

## PREDATORY BEHAVIOR IN *LITHOPHANE QUERQUERA* AND OTHER SPRING CATERPILLARS

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**ABSTRACT.** Predatory tendencies are widespread among relatively polyphagous noctuid larvae feeding on spring foliage of forest trees but not among their more host-specific relatives. Prey capture behavior of *Lithophane querquera* is complex and highly stereotyped. Predation may be especially important during defoliator outbreaks since larvae can change from eating foliage to eating defoliators.

It is well known among lepidopterists that certain larvae will engage in cannibalism, especially under crowded laboratory conditions or if deprived of their normal food. Some noctuid species are reportedly largely predatory in nature, e.g., *Cosmia* and *Enargia* spp. (Forbes, 1954). However, little consideration has been given to the ecological significance of facultative larval predation and I am aware of no published accounts of specialized predatory behavior patterns in the Noctuidae or in other facultatively predacious Lepidoptera.

I have reared many thousands of noctuid larvae and although studying cannibalism was not a primary purpose of such rearings, some relevant observations were made and I suggest some ecological implications of these predatory tendencies.

Among the Lithophanini (Noctuidae: Cuculliinae) predatory tendencies are quite widespread in certain genera, but nearly absent in others. Species showing no predatory (i.e., cannibalistic) tendencies even in crowded, confined, laboratory conditions included: five species of *Metaxaglaea* (two presently undescribed), *Chaetaglaea sericea* (Morrison), *C. tremula* (Harvey), *Epiglaea decliva* Grote, *E. apiata* Grote, *Eucirroedia pampina* (Guenée), *Pyreferra pettiti* (Grote), *P. hesperidago* (Guenée), *P. citrombra* Franclemont, *Lithophane semiusta* (Grote), *L. patefacta* (Walker) (from Wisconsin), *L. signosa* (Walker), *Eupsilia morrisoni* (Grote) and *Homoglaea hircina* Morrison. Species showing slight to moderate predatory tendencies, at least when crowded, included: *Eupsilia sidus* (Guenée) (only when starving, larvae observed in sleeves only), *E.* species near *cirripalea* (late last instar only, including when sleeved), *E. vinulenta* (Grote) (late last instar only), *Xylena curvamacula* (Morrison), *Lithophane bethunei* (Grote and Robinson) (especially third and fourth instars), *L. innominata* (J. B. Smith), *L. hemina* (Grote) (seldom if ever when sleeved), *L. petulca* (Grote), *L. grotei* (Riley) (especially third and fourth instars, including sleeved larvae),

*Sericaglaea signata* (French) (last instar only, not when sleeved) and *Jodia rufago* Hübner (rarely, only if food was wilting). Species showing extreme predatory tendencies (i.e., it was rarely possible to rear more than one per container) were: *Lithophane baileyi* (Grote), *L. tepida atincta* (J. B. Smith), *L. querquera* (Grote) (sleeved larvae also highly predacious), and a fourth *Lithophane* species that ranges from southern New Jersey southward and has generally been included with *L. patefacta* in collections and by Forbes (1954).

All of the observations reported above were in crowded, laboratory conditions except where noted. The cuttings used as food cannot be considered optimal (Schweitzer, 1977) even though they were very seldom visibly wilted. Sleeved larvae had natural quality food but were crowded, about 25–50 per 51 × 82 cm sleeve. However, at least under stress conditions, those species indicated as predatory could be expected to eat other caterpillars in the field. Except for *Eupsilia sidus* and probably *Jodia rufago*, all of them ate other larvae even when suitable foliage was available. Furthermore, *L. bethunei* is known to be a predator on *Malacosoma* pupae in the field (Sanders and Dustan, 1919). The Eurasian *Eupsilia transversa* (Linnaeus) is also reportedly predacious in the field (Stokoe and Stovin, 1948). Sleeved larvae of all species of *Metaxaglaea*, *Chaetaglaea*, *Pyreferra* and *Homoglaea* were found to be non-predacious even after 24–48 hours of starvation.

Further information on larvae of most of the above species can be found elsewhere (Forbes, 1954; Schweitzer, 1974, 1977). Exceptions are *Lithophane signosa* which feeds only on *Platanus occidentalis* and one of the undescribed *Metaxaglaea* which accepts and grows (but not well) on a variety of woody plants (its natural host is unknown). Table 1 summarizes the feeding habits of predatory and non-predatory species.

