. Koch of section *§Apocarya*, but this foodplant was not used in arenas due to lack of material (pecan is not native to Connecticut).

The other 14 *Catocala* species preferred *Carya* to other foodplant genera (see below for responses to *Carya cordiformis*, which was usually omitted as a food choice in their arenas). All but *epione* consumed more *C. ovata* than any other *Carya*, and larvae of 5 of the 14 species — *angusi*, *habilis*, *judith*, *obscura*, and *residua* — showed quite pronounced preferences for *C. ovata*. This penchant for *C. ovata* is quantified in Figure 1 by a "preferred foodplant index" (PFI), which is here defined as the amount of *C. ovata* consumed divided by the sum of all *Carya* consumed. The PFI is higher for the set of five species including *angusi*, *habilis*, *judith*, *obscura*, and *residua* than for the remaining nine *Carya* feeders (u=0, n1=5, n2=9, p<.05 by Mann-Whitney U-test).

It is notable that only *epione* did not eat substantially more *C. ovata* than other *Carya*. In contrast to the other 13 *Carya* feeders examined (especially the taxa with larger numbers of arena tests), *epione* did not consume *Juglans* as its second-ranking food item next to *Carya*. In fact, *epione* was the only Juglandaceae feeder that ate significantly less *Juglans* than it did its Type I *Quercus*/*Populus* controls (u=12, n1=8, n2=8, p<.05 by Mann-Whitney U-test; the amounts of control food eaten were nevertheless meager).

Among the *Carya §Eucarya*-feeding *Catocala*, the preference for *C. ovata* is pronounced, and it is thus germane to ask: what preferences do these larvae exhibit if *C. ovata* is unavailable in arenas? Several additional arenas were run in which *Carya cordiformis* replaced *C.*

ovata. In such arenas, test larvae of *judith*, *palaeogama*, and *residua* each increased their consumption of *C. tomentosa* and *Juglans*, while refusing to eat *Carya cordiformis*. Indeed, in other no-choice rearing situations, unfed first instars of all North American *Carya §Eucarya*-preferring *Catocala* refuse to feed significantly on *Carya §Apocarya* when only it is offered (my unpublished rearing and field data; see also below under sleeve results). Larvae of *neogama* also refused to feed on *Carya cordiformis* (see above); larvae of two *piatrix* broods accepted this plant, although they did not feed as readily as when *Juglans* was offered.

Larvae of *luctuosa* (one arena test only) preferred *C. ovata* two to one over all other foods, but the larvae ate much less leaf material *in toto* than did larvae of all the other *Catocala* species tested. Moreover, *luctuosa* is the only *Carya §Eucarya*-preferring Juglandaceae-feeding *Catocala* that showed poor (40-60 percent) survival as larvae when reared on *C. ovata* indoors in the lab (the survival rate I obtain when rearing all other *Carya* feeders indoors is never less than 75-80 percent). Initial field work with *luctuosa* in Tennessee in 1987, and its geographic distribution in the Nearctic indicate that this *Catocala* likely specializes on shellbark hickory, *Carya laciniosa* (Michx.) Loud of section *§Eucarya*.

Test larvae of three of the Juglandaceae feeders were offspring from a single mother: *dejecta*, *nebulosa*, and *ulalume*. Significant ($p<.05$ by ANOVA) between-brood differences in preference existed for five of the remaining species: *epione*, *habilis*, *obscura*, *palaeogama*, and *retecta*. The significances for *habilis* and *obscura* were traceable to one evening of tests in 1980, in which the arenas became waterlogged (the larvae rested on and ate mostly *Juglans*). The between-brood differences were more robust for *epione*, *palaeogama*, and *retecta*. These three species also show the widest breadth in foodplant preference as both young and mature larvae (see below). However, no consistent patterns emerged when the known oviposition histories of the brood mothers were compared to the foodplant preferences of their larvae (see Gall, 1991b; the principal finding being that *C. ovata* best supports larval growth, regardless of female oviposition history).

3. SALICACEAE-FEEDING *CATOCALA*

Figure 2 shows foodplant preferences for the 7 Salicaceae-feeding *Catocala* (data are from a total of 47 arena tests, involving offspring of 12 different females).

Only *cara* preferred willows over poplars. Larvae of *cara* did not discriminate among the willows offered. The introduced lombardy poplar, *Populus nigra* var. *italica*, was the first-ranked food item for *amatrix*, *meskei*, and *unijuga*, but for only *amatrix* was this significantly so (I regularly collect larvae of *amatrix* on this plant in the city of New Haven). Larvae of *concumbens*, *parta*, and *relicta* all ate *Populus deltoides* as their first-ranked food, with this pattern being significant for *concumbens* and *relicta*. All Salicaceae-feeding species except for *meskei*

