

When good bugs go bad: intraguild predation by *Jalysus wickhami* on the parasitoid, *Cotesia congregata*

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Abstract

We report a case of direct intraguild predation involving an insect predator and parasitoid in an agricultural system. The spined stilt bug, *Jalysus wickhami* Van Duzee, feeds on eggs of the tobacco hornworm, *Manduca sexta* L., and also on prepupal and pupal stages of the gregarious hornworm parasitoid, *Cotesia congregata* (Say). In two separate trials, mean mortality of attached parasitoids was significantly lower (66%, 73%) than that of their detached siblings (97%, 96%) after a 3 day exposure to stilt bugs, demonstrating that attachment to the host offered some protection against predation. In no-choice experiments, prepupal parasitoids suffered greater mortality (0 day-old=61%, 1 day-old=65%) than pupal parasitoids (2 day-old=50%, 3 day-old=14%). When offered in combination with 0 or 2 day-old hornworm eggs, respective mortality of 0, 1, 2 and 3-day-old pupal parasitoids showed a similar pattern (67%, 63%, 33% and 23%). In another experiment, mortality of 0-day-old pupal parasitoids (64%) was greater than that of 3 day-old pupal parasitoids (38%). Mortality of pupal parasitoids was not affected by the availability of hornworm eggs, a highly acceptable food. Younger pupal parasitoids (= prepupae) probably suffered greater mortality because they were more easily fed on by stily bugs than older (pupated) ones. Because *C. congregata* overwinters in the prepupal stage, it may be particularly vulnerable to attack late in the season when stilt bug populations are large and hornworm eggs are relatively uncommon.

Introduction

Intraguild predation, 'the killing and eating of species that use similar resources and thus are potential competitors' (Polis & Holt, 1992), is a common and significant occurrence within a variety of terrestrial and aquatic communities (Polis & Holt, 1992; Polis et al., 1989). With the exception of a few studies, intraguild predation has been rarely reported or studied in insect communities, despite its important implications for biological control (Rosenheim et al., 1995). Indirect intraguild predation appears to be relatively common, e.g., when a predator feeds on an herbivorous host which has also been parasitized. However, only one case of direct predation of an insect predator on

a developing parasitoid is reported in the literature. In this single example, intraguild predation by the warehouse pirate bug, *Xylocoris flavipes* (Reuter) (Hemiptera: Anthocoridae), on *Bracon hebetor* (Hymenoptera: Say), an ectoparasitoid of the stored-product pest, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), significantly reduces both parasitoid and moth populations (Press et al., 1974).

The spined stilt bug, *Jalysus wickhami* Van Duzee (= *J. spinosus* (Say) (Hemiptera: Berytidae), in the eastern USA prior to 1981; Wheeler & Henry, 1981), feeds on live and dead arthropods associated with its numerous host plants, as well as on plant juices. First reported as a phytophagous pest of tomato (Somes, 1916), its host plants are typically 'glandular-hairy' herbs in



the Solanaceae, Malvaceae, Scrophulariaceae, Oxalidaceae and Onagraceae (Wheeler & Henry, 1981). One of its more common host plants is tobacco, *Nicotiana tabacum* L., on which its activity as a predator was first observed (Gilmore, 1938). Plant feeding alone does not support stilt bug populations and a prey source is required for proper development and fecundity (Elsey & Stinner, 1971). Spined stilt bugs prey on tobacco aphids, *Myzus nicotianae* Blackman (Homoptera: Aphididae) (Kulash, 1949; Lawson, 1959), and on the eggs of several lepidopterans including tobacco budworms, *Heliothis virescens* (F.) (Lepidoptera: Noctuidae) (Elsey, 1972a) and hornworms, *Manduca* spp. (Lawson, 1959) (Lepidoptera: Sphingidae). As egg predators, spined stilt bugs contribute greatly to the overall natural biological control of lepidopterans on tobacco, especially in the piedmont areas of North Carolina and Virginia (Lawson, 1959; Elsey, 1973; Semtner, 1979).

In 1988, we observed adults and late instar nymphs of *J. wickhami* on parasitized hornworm larvae on tobacco plants at the Tobacco Research Station in Oxford, NC. The stilt bugs appeared to be feeding on cocoons of *Cotesia congregata* (Say) (Hymenoptera: Braconidae), a major parasitoid of *M. sexta*, also reported anecdotally by Lawson (1959).

The biology of *C. congregata* is fairly well known. This gregarious larval endoparasitoid attacks sphingids on various plants but its major hosts are *Manduca* spp. in tobacco-growing areas, where it is sometimes the only hymenopterous parasitoid of *M. sexta* (Kester & Barbosa, 1991a). At the completion of their larval development, parasitoids egress through the host cuticle and spin cocoons. Non-diapausing parasitoids pupate within their cocoons ca. 2 days after spinning and emerge as adults 2 to 4 days later (Kester, unpubl.). Although most cocoons remain attached to the host larva, some are dislodged and fall on to the leaves of the surrounding plant or the ground below. In the field, most parasitized hornworm larvae survive as mobile, non-feeding larvae until after the emergence of parasitoid adults when they succumb to death through starvation. Parasitoid cocoons are typically available to potential predators or hyperparasitoids in three ways: (1) attached to a living and mobile host larva, (2) detached, on a leaf or other plant surface, or (4) detached and on the ground below the plant (Kester & Barbosa, 1991b).

