

**Response of Predaceous Arthropods to Chemically Defended
Larvae of the Pyralid Moth *Uresiphita reversalis* (Guenée)
(Lepidoptera: Pyralidae)**

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ABSTRACT: Extensive observations of aposematic *Uresiphita reversalis* (Guenée) larvae feeding on sky-blue lupine *Lupinus cumulicola* Small in February in south Florida revealed a low incidence of predation by natural arthropod enemies. Three species of spiders, the wolf spiders *Lycosa ceratiola* Gertsch & Wallace and *L. osceola* Gertsch & Wallace and the crab spider *Misumenops* sp., rejected *U. reversalis* larvae that were offered to them in laboratory predation tests. However, the green lynx spider *Peucectia viridans* (Hentz) and the assassin bug *Zelus longipes* (L.) were found to feed on the caterpillars. Bioassays with the wolf spider *L. ceratiola* confirmed previous studies showing that the larval integument possess potent antifeedant properties, most likely because it contains quinolizidine alkaloids of dietary origin.

In winter the sandhills on south-central Florida's Lake Wales Ridge undergo a pronounced seasonal change as many xerophytic trees and shrubs shed their leaves and herbaceous plants wither or die back (Abrahamson et al., 1984). This time of year corresponds to the second half of the 6-month long dry season when available moisture in the excessively well-drained upland soils is minimal. Hence, it is remarkable to observe sky-blue lupines (*Lupinus cumulicola* Small) growing and blooming profusely in February, especially in recently burned or cleared sandhill ecosystems (Dunn, 1971; Abrahamson et al., 1984). In addition, although many herbivorous insects visit lupines during the day or night, almost none of them consume the tender foliage (J. Carrel, pers. obs.), presumably because the peripheral tissues contain high concentrations of poisonous quinolizidine alkaloids (QA) (Wink et al., 1991; Wink, 1992). But there is one notable exception to this generalization.

Caterpillars of the pyralid moth *Uresiphita reversalis* (Guenée) feed extensively on sky-blue lupines in ridge sandhills of Florida, sometimes resulting in defoliation of individual plants. This moth is a multivoltine species recorded widely in North America, especially in coastal regions, that specializes in feeding on legumes in the tribe Genisteae (Kimball, 1965; Munroe, 1976; Bernays and Montllor, 1989; Montllor et al., 1990). The larvae (second to fifth instars) are highly aposematic: they are brightly colored, they feed in groups during daytime on exposed leaf surfaces, and they are relatively inactive even on hot days (Bernays and Montllor, 1989; J. Carrel, unpubl. obs.). As a chemical defense, the larvae selectively sequester bitter tasting and toxic QA from the leguminous hosts and concentrate them predominantly in their integument (Montllor et al., 1990, 1991; Wink et al., 1991; Wink, 1992). But field studies conducted in California reveal that, despite the presence of defensive chemicals, mortality of the first four instars is high (~70% of larvae die in the 3-4 wk required to develop from hatching to fifth instar). Much of the larval mortality is attributable directly to predation by anthocorid bugs, vespidae wasps, chrysopid larvae, salticid spiders, and thomisid spiders (Bernays and Montllor, 1989). For reasons that are not fully evident, fifth instar larvae are virtually devoid of predation by arthropods, birds, and other enemies (Bernays and Montllor, 1989).

I wished to evaluate the effectiveness of the chemical defense in *U. reversalis* larvae against predaceous arthropods they naturally encounter while feeding on *L. cumulicola* in the ridge sandhill ecosystems of Florida. First, I made extensive field observations in an attempt to document natural attacks on larvae. Second, I performed predation tests in the laboratory to determine the course and outcome of attacks on larvae by natural enemies. Finally, I conducted antifeedant bioassays using extracts prepared from larvae.