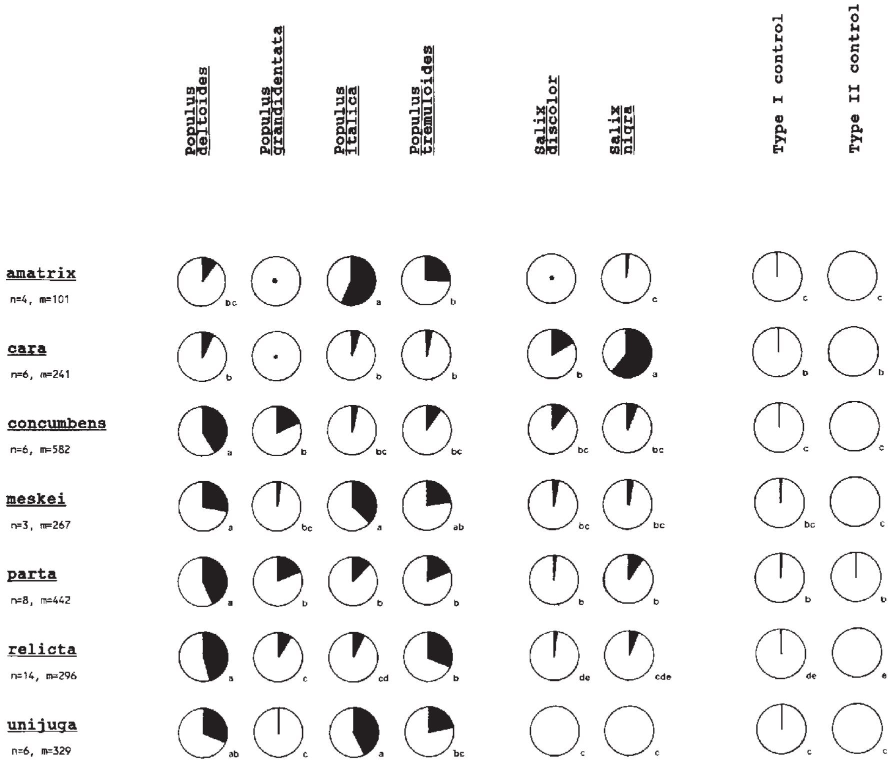


Fig. 2. Foodplant arena results with previously unfed larvae of Salicaceae-feeding Catocala. Areas of pies proportional to amounts (percent) of food eaten; dot in center = food not offered. Pies having the same subscripted letters are not significantly different at the 0.05 level (Tukey HSD tests). N = total number of arena tests. M = mean amount of food eaten per arena in square mm.

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ate more of the Type I control (*Carya*/*Quercus*) than the Type II control, and no species ate more Type I control than any salicaceous food.

Three of the Salicaceae feeders were represented by a single mother: *cara*, *concumbens*, and *meskei*. Of the remaining four species, only *relicta* showed significant (p<.05 by ANOVA) between-brood differences in preference. The oviposition histories of the *relicta* brood mothers were not known.

4. *Quercus*-feeding *Catocala*

Figure 3 shows foodplant preferences for the 5 *Quercus*-feeding *Catocala* (data are from a total of 36 arena tests, involving larvae from 12 different females).

The foodplant preferences of the oak-feeding species were less sharply defined than those of either the Juglandaceae or Salicaceae feeders.

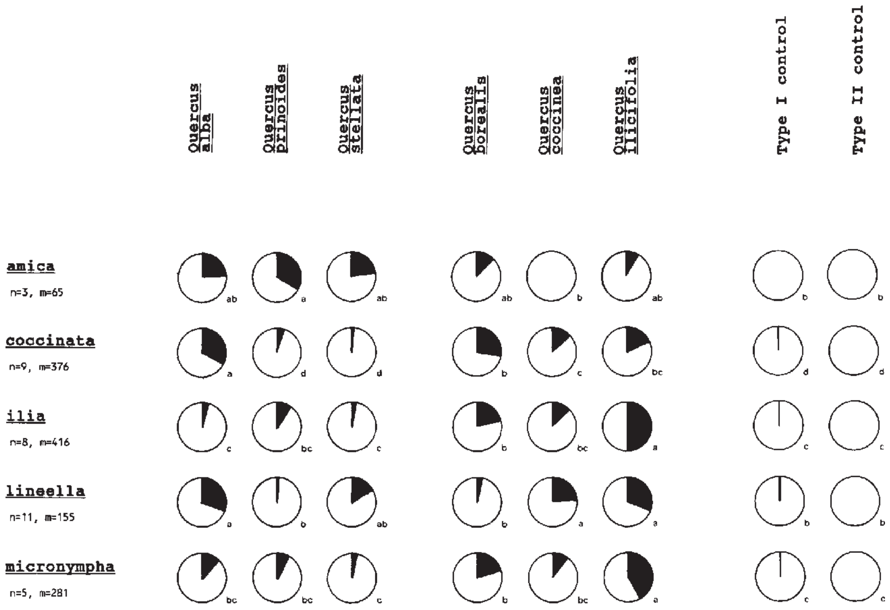

Fig. 3. Foodplant arena results with previously unfed larvae of Quercus-feeding Catocala. Areas of pies proportional to amounts (percent) of food eaten. Pies having the same subscripted letters are not significantly different at the 0.05 level (Tukey HSD tests). N = total number of arena tests. M = mean amount of food eaten per arena in square mm. Quercus (Lepidobalanus) at left, Quercus (Erythrobalanus) at center.