Of the highly predatory species only *L. querquera* has been studied in detail. I have reared nine broods, all highly cannibalistic. The last instar larvae seem to prefer caterpillars but accept most deciduous tree leaves and also various rosaceous fruits and flowers. The frequency of predatory behavior, even at low densities, as well as the stereotyped behavior described below strongly indicates this species is at least substantially predacious under natural conditions.

Based on observations of 25–30 *L. querquera* (two broods), larvae exhibited the following behavior toward prey (various noctuid or decapitated *Tenebrio* larvae). When the prey approaches the larva, or is dropped near it, the larva raises its anterior portion slightly and begins waving to each side, usually rather slowly. When contact is made, the prey is grasped with the true legs and the attacker works quickly to the caudal region where the initial bite is made (Fig. 1), except in the case

TABLE 1. Larval feeding patterns of predacious and non-predacious Lithophanini. Polyphagous species are those feeding regularly on two or more plant families, facultatively polyphagous species are those appearing to have definite food preferences and restricted feeders can complete development only on a limited array of plants (see Schweitzer, 1977).

Predatory tendency	Genus	Feeding pattern			
		Polyphagous	Facultatively polyphagous	Restricted	Uncertain
None	<i>Lithophane</i>	0	2	1	
	<i>Pyreferra</i>	—	—	3	
	<i>Eupsilia</i>	1	0	—	
	<i>Homoglaea</i>	—	—	1	
	<i>Metaxaglaea</i>	1	0	3	1
	<i>Epiglaea</i>	—	1	1	
	<i>Chaetaglaea</i>	—	2	—	
	<i>Eucirroedia</i>	—	—	—	1
	total non-predacious	2	5	9	2
Slight to moderate	<i>Xylena</i>	1	0	0	
	<i>Lithophane</i>	4	1	0	
	<i>Eupsilia</i>	2	1	—	
	<i>Sericaglaea</i>	1	—	—	—
	<i>Jodia</i>	—	—	1	
Extreme	<i>Lithophane</i>	3	1?	0	
	total predacious	11	3	1	0

Note: The symbol — indicates no species in that genus exhibits the indicated feeding strategy in the eastern United States; 0 indicates that no species exhibiting a particular feeding pattern was found to fit into the predation category indicated.

of decapitated *Tenebrio* in which case feeding usually starts at the wound. Frequently the entire prey is eaten, but rather often the head capsule is discarded. Prey may vary considerably in size range and can be larger than the attacker. Occasionally *L. querquera* larvae encounter non-moving prey and bite into the caudal portion quickly, omitting the waving motions. The advantage of grasping the prey caudally may be that this prevents it from jumping or dropping away. Both *L. querquera* and *L. t. atincta* larvae have also been observed to turn and run down moving caterpillars.

Table 2 presents data from an experiment designed to determine if *L. querquera* larvae could grow well on an exclusively vegetable diet. All larvae hatched 16 May 1975 and were reared individually in 230 ml glass jars. Food was primarily foliage of *Pyrus × purpurea* for the first five instars. Thereafter, half of the larvae were maintained on this diet, with fresh food daily, during the last instar. The others were also given noctuid or decapitated *Tenebrio* larvae about every second day. These prey larvae were always eaten, and were often taken within 4 or 5

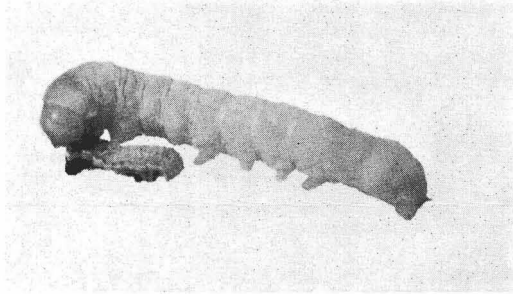


Fig. 1. Last instar larva of *Lithophane querquera* (Southford, New Haven Co., CT.) beginning to eat a third instar *Xylena curvimacula* (Sunderland, Franklin Co., MA.) (Photo by William Sacco, Peabody Museum Photography Laboratory: twice life size).

seconds. In many cases small amounts of foliage were subsequently eaten. The final body weights are very close for both groups and neither survival nor growth rates (based on maturation date) differ statistically. Thus *L. querquera* larvae are clearly not obligately predatory. It is somewhat surprising that no advantage can be shown for the predators. Perhaps the *Tenebrio* larvae which constituted over half of the prey are a poor food, or the *Pyrus* may be exceptionally suitable.

Predatory behavior probably serves to reduce the effects of competition

TABLE 2. Comparisons of body weights for sibling *L. querquera* larvae fed foliage vs. mixed foliage-insect diets during their last instar. Weights were taken the afternoon following the last night of feeding and are in grams.