Materials and Methods

Study area

The Archibold Biological Station (ABS) is located near the southern terminus of the Lake Wales Ridge in Highlands County, Florida (27° 11'N lat., 81°21'W long.), 12 km south of the town of Lake Placid. The sandhill at ABS is located on the crest and upper slopes of Red Hill, a relictual sandridge consisting of beach and dune sands from the Plio-Pleistocene that rises from 45 to 68 m above mean sea level. The southern ridge sandhill community has a tree layer comprised of south Florida slash pine (*Pinus elliottii* var. *densa* Little and Dorman), turkey oak (*Quercus laevis* Walter), scrub hickory (*Carya floridana* Sargent), and an occasional sand pine (*P. clausa* Chapman). The shrub layer is dominated by three oaks (*Q. myrtifolia* Willdenow, *Q. geminata* Small, and *Q. chapmanii* Sargent), two palmettos (*Serenoa repens* Small and *Sabal etonia* Swingle), and rusty lyonia (*Lyonia ferruginea* Nuttall). Wire grass (*Aristida stricta* Michaux), broom sedges (*Andropogon* spp.), and many other plants are present in the ground layer, but generally the importance value of any single herbaceous species is minor (Abrahamson et al., 1984; Myers, 1985; Myers and White, 1987; Menges and Salzman, 1992). The site was never commercially logged or turpented and it was not burned from 1927 until 1991 when prescribed burns were conducted as part of the ABS fire management plan (Myers, 1985; Main and Menges, 1997).

Field observations

Over the course of seven winters (February in 1992, 1993, 1994, 1995, 1998, 1999, and 2000) I spent 1-3 hr periods during daytime and nighttime continuously observing *U. reversalis* larvae on lupines in order to document interactions with predatory arthropods. Because many spiders and other predators in Florida scrub and sandhill habitats are nocturnally active, I reasoned that observations had to be made from early morning until late at night (0700-2400 hr). At night I used a headlamp and a lantern for illumination. I nonrandomly selected plants each having twelve or more larvae and, due to year-to-year phenological variations, over the course of the study I was able to observe aggregations of larvae representing all five instars.

Predatory arthropods were collected alive in vials and taken to the laboratory at ABS for taxonomic identification. Representative specimens of *U. reversalis* and other arthropods were deposited in the collection of invertebrates at ABS.

Predation tests in the laboratory

I collected twenty individuals each of four spider species and one bug species (Table 1) in the ridge sandhill habitat and brought them alive back to the laboratory at ABS for use in no-choice predation tests. The two species of wolf spiders (Araneae: Lycosidae) were collected at night in February 1995 after they had emerged from their burrows to forage on sand near lupines. Although these spiders are most commonly found on the ground, it is not unusual to detect them by their reflective eye-shine sitting 0.5-1.0 m above ground in vegetation (J. Carrel, unpubl. obs.; Eisner and Eisner 1991). Individuals of the other two spiders (Araneae: Thomisidae and Oxyopidae) and the assassin bug

(Hemiptera: Reduviidae) were collected during daytime in February 2000 on lupine plants. The four spider species typically ambush their prey; they do not use silk for prey capture.

Each predator was caged singly in a translucent plastic container lined on the bottom with moistened filter paper for 1-2 days without food at 22-27°C under fluorescent illumination (14hr L:10hr D) before it was offered an *U. reversalis* larva. After this acclimation period was complete, I presented one fourth or fifth instar larva to each of the large wolf spiders. Because the thomisid and oxyopid spiders were small (Table 1), I gave each of them either a first, second, or third instar larva. Finally, I offered second, third, or fourth instar larvae to the medium-size assassin bugs. I weighed all animals before tests. After tests I measured the lengths of the *Zelus longipes* (L.) (Hemiptera: Reduviidae) beaks using a micrometer.

I followed the same protocol for all feeding tests. After introducing an active *u. reversalis* larva into a predator's cage, I watched continuously for 2 hr and recorded whether an attack occurred, the outcome of each attack, and the duration of feeding after initiation of a successful attack. If predation did not occur during a test, I subsequently confirmed that the predator was hungry and physically capable of feeding by successfully getting it to eat either a cultured small mealworm (larva of *Tenebrio molitor* L. (Coleoptera: Tenebrionidae)) or a wild fruit fly (*Drosophila* sp. (Diptera: Drosophilidae)). I observed the condition of each predator at 24 and 48 hr after tests were completed to determine whether exposure to alkaloid-laden caterpillars might induce morbidity or death.

Antifeedant bioassays

To demonstrate that the deterency of *U. reversalis* larvae was chemically based, I conducted antifeedant tests in February 1998 with extracts of larvae administered orally to wolf spiders using the protocol of Carrel and Eisner (1984). Adapting the chemical procedures of Montllor et al. (1991) and Wink et al. (1991), 50 whole fourth and fifth instar larvae, unfed for 2 days to eliminate stomach contents were frozen, thawed, and ground in a mortar in 0.5 M HCl. The slurry was made alkaline with 6 N NaOH and extracted twice with 5 ml CH₂Cl₂, yielding alkaloids in free base form. The CH₂Cl₂ extract was air dried and dissolved in 200µl methanol. Similar extracts were made of the integument plus head or the remaining tissues (primarily gut) removed from an additional 50 unfed, thawed larvae.