Larvae of *amica* consistently distinguished between the two oak subgenera, it being a *Quercus* (*Lepidobalanus*) feeder (but note the small number of arenas). The cosmopolitan Nearctic *ilia* showed a tendency toward *Quercus* (*Erythrobalanus*), eating *Q. ilicifolia* significantly more than other foods. Larvae of *coccinata*, *lineella*, and *micronympha* did not discriminate crisply between the two oak subgenera, although *micronympha* did eat significantly more *Q. ilicifolia* than other foods. All species ate more Type I control (*Carya/Populus*) than Type II, and none ate more Type I control than any oak.

Each of the oak-feeding *Catocala* species was represented by offspring of more than one mother. No species showed significant between-brood differences in preference (p>.50 by ANOVA).

Arena Tests: Partially Grown Larvae

1. Effects of larval age

For 7 Juglandaceae and 3 Salicaceae feeders, foodplant arenas were also run for third and fourth instar larvae. Because of the confounding effects of leaf age and leaflet position (see Gall, 1987, and below), only terminal leaflets were used as food items in arenas with mid instar

Table 2. Foodplant preference in Catocala as a function of larvae age. PFI = preferred foodplant index, here measuring preference for favorite food of the first instar larvae compared to other foods (the greater the PFI the greater the preference). N = total number of arenas. PFI declines between first and middle instars, as foodplant preference broadens.

	Young Larvae		Mature Larvae			
Species	PFI	n	PFI	n	PFI Change	Preferred First Instar Food
epione	0.75	11	0.41	4	- 0.34	Carya glabra
habilis	1.12	8	0.83	3	- 0.29	Carya ovata
judith	1.06	11	0.94	2	- 0.08	Carya ovata
obscura	1.95	8	2.13	2	+ 0.18	Carya ovata
palaeogama	0.81	13	0.37	6	- 0.44	Carya ovata
residua	2.69	8	2.49	2	- 0.20	Carya ovata
retecta	0.93	17	0.59	8	- 0.34	Carya ovata
amatrix	0.97	4	0.75	5	- 0.22	Populus italica
parta	0.60	8	0.36	3	- 0.24	Populus deltoides
relicta	0.60	14	0.54	4	- 0.06	Populus deltoides

Salicaceae-feeding *Catocala*. Both *Juglans* and *Carya cordiformis* were eventually eliminated from tests involving mid-instar Juglandaceae feeders, since it proved impossible to assess objectively the age of leaflets from these indeterminate foliating trees (responses of particular Juglandaceae feeders varied, but most could be shifted back and forth at will from eating large or small quantities of *Juglans*, depending upon the leaflets selected).

With these caveats on leaf age in mind, Table 2 shows mid-instar foodplant preferences for 7 Juglandaceae feeders (*epione*, *habilis*, *judith*, *obscura*, *palaeogama*, *residua*, *retecta*) and 3 Salicaceae feeders (*amatrix*, *parta*, *relicta*). The foodplant use is expressed in Table 2 as a "preferred foodplant index" (PFI), as described earlier, but with the numerator of the index here being the foodplant species eaten most by the first instars. The PFI decreased in 9 of 10 cases, indicating that foodplant preference broadened as larvae aged (t=3, n=10, p<.05, Wilcoxon test).

2. EFFECTS OF LEAF AGE

There is a natural dichotomy between the Salicaceae and Juglandaceae in the timing of leaf appearance in the field. Plants in the Juglandaceae are principally determinate foliators i.e., all leaves break from the bud at the same time of year (true for all *Carya* tested here; *Juglans* and *Carya cordiformis* are semi-determinate foliators). The salicaceous plants are indeterminate foliators, with new leaves being produced in most species throughout at least the first half of the growing season.

To determine the influence of leaf age on mid instar larvae of the Salicaceae feeders, arenas were constructed in which a young leaf was used for only one food item, and old leaves for all others. Young leaves were defined here as those immediately adjacent to the growing meristem of branch termini, and old leaves as the most basal on the same shoots. Several such tests were carried out on larvae of *amatrix*, *cara*, and *parta*, with a different food item being "young" in each arena.

Young leaves were greatly preferred over old leaves (Table 3), in accord with the findings of most other published studies on the influence of leaf age on caterpillar feeding (e.g., Schweitzer, 1979). Leaf age nearly completely overrides the usual foodplant preferences in each of these three *Catocala* species (cf. Figure 2; note especially the shifting between the two Salicaceae genera, *Populus* and *Salix*). Moreover, when presented with only old leaves in arenas, mid instar larvae of all three *Catocala* either consumed vastly lower amounts of food, or rejected the choice items entirely.

Sleeve Rearings: Survival

1. Juglandaceae-feeding *Catocala*

Field rearing experiments were conducted with 11 of the 19 Juglandaceae feeders whose preferences were assayed in arenas: *angusi*, *epione*,

Table 3. Arena preference tests for young versus old leaves, with Salicaceae-feeding Catocala. Values in table are percents of food eaten. In each arena, leaves of only one food item were young, all others old (as defined in text). N = total number of arenas. Young leaves are preferred over old leaves, and leaf age overrides the usual foodplant preferences of each Catocala species (cf. Figure 2).