Date matured	Food in last instar	
	Foliage (N = 16)	Insects and foliage (N = 17)
16 June	.2818	
17 June	.3203	
18 June		.2856
19 June	.2627	.2842
21 June	.2813	.2822
22 June	.2260	
23 June	.2727	.2614, .2377
26 June	.2119	.1952, .2801, .2480
27 June		.3363, .2331
28 June	.2802, .2556	.2610
29 June		.2631
3 July		.2338
mean weight	.2658	.2617
% survival	56.3	76.5

Comparison of survival data gives  $\chi^2 = 1.58$ ,  $p \gg .05$ . Comparison of maturation dates by a Mann-Whitney U-test (Siegel, 1956; 2 tailed large sample procedure) gives  $U = 39.5$ ,  $p = .1936$ .

for food from other caterpillars in certain situations. Even before the disturbance brought on by European man and the pests he has imported to North America, occasional spring canopy defoliation probably occurred in the eastern deciduous forests. Likely defoliators would include the several Geometridae commonly known as canker worms (Craighead, 1950). In fact, *Lithophane* larvae themselves occasionally cause local canopy defoliation (Craighead, 1950; Rings, 1968, 1973). A facultative predator (or cannibal) could switch from eating foliage to eating defoliators during outbreak periods. It is not known whether any lithophanine larvae will eat gypsy moth (*Lymantria dispar* [Linnaeus]) larvae, but usually defoliations caused by that species occur after most *Lithophanini* have finished feeding. It is interesting to note that one of two generalized feeders (Table 1) listed as nonpredatory, *Eupsilia morrisoni*, apparently feeds on understory plants in its late instar (Rings, 1969) and thus would be little affected by canopy defoliation.

Apparently, however, it is difficult for specialized feeding larvae to evolve (or retain) predatory behavior since nine out of ten restricted feeders (and most others with distinct preferences) are non-predatory (Table 1). In addition, I find no evidence of cannibalism among ten early feeding species of *Catocala* I have reared. Larvae of this genus are highly specialized feeders and none is reported as cannibalistic even in confinement (Sargent, 1976). Furthermore, the clear lack of cannibalism among crowded *Lithophane signosa* and less crowded *L. semiusta* and *L. patefacta* (whose very near relatives include predacious species) suggests this tendency may be lost as specialized feeding habits evolve, assuming that these species evolved from more generalized relatives. This assumption is questionable for *L. semiusta* but seems very likely for the others.

At the other extreme *L. querquera* represents a generalist that has evolved into a substantially predacious niche. In addition to the behaviors already described, it seems to differ from other *Lithophanini* by being somewhat more active, both nocturnally and diurnally. Presumably, increased locomotor activity increases the chance of encountering suitable prey.

Another interesting feature of *L. querquera* that perhaps related to its hyperactivity is its unusual coloration. This species may be warningly or mimetically colored since, unlike all other known *Lithophane* larvae, *L. querquera* larvae do not appear to be cryptic. They are greyish or bluish to whitish with a bright yellow pattern (Schweitzer, 1974, 1977). The color and pattern, however, are quite close to those of *Pyreferra ceromatica*, *hesperidago*, and *citrombra*. These three feed almost entirely on *Hamamelis virginiana* in southern New England (Schweitzer, 1977),

where they are easily found on the undersides of the leaves in May and June.<sup>1</sup> Possibly they derive some toxic or noxious substance from this plant and are mimicked by the less numerous, but presumably edible, *L. querquera* larvae. The possibilities of mimicry or unpalatability could be investigated experimentally if stock of these species were available.

The predatory habits of noctuid larvae have received very little attention from ecologists or entomologists. A more precise system of classifying predatory tendencies could be devised. The observations presented here suggest that predatory tendencies may be an important factor favoring non-restricted feeding habits among spring canopy feeding noctuid larvae. It seems likely that the impact of severe competition for food would be less for such larvae than for their restricted, non-predatory relatives. Experimental studies of predation during simulated cankerworm outbreaks will be reported elsewhere. In some instances cannibalism may be an important mechanism of self-regulation.

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<sup>1</sup> *P. citrombra* is reportedly a *Corylus* feeder (Forbes, 1954), but southern New England larvae accept only *Hamamelis* (2 spp.) and I have collected them on *H. virginiana* in Massachusetts and at Philadelphia, Pennsylvania. *P. ceromatica* has apparently not been collected in New England or neighboring regions for about 60 years, but was once fairly common there.