I thoroughly mixed each of the three methanolic extracts separately with 400 µl aqueous egg albumin and applied 6µl of each milky solution to the chelicers and prey of *Lycosa ceratiola* Gertsch & Wallace (Araneae: Lycosidae) wolf spiders (n=25/extract) soon after they began to eat mealworms. This dosage was approximately the equivalent of the total alkaloids from one-half *U. reversalis* larva per test spider (assuming 100 % extraction efficiency). Using the same criteria as Carrel and Eisner (1984), I scored rejection of a mealworm within 3 min of application as an antifeedant response. I tested methanolic egg albumin as the solvent control (n = 25 spiders). As in predation tests, I observed the condition of each spider at 24 and 48 hr after tests were completed to determine if any were moribund or dead.

Statistical analyses were performed on SYSTAT (Wilkinson, 1989).

Results

Field observations of predation

Over the course of seven winters (February in 1992, 1993, 1994, 1995, 1998, 1999, and 2000), I observed many *U. reversalis* larvae on lupines in ridge sandhill habitats for a total of 130 hr during the day and 64 hr during the night. Only once during this time did I see an attack by a predator on a caterpillar. One afternoon I noticed a subadult assassin bug *Z longipes* apparently stalking a third

Table 1. Description of four spiders and one bug used in predation tests with *U. reversalis* larvae.

Family (Common name)	Species	Number and stage	Body mass (mg. $\bar{X} \pm \text{SEM}$)
Lycosidae (Wolf spiders)	<i>Lycosa ceratiola</i> Gertsch & Wallace	20 adult females	355 ± 17
	<i>L. osceola</i> Gertsch & Wallace	20 adult females	1160 ± 61
Thomisidae (Crab spiders)	<i>Misumenops</i> sp.	10 adult females & 10 adult males	9.2 ± 1.6
Oxyopidae (Lynx spiders)	<i>Peucetia viridans</i> (Hentz)	20 immatures	2.0 ± 0.1
Reduviidae (Assassin bugs)	<i>Zelus longipes</i> (L.)	4 adults & 16 subadults	23.2 ± 1.4

instar larva. The bug slowly approached the larva while it was chewing a small hole in the leaf's upper epidermis. At a distance of a few mm, the bug quickly pierced the larva with its beak and then lifted it with the forelegs. The larva soon stopped writhing and the pair remained motionless in this posture for about 1 hr as the bug sucked its meal from the limp, ever shrinking caterpillar.

The absence of attacks on *U. reversalis* larvae was not simply a reflection of the absence of predators in winter. In addition to the predators listed in Table 1, I noticed small ants, *Monomorium viridum* Brown (Hymenoptera: Formicidae), commonly moving along trails on stems to forage in the inflorescences of lupines. Other ants, such as *Camponotus* sp. (Hymenoptera: Formicidae), were also seen walking on lupines during the daytime. Also, I detected a few trash-carrying chrysopid larvae (Neuroptera) crawling on lupine leaves but I failed to detect remains of caterpillars in their adornments. One night I found a green tree frog *Hyla cinerea* (Schneider) sitting on a lupine leaf near an aggregation of larvae, but it did not approach the insects; the next morning the frog was still there and the number of larvae on the plant had not changed. The frog was the only vertebrate I saw actually on a lupine.

Predation tests in the laboratory

Of 40 wolf spiders, equal numbers of *L. ceratiola* and *L. osceola* Gertsch & Wallace, given large *U. reversalis* larvae, all attacked but none of them visibly harmed the caterpillars (Table 2). Spiders initially pounced upon crawling larvae with their forelegs and pedipalps, but within 1-3 sec they released the insects. Spiders never grasped the larvae strongly enough with their chelicers to pierce the integument. After quickly releasing the insects, spiders usually walked away and assumed their resting posture. In most instances this behavioral sequence was repeated by wolf spiders several

Table 2. Outcome of attacks by five predators on *U. reversalis* larvae.