Species	n	Young Leaves:	Populus deltoides	Populus italica	Populus tremuloides	Salix nigra
amatrix	2	Populus deltoides	0.94	0.06	0.00	0.00
	2	Populus italica	0.04	0.94	0.01	0.01
	1	Populus tremuloides	0.14	0.10	0.75	0.01
	1	Salix nigra	0.27	0.53	0.02	0.18
cara	2	Populus deltoides	0.92	0.01	0.00	0.07
	3	Populus italica	0.00	0.89	0.00	0.11
	1	Populus tremuloides	0.00	0.01	0.97	0.02
	3	Salix nigra	0.00	0.03	0.16	0.81
parta	1	Populus deltoides	0.97	0.02	0.00	0.01
	1	Populus italica	0.04	0.73	0.21	0.02
	1	Salix nigra	0.02	0.02	0.07	0.89

habilis, *lacrymosa*, *neogama*, *obscura*, *palaeogama*, *piatrix*, *residua*, *retecta*, and *vidua*. The numbers of different broods involved in these rearings were 1, 2, 1, 1, 2, 2, 3, 1, 3, 2, and 1, respectively. Two additional sleeve experiments (broods *habilis* A79 and *retecta* A79) were halted early in 1980 due to defoliation of the study sites by gypsy moth larvae. Censuses were taken both early and late in the season for several sleeve tests, affording insights into changes in survival and growth rates as a function of time spent on particular foodplants.

Among the two *Juglans* feeders, *piatrix* survived equally as well in the field on *Juglans* as on *Carya* (Table 4). Two attempts were made at rearing *neogama* brood B79 on *C. ovata* and *Juglans nigra*: experiment B791 was started with third instars that had previously been fed *Juglans nigra*, while B792 was started with previously unfed first instars. Larvae in each of these experiments refused to eat *C. ovata*, and died within several days; over half the larvae on *J. nigra* in each corresponding sleeve pupated successfully (Sargent, 1982, found ca. 50 percent survival of Massachusetts *neogama* on *C. ovata* in laboratory cage rearings). Larvae of *neogama* broods X80, A85, and A86 also refused to eat *Carya cordiformis* in the laboratory.

Among the *Carya* feeders tested, *angusi*, *habilis*, *obscura*, *residua*, *retecta*, and *vidua* survived best on *C. ovata* (Table 4). For each of these species, survival was generally next best on *C. glabra*; however, in none was survival significantly higher on *C. ovata* than on the second ranked food. Larvae of *angusi*, *obscura*, and *residua* died on *C. tomentosa* (all deaths were in the first instar; note that these three species showed the strongest arena preferences for *C. ovata*). Survival was moderate on *Juglans nigra* for *residua* and *vidua*, and high for the other taxa. Survival was uniformly high on all plants early in *retecta* brood E81, but significant mortality occured between the two censuses on *C. tomentosa* and *C. glabra* ($p<.05$ for each by G-tests).

Of the remaining *Carya* feeders, *epione* survived equally well on all juglandaceous foodplants; *C. ovata* ranked first and fourth in each of the two broods, respectively. For *palaeogama*, survival was highest on *C. ovata* only in brood E80. Survival on *C. glabra* ranked variously, with larvae surviving poorly on it in brood A80, but well in E80. Broods A80 and E80 fared poorly on *C. tomentosa*, but brood B81 survived best on this plant. Brood *palaeogama* A79 (not shown in Table 4; 25 larvae started per sleeve) was the only 1980 sleeve experiment in which all larvae pupated prior to heavy gypsy moth defoliation. Survival in the A79 brood did not vary among *C. ovata*, *C. glabra*, and *C. tomentosa* (0.52, 0.72, and 0.48, respectively; $p>.15$ by G-test).

An intensive effort was made to force larvae of *palaeogama* broods A80 and E80 on *Carya cordiformis* and *Quercus ilicifolia*. These rearings were done in the laboratory, under much more favorable conditions for growth than in the field. All 25 larvae started from each brood refused to feed on *C. cordiformis*, and died in the first instar. Of the 25 brood A80 larvae started on *Q. ilicifolia*, 24 died in the first instar; a single *palaeogama* A80 larva grew sluggishly on this oak through the first two instars, only to die while molting into the third instar.

Because the life histories of *subnata* and *nebulosa* were unknown prior to this work, all their broods were reared primarily in the laboratory on the preferred foodplant, *Carya cordiformis*, to obtain maximal series of preserved immatures for later taxonomic work. This left few larvae with which to attempt no-choice rearings, and I opted to place a few larvae of *subnata* in the field on foodplants other than *C. cordiformis*. No *subnata* brood B80 larvae survived past the first instar in sleeves on *Carya ovata*, whereas 6 pupated successfully on *J. nigra* but gave malformed adults (15 larvae started per sleeve). Of 10 brood A80 larvae started on *Juglans cinerea*, only 5 survived through the first instar, and all died by the fourth (implicit in the discussions here, of course, since there were no *C. cordiformis* sleevings, is that this plant would have best supported larval development of *subnata* in the field, as it does in the lab).

2. OTHER *CATOCALA* GROUPS

The biology of the Juglandaceae feeders was emphasized for this larval research, and hence comparable sleeve rearings for *Catocala* species in other foodplant groups have yet to be conducted. Two broods were started in 1981 with the oak-feeding *ilia*, but no larvae of either brood survived beyond the third instar on any of the *Quercus* foodplants. I suspect that these rearings were initiated too late in the season (8 May 1981), and that the leaf physiologies had already become unsuitable for the larvae (egg hatch of this species in New Haven County is typically during the last few days of April, and 1981 was an early spring). In 1983, I confined larvae of *parta* brood A82 and *relicta* brood A82 in the laboratory on several of their salicaceous foodplants. There were significant differences in mortality among foodplants during the first instar (Table 5; census at second instar). The patterns resembled the respective first instar arena preferences (cf. Figure 2), each species surviving best on *Populus deltoides*.

Sleeve Rearings: Development Rates

There was a quite close correspondence between survival and growth rate in the no-choice rearing studies. Among the *Carya* feeders, growth was most rapid on *C. ovata* in all broods except for *palaeogama* B81, and significantly so in most (Table 4; growth in *palaeogama* B81 was fastest on *C. glabra*). Growth in *palaeogama* A79 (not shown in Table 4) was significantly faster on *C. tomentosa* and *C. ovata* compared to *C. glabra* (median pupation dates of 4, 6, and 11 July 1980, respectively; $p<.05$ for difference of *glabra* against each other hickory, Mann-Whitney U-tests).

Growth was also most rapid on *C. ovata* in the two 1980 rearing experiments that were halted due to gypsy moth defoliation (*habilis* A79, *retecta* A79). Of 25 *retecta* A79 larvae, all 20 survivors on *C. ovata* had pupated prior to 15 July, whereas only two of those on *C. glabra* and none on *C. tomentosa* had done so. Five of 25 *habilis* A79 larvae had pupated by this date; no larvae on *C. glabra* or *C. tomentosa* had yet done so, and these were all at least one full instar behind the larvae on *C. ovata*.

The length of the larval period was shortest for *epione* (ca. 25-40 days), longest for *angusi*, *habilis*, and *obscura* (each ca. 50-75 days), and intermediate for the others (ca. 30-60 days). The egg of *epione* (and hence its first instar larva) is considerably larger than those of the other *Carya* feeders treated here, and *epione* larvae also pass through only 5 instars compared to 6-7 instars in the other species. These factors account for the rapid development in *epione* (timing of egg hatch for all *Carya* feeders in southern Connecticut is the same; Schweitzer, 1982, and in preparation). Larvae of *angusi*, *habilis*, and *obscura* simply grow more slowly than the other species.

Lastly, among the *Juglans*-feeding species, growth was faster on *Juglans nigra* than on *J. cinerea* for *neogama* X80 (Table 4). This was also the case for *piatrix*, in which growth was much slower still on *Carya*.

SUMMARY

General Trends in Foodplant Specificity

A principal finding here is that *Catocala* larval foodplant preferences appear to be absolute along foodplant family lines. In choice situations (arenas), larvae of 14 species of Juglandaceae, Salicaceae, and Fagaceae feeders accurately discriminate against foods foreign to their own foodplant array. In no-choice situations (sleeve and laboratory rearings), these same *Catocala* larvae die if confined on foodplants from plant families other than their own.

Limitations to larval foodplant acceptability also exist within each foodplant family examined, but the crispness of such infra-familial foodplant preferences is variable. Hence, preferences are least circumscribed for Fagaceae (two subgenera of *Quercus* tested), moderately so for Salicaceae (two genera tested), and sharply delimited for Juglandaceae (two genera, and two sections of *Carya* tested).

Age-specific influences on foodplant preferences were noted for both the larvae and their foodplants. For 9 of 10 *Catocala* species studied, larval foodplant preferences broadened from the first instar to the third/fourth; and for *Populus*, *Salix*, *Carya*, and *Juglans* foodplants, young leaves were preferred to mature leaves.

Specificity Among Juglandaceaous Foodplants

The taxonomic divisions within Juglandaceae (*Juglans*, the two sections of *Carya*) define boundaries to foodplant acceptability for the 19 Juglandaceae-feeding *Catocala* studied here. Two species prefer *Juglans* (*neogama*, *piatrix*); two prefer section *§Apocarya* of *Carya* (*nebulosa*, *subnata*); and the remaining 15 prefer section *§Eucarya* of *Carya* (*angusi*, *dejecta*, *epione*, *flebilis*, *habilis*, *insolabilis*, *judith*, *lacrymosa*, *luctuosa*, *obscura*, *palaeogama*, *residua*, *retecta*, *ulalume*, *vidua*).