Predator	No. used in tests	No. that attacked a larva	No. that killed a larva
<i>Lycosa ceratiola</i>	20	20	0
<i>L. osceola</i>	20	20	0
<i>Misumenops</i> sp.	20	0	0
<i>Peucetia viridans</i>	20	7	7
<i>Zelus longipes</i>	20	20	20

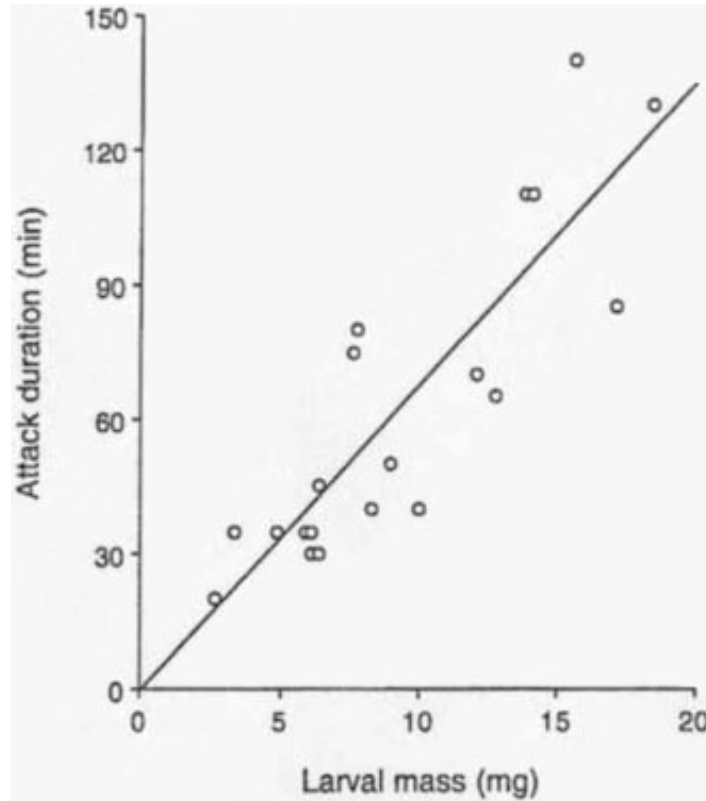


Fig 1. Duration of feeding by assassin bugs (*Z. longipes*) is a positive function of body mass of *U. reversalis* larvae. Best-fit regression line is shown (N = 20 adult or subadult bugs, $Y = -0.7934 + 6.7685 X$, $R^2 = 0.747$, $P < 0.0001$).

times within 0.5 hr. Toward the end of the test period the wolf spiders ignored the moving insects unless one crawled into a spider's leg, whereupon the spider quickly extended its appendage to flick the larva away.

As indicated in Table 2, crab spiders *Misumenops* sp. (Araneae: Thomisidae) never attacked *U. reversalis* larvae. These spiders spent most of the test period sitting motionless with their legs retracted in the typical thomisid sit-and-wait attack posture. When larvae crawled up to them and made contact, which happened often, the crab spiders flicked them away in a manner identical to the behavior shown by wolf spiders.

Most green lynx spiders *Peucetia viridans* (Hentz) (Araneae: Oxyopidae) either ignored caterpillars or, if contacted by larvae, walked away from them. However, of the 20 oxyopids tested, seven spiders attacked and killed *U. reversalis* larvae (Table 2). After the initial bites, spiders held their prey in their chelicers for a long time ($\bar{X} \pm \text{SEM} = 250 \pm 20$ min, range 140–380 min), occasionally altering the location of their bites on the caterpillars' bodies. When feeding was complete larvae were reduced to tiny pellets, each consisting of a head capsule pressed against the shriveled integument. The seven *U. reversalis* caterpillars eaten by *P. viridans* were first instar larvae, whereas the thirteen uneaten caterpillars were second or third instar larvae. This suggests first instar larvae may be vulnerable to predation for hours or days after eclosion until they feed on lupine tissues and sequester defensive chemicals in their integument. These observations may also explain why first instar larvae are not aposematic, unlike subsequent immature stages.

All twenty assassin bugs attacked *U. reversalis* larvae in laboratory tests. The sequence of feeding behavior was similar to that seen in the field. Duration of feeding by *Z. longipes* ($\bar{X} \pm \text{SEM} = 63 \pm 8$ min, range 20–140 min) was positively correlated with body mass of the caterpillar prey (Fig. 1), but it

Table 3. Results of antifeedant bioassays with extras of *U. reversalis* larvae applied to chelicers of wolf spiders *Lycosa ceratiola*. ($X^2_c = 52.82$, $N = 100$, d.f. = 3, $P < 0.0001$).

Extract	Number of spiders	
	Antifeedant. response	No. response
Entire larvae	22	3
Larval integuments and heads	24	1
Larval guts	3	22
Solvent control	5	20

was not related to body mass (see Table 1) or beak length (3.0 ± 0.1 mm, range 2.6–3.6 mm) of the predator (MLGH/Regression test, $t = 0.48$, $P = 0.63$ for each variable).

All predators ($n = 100$) were alive and active at 24 and 48 hr after tests were completed.

Antifeedant bioassays

It is clear from the data (Table 3) that substances extracted from the integument of *U. reversalis* larvae were potent antifeedants when applied to the mouthparts of wolf spiders *L. ceratiola*. Moreover, the extract of larval guts was not deterrent relative to the solvent control. These results are fully consistent with previous findings on the protective role of plant-derived QA in the integument of this caterpillar, as mentioned in the introduction. Furthermore, all wolf spiders ($n = 100$) were alive and apparently normal 24 and 48 hr after being tested.

Discussion

The low incidence of observable predation on wild *U. reversalis* larvae in the sandhill habitat was unexpected. Bernays and Montllor (1989), watching these larvae on *Cytisus* plants from dawn to dusk in summer, recorded up to 20% of young larvae were taken by minute pirate bugs (Hemiptera: Anthocoridae) and wasps (Hymenoptera: Vespidae). Moreover, adult green lynx spiders *P. viridans* are known to feed both day and night in summer on many other arthropods found on low vegetation in Florida and other states (Randall, 1982; Nyffeler et al., 1987). I suspect the primary reason for my failure to detect predation in the field is attributed to the season of my work. In winter in Florida large carnivorous arthropods probably are relatively uncommon or inactive. Because it is the dry season, many insects and spiders are in diapause or in early developmental stages of their life cycles, such as the green lynx spiders I found. In addition, low air temperatures may restrict foraging activity by some spiders but not others (Pulz, 1987). According to long-term records from the ABS weather station, ambient temperatures in February frequently dip below 15°C by dusk. Previous work at ABS demonstrated that nocturnal emergence and foraging by *L. ceratiola* and *L. osceola*, the large wolf spiders used in this study, is inhibited sharply whenever the air temperature drops below 20°C (Carrel, 1980; J. Carrel and T. Eisner, unpubl.). On the other hand, recent studies show that hunting performance by the crab spider *Misumenops asperatus* (Hentz) (Araneae: Thomisidae), which is both diurnally and nocturnally active on flowers, is thermally insensitive over a broad temperature range (10–40°C) (Schmalhofer and Casey, 1999). Hence, even though I did not actually observe encounters in the field, it seems reasonable to suspect that crab spiders and green lynx spiders might attack small *U. reversalis* larvae on lupines.

Results of laboratory tests reported here lend support to field observations that indicate

larvae are well protected from large, voracious wolf spiders (*L. ceratiola* and *L. osceola*) because their integument is replete with extractable antifeedant substances. Larvae of another moth, *Utetheisa ornatrix* (family Arctiidae), found commonly at the Archbold Biological Station, possess pyrrolizidine alkaloids that are also deterrent to *L. ceratiola* and perhaps generally to spiders as a group (Eisner and Eisner, 1991). However, unlike the almost instantaneous rejection of *U. reversalis* larvae noted in my study, these spiders seize and hold field-caught *U. ornatrix* larvae for nearly a minute before releasing them unharmed (Eisner and Eisner, 1991). I suspect the difference in the rapidity of response by wolf spiders reflects the fact that defensive alkaloids in *U. reversalis* larvae are concentrated peripherally in the integument, whereas the alkaloids in *U. ornatrix* larvae are dispersed throughout the body. The *U. reversalis* defensive mechanism may be much faster, and hence potentially more effective than the *U. ornatrix* defensive mechanism against many predators, but there clearly are drawbacks to the former. First, as was proven by the assassin bugs and the green lynx spiders, *U. reversalis* larvae suffer from the Maginot Line Fallacy: once an enemy—whether predator or parasitoid—manages successfully to breach the integument, there are no further lines of defense and the larva is doomed. In contrast, one might expect that the *U. ornatrix* defensive mechanism would prove effective against *Zelus* and other enemies with piercing/sucking mouthparts and perhaps even many parasitoids. Second, the *U. reversalis* defensive mechanism precludes retention of defensive chemicals into the adult stage where they can continue to afford protection. Hence, unlike *Utetheisa* moths (Eisner and Meinwald, 1995), one would anticipate that *U. reversalis* adults are very vulnerable to attack by web-building spiders and other nocturnal predators. Tests of these ideas are underway.

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