The capacity of larvae to cross these foodplant boundaries clearly differs. The ability to feed largely successfully on *Juglans*, for example, is shared by all 19 species examined. Among the two *Juglans* feeders, larvae of *piatrix* feed successfully on *Carya*, but those of *neogama* do not; among the *Carya* section *§Apocarya* feeders, larvae of both *nebulosa* and *subnata* are unable to feed on *Carya* section *§Eucarya*, and feed poorly at best on *Juglans*; and no *Carya* section *§Eucarya* feeder could feed successfully on *Carya* section *§Apocarya*. Hence, a foodplant shift from either section of *Carya* to *Juglans* appears easier than the converse. A shift from *Carya* section *§Eucarya* to *Carya* section *§Apocarya* seems at least as difficult as a shift from *Juglans* to *Carya*.

Of interest in this context is foodplant use (my unpublished rearing and field data) by the remaining 7 Nearctic Juglandaceae-feeding *Catocala* not treated in detail above: *agrippina* Strecker, *atocala* Brou, *consors* Smith, *maestosa* Hulst, *robinsoni* Grote, *sappho* Strecker, and *serena* Edwards. Throughout their ranges, each of *consors*, *robinsoni*, *serena*, and *sappho* have been reliably recorded only on *Carya*, with *robinsoni* and *serena* being limited to *C. ovata*. In the southcentral and southeastern USA, *maestosa* feeds primarily on *Carya illinoiensis* and *C. aquatica* (Mich.) Nutt. (both of *Carya* section *§Apocarya*); in southern New Jersey, near this moth's northeastern geographic limit, both *Juglans* and (planted) *Carya illinoiensis* are used as foods. Larvae of *agrippina* use *C. aquatica*, and rarely *C. illinoiensis*. Foodplant use by the recently described *atocala* (a sibling of *agrippina*) remains unreported, but *C. aquatica*, *C. illinoiensis*, and *C. myristiciformis* (Michx.) Nutt. (of *Carya* section *§Apocarya*) are the only juglandaceous plants present where the moth flies in Arkansas and Tennessee, and *atocala* will doubtless prove to use one of these.

Hence, only 6 of the 25 Nearctic Juglandacae-feeding *Catocala* prefer foodplants other than *Carya* (7 of 26 if one includes *atocala*). The remaining 19 prefer *Carya*, and each of these feeds heavily on shagbark hickory, *C. ovata*, usually preferring it over other *Carya*. A subgroup of 7 of these 19 species — *angusi*, *habilis*, *judith*, *obscura*, *residua*, *robinsoni*, *serena* — is intimately associated with the biology of C. *ovata*. Their larvae show the strongest arena preferences for *C. ovata*, and fare the worst of all 19 *Carya* feeders on plants other than *C. ovata* in no-choice sleeve rearings. Foodplant preference also probably broadens least in this array of *C. ovata* specialist species as larvae mature (u=0, n1=4, n2=3, p=0.05 by 1-tailed Wilcoxon test on data in Table 4).

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Table 4. No-choice field rearing results with Juglandaceae-feeding Catocala larvae. Developmental stage abbreviations: PU = pupa; PP = prepupa; U2 = late ultimate instar; U1 = early ultimate instar; P2 = late penultimate instar; P1 = early penultimate instar; A2 = late antepenultimate instar; A1 = early antepenultimate instar; E2 = late ante-antepenultimate instar; E1 = early ante-antepenultimate instar. Growth rates among sleeves analyzed by Kruskal-Wallis tests, survival among sleeves by G-tests (sleeves having same "Group" letter are not significantly different at the 0.05 level).

		Developmental Stage at Census										Growth Rate		Survival		
Species-brood	Foodplant	E1	E2	A1	A2	P1	P2	U1	U2	PP	PU	Rank	Group	N	%	Group
	Carya glabra	1	3	7	9	7	0	0	0	0	0	3	b,c	27/50	0.54	b
angusi-A86	Carya ovata	0	0	0	0	11	10	0	0	0	0	1	a	21/25	0.84	a
	Carya tomentosa	0	0	4	0	0	0	0	0	0	0	4	c	4/25	0.16	c
(late census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/25	0.00	d
	Juglans nigra	0	0	2	2	11	1	0	0	0	0	2	a,b	16/25	0.64	a,b
	Carya glabra	0	0	0	0	3	1	13	8	0	0	3	a	25/30	0.83	a
epione-A81	Carya ovata	0	0	0	0	0	1	2	9	0	0	1	a	12/15	0.80	a
	Carya tomentosa	0	0	0	0	0	0	6	7	0	0	2	a	13/15	0.86	a
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	11	3	0	0	0	0	4	b	14/15	0.93	a
	Carya glabra	0	0	2	4	4	6	0	0	0	0	3	a,b	16/20	0.80	a
epione-A84	Carya ovata	0	0	0	1	2	7	0	0	0	0	1	a	10/10	1.00	a
	Carya tomentosa	0	0	0	2	3	3	0	0	0	0	2	a,b	8/10	0.80	a
(early census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	2	4	2	0	0	0	0	0	4	b	8/10	0.80	a
	Carya glabra	0	0	0	0	0	0	6	9	0	0	4	b	15/20	0.75	a
epione-A84	Carya ovata	0	0	0	0	0	0	0	6	4	0	1	a	10/10	1.00	a
	Carya tomentosa	0	0	0	0	0	0	0	7	1	0	2	a,b	8/10	0.80	a
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	0	0	2	5	0	0	3	b	7/10	0.70	a
	Carya glabra	0	0	6	8	2	0	0	0	0	0	3	c	16/20	0.80	a
habilis-A84	Carya ovata	0	0	0	0	0	4	2	0	0	0	1	a	6/10	0.60	a
	Carya tomentosa	0	0	0	0	0	0	0	0	0	0	.	.	0/10	0.00	b
(late census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/10	0.00	b
	Juglans nigra	0	0	0	2	4	1	0	0	0	0	2	b	7/10	0.70	a
	Carya glabra	0	0	5	3	6	0	0	0	0	0	4	a	14/15	0.93	a
lacrymosa-A87	Carya ovata	0	0	0	5	5	3	1	0	0	0	1	a	14/15	0.93	a
	Carya tomentosa	0	0	0	2	7	1	0	0	0	0	2	a	10/15	0.67	a
(early census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/15	0.00	b
	Juglans nigra	0	0	1	3	7	1	0	0	0	0	3	a	12/15	0.80	a
	Carya glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
neogama-B791	Carya ovata	0	0	0	0	0	0	0	0	0	0	.	.	0/13	0.00	b
	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
(late census)	Juglans cinerea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	0	0	0	0	0	7	1	a	7/13	0.54	a
	Carya glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
neogama-B792	Carya ovata	0	0	0	0	0	0	0	0	0	0	.	.	0/09	0.00	b
	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
(late census)	Juglans cinerea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	1	3	3	2	0	0	1	a	9/09	1.00	a

		Developmental Stage at Census										Growth Rate		Survival		
Species-brood	Foodplant	E1	E2	A1	A2	P1	P2	U1	U2	PP	PU	Rank	Group	N	%	Group
	Carya glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
neogama-X80	Carya ovata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/25	0.00	b
(late census)	Juglans cinerea	0	0	0	0	2	9	2	0	0	0	2	b	13/25	0.52	a
	Juglans nigra	0	0	0	0	0	2	10	7	0	0	1	a	19/25	0.76	a
	Carya glabra	0	4	12	15	9	0	0	0	0	0	2	a	40/50	0.80	a
obscura-A83	Carya ovata	0	0	9	6	6	0	0	0	0	0	1	a	21/25	0.84	a
	Carya tomentosa	0	0	0	0	0	0	0	0	0	0	.	.	0/25	0.00	c
(early census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	4	3	6	0	0	0	0	0	0	0	3	b	13/25	0.52	b
	Carya glabra	0	0	0	4	12	9	13	2	0	0	3	b	40/50	0.80	a
obscura-A83	Carya ovata	0	0	0	0	0	2	6	12	0	0	1	a	20/25	0.80	a
	Carya tomentosa	0	0	0	0	0	0	0	0	0	0	.	.	0/25	0.00	c
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	2	7	4	0	0	0	2	b	13/25	0.52	b
	Carya glabra	0	0	2	1	1	0	0	0	0	0	2	b	4/30	0.13	b
obscura-A83	Carya ovata	0	0	0	1	1	3	2	0	0	0	1	a	7/15	0.47	a
	Carya tomentosa	0	0	0	0	0	0	0	0	0	0	.	.	0/15	0.00	b
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Carya glabra	0	0	0	2	3	3	7	0	0	0	3	a	15/50	0.30	b
palaeogama-A80	Carya ovata	0	0	0	0	0	2	5	6	0	0	1	a	13/25	0.52	a,b
	Carya tomentosa	0	0	0	0	1	0	1	0	0	0	4	a	2/25	0.08	c
(late census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/25	0.00	c
	Juglans nigra	0	0	0	0	0	4	6	4	0	0	2	a	14/25	0.56	a
	Carya glabra	0	0	1	5	4	0	0	0	0	0	2	b	10/22	0.45	a
palaeogama-E80	Carya ovata	0	0	0	0	0	1	5	1	0	0	1	a	7/11	0.64	a
	Carya tomentosa	0	0	2	2	0	0	0	0	0	0	3	b	4/11	0.36	a,b
(late census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/11	0.00	b
	Juglans nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Carya glabra	0	1	10	18	15	2	0	0	0	0	1	a	46/50	0.92	a
palaeogama-B81	Carya ovata	0	0	1	20	2	0	0	0	0	0	2	a	23/25	0.92	a
	Carya tomentosa	0	4	8	8	5	0	0	0	0	0	4	a	25/25	1.00	a
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	3	15	2	0	0	0	0	0	3	a	20/25	0.80	a
	Carya glabra	0	0	0	2	7	0	0	0	0	0	4	c	9/10	0.90	a
piatrix-A82	Carya ovata	0	0	0	0	6	2	0	0	0	0	3	b,c	8/10	0.80	a
	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
(early census)	Juglans cinerea	0	0	0	0	3	5	0	0	0	0	2	a,b	8/10	0.80	a
	Juglans nigra	0	0	0	0	0	2	4	2	0	0	1	a	8/10	0.80	a
	Carya glabra	0	0	0	0	4	4	0	0	0	0	4	c	8/10	0.80	a
piatrix-A82	Carya ovata	0	0	0	0	0	2	6	0	0	0	3	b	8/10	0.80	a
	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
(late census)	Juglans cinerea	0	0	0	0	0	0	0	5	1	2	2	a	8/10	0.80	a
	Juglans nigra	0	0	0	0	0	0	0	1	1	5	1	a	7/10	0.70	a
	Carya glabra	0	0	0	3	21	2	0	0	0	0	2	b	26/40	0.65	a,b
residua-A83	Carya ovata	0	0	0	0	6	11	0	0	0	0	1	a	17/20	0.85	a
	Carya tomentosa	0	2	1	5	0	0	0	0	0	0	3	c	8/20	0.40	b
(early census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	3	7	4	0	0	0	0	0	0	4	c	14/20	0.70	a,b

		Developmental Stage at Census										Growth Rate		Survival		
Species-brood	Foodplant	E1	E2	A1	A2	P1	P2	U1	U2	PP	PU	Rank	Group	N	%	Group
	Carya glabra	0	0	0	0	0	1	16	3	0	0	3	c	20/40	0.50	b
residua-A83	Carya ovata	0	0	0	0	0	0	0	5	11	0	1	a	16/20	0.80	a
	Carya tomentosa	0	0	2	0	6	0	0	0	0	0	4	d	8/20	0.40	b
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	0	0	4	10	0	0	2	b	14/20	0.70	a,b
	Carya glabra	0	2	3	7	0	0	0	0	0	0	3	b	12/30	0.40	a,b
residua-B80	Carya ovata	0	0	0	0	0	4	3	3	0	0	1	a	10/15	0.67	a
	Carya tomentosa	0	0	0	0	0	0	0	0	0	0	.	.	0/15	0.00	c
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	1	1	0	0	0	0	0	2	b	2/15	0.13	b,c
	Carya glabra	1	4	7	4	10	0	0	0	0	0	2	b	26/40	0.65	a
residua-D80	Carya ovata	0	0	0	0	0	2	4	11	0	0	1	a	17/20	0.85	a
	Carya tomentosa	0	0	0	0	0	0	0	0	0	0	.	.	0/20	0.00	b
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Carya glabra	0	1	11	14	1	0	0	0	0	0	1	a	27/40	0.67	a
retecta-E81	Carya ovata	0	3	3	10	0	0	0	0	0	0	2	a	16/20	0.80	a
	Carya tomentosa	11	7	0	0	0	0	0	0	0	0	4	b	18/20	0.90	a
(early census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/20	0.00	b
	Juglans nigra	0	0	9	5	0	0	0	0	0	0	3	a	14/20	0.70	a
	Carya glabra	0	0	0	0	0	0	2	4	6	5	2	a	17/40	0.42	b
retecta-E81	Carya ovata	0	0	0	0	0	0	0	1	5	9	1	a	15/20	0.75	a
	Carya tomentosa	0	0	0	0	0	1	8	0	0	0	3	b	9/20	0.45	a,b
(late census)	Carya cordiformis	0	0	0	0	0	0	0	0	0	0	.	.	0/20	0.00	c
	Juglans nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Carya glabra	0	0	0	1	11	3	0	0	0	0	3	a,b	15/20	0.75	a
retecta-C84	Carya ovata	0	0	0	0	3	4	1	0	0	0	1	a	8/10	0.80	a
	Carya tomentosa	0	0	0	0	6	1	0	0	0	0	2	a,b	7/10	0.70	a
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	2	6	1	0	0	0	0	4	b	9/10	0.90	a
	Carya glabra	0	1	10	12	1	0	0	0	0	0	4	b	24/30	0.80	a
vidua-A82	Carya ovata	0	0	0	3	8	3	0	0	0	0	2	a	14/15	0.93	a
	Carya tomentosa	0	1	1	2	6	0	0	0	0	0	3	a,b	10/15	0.67	a,b
(early census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	1	3	1	0	0	0	0	1	a	5/15	0.33	b
	Carya glabra	0	0	0	1	1	6	7	7	0	0	3	b	22/30	0.73	a
vidua-A82	Carya ovata	0	0	0	0	0	0	0	10	2	1	1	a	13/15	0.86	a
	Carya tomentosa	0	0	0	0	0	1	7	1	0	0	4	b	9/15	0.60	a,b
(late census)	Carya cordiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Juglans nigra	0	0	0	0	0	0	4	1	0	0	2	b	5/15	0.33	b

Table 5. No-choice laboratory rearing results with Salicaceae-feeding Catocala larvae. Census taken at second instar, number of larvae per rearing container not equalized at start. Foodplants having same "Group" letter are not significantly different at the 0.05 level (G-tests).

Species-brood	Survival	Populus deltoides	Populus grandidentata	Populus italica	Salix nigra
parta-A82	live	52	.	7	1
	dead	13	.	14	12
	Group	a	.	b	b
relicta-A82	live	22	7	13	0
	dead	8	11	4	10
	Group	a	b	a	c

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