In this study, we addressed three questions: 1) Do pupal parasitoids attached to their hosts suffer less mortality due to predation by stilt bugs than ones that

are detached? 2) Do younger pupal parasitoids suffer greater mortality due to predation by stilt bugs than older pupae? 3) Is *C. congregata* a relatively acceptable food source for *J. wickhami*? Unless directly specified, we use the term 'parasitoid pupae' as a general term for both prepupal ('young pupae') and pupal ('older pupae') parasitoids within cocoons.

Materials and methods

Microscopic observations of both adults and late-instar nymphs were made to confirm our observations of apparent predation by the spined stilt bug, *J. wickhami*, on pupae of the hornworm parasitoid, *C. congregata*. Unless otherwise stated, stilt bugs were offered prey (parasitoid pupae or hornworm eggs) and/or tobacco leaf ('NC2326') in Petri dishes (15.2 cm diam., 2.5 cm deep) and held in a growth chamber at ca. 27 °C and L14:D10 for 3 days. Tobacco was grown in a greenhouse without pesticides. Parasitoid pupae were examined daily for emergence over a one-week period following removal of stilt bugs. As indicated in table footnotes, parasitoid mortality was compared among the treatment groups in each experiment by analysis of variance (ANOVA); resulting means were compared using the Waller-Duncan k-ratio *t*-test or orthogonal contrasts using SAS (SAS Institute, 1985; SAS Institute, 1987). To meet assumptions for parametric analysis, results were analyzed for 'percent survival' but are reported for 'percent mortality' (100 - percent survival). Unless otherwise stated, all other assumptions for parametric analyses were met.

Experiment 1. In this experiment, we tested the hypothesis that pupal mortality of *C. congregata* attached to their hosts would suffer less mortality due to predation by *J. wickhami* than detached parasitoids. Stilt bugs used in this experiment were collected from *Nicotiana rustica* var. *brasilia* Schrank, a preferred hostplant of *J. wickhami* (Jackson et al., 1989), and included a mixture of 5th instar nymphs and adults. Parasitized hornworms were collected from 'Coker 176' flue-cured tobacco at the Tobacco Research Station, Oxford, NC in August 1988. Parasitoid cocoons from a single cohort, i.e., attached to a single host, were randomly assigned to a petri dish in one of three treatment groups each containing a tobacco leaf: (1) attached cocoons, one stilt bug per two cocoons, (2) detached cocoons, one stilt bug per two cocoons, and (3) detached cocoons only. Because the number of

cocoons varied within each cohort (36 to 114 parasitoid cocoons per host), replicates contained 8 to 38 parasitoid cocoons. Detached cocoons were distributed evenly on the surface of the tobacco leaf. Insects were arranged on a laboratory bench and held at ambient temperature (ca. 27 °C) under constant light. Constant light was chosen over constant dark, the only options in the laboratory space available at the time. This same experiment was repeated in September 1988 using a constant number (20) of parasitoid cocoons per replicate. Data for the two trials were analyzed separately.

Experiment 2. In this experiment, we tested the hypothesis that mortality of pupal *C. congregata* due to predation by adults of *J. wickhami* would be greater for younger pupae than for older pupae of *C. congregata*. Treatment groups consisted of 0 (newly-spun), 1, 2 or 3 day-old pupae with or without adult stilt bugs for a total of eight treatment groups. Each of the 40 replicates contained 20 cocoons arranged evenly on the surface of a tobacco leaf within a petri dish; each experimental replicate contained ten bugs. Dishes were held in a growth chamber at ca. 27 °C and L14:D10.

Spined stilt bugs used in Experiments 2, 3, and 4 were reared in the laboratory on previously frozen tobacco hornworm eggs placed on tobacco leaf, as described by Elsey & Stinner (1971) and Jackson & Lam (1989). Parasitoid pupae were from a laboratory colony maintained on tobacco hornworm larvae for over ten generations using methods modified from those of Postley & Thurston (1974) and Barbosa et al. (1991). Tobacco hornworms were reared by the procedures of Baumhover (1985).

Experiment 3. This experiment was performed using two age classes of parasitoid pupae, 0 day old (pre-pupae) and 3-day-old pupae (probably all pupae) to confirm the strong trend suggested by results of Experiment 2 (see Results). Methods of the two experiments were the same except that Experiment 3 was repeated 26 times over a six month period in 1991.

Experiment 4. In this experiment, we determined the relative acceptability of pupal *C. congregata* for adults of *J. wickhami*, compared to hornworm eggs, a highly acceptable food. Because acceptability of hornworm eggs for stilt bugs is reportedly affected by age (Elsey, 1972b), treatment groups contained 0 or 3-day-old hornworm eggs in combination with 0, 1, 2 and 3-day-old parasitoid pupae. Ten replicates were established for each of the eight treatment groups; each replicate

Table 1. Effect of predation by the spined stilt bug, *Jalysus wickhami*, on pupal survival of *Cotesia congregata* (mean percent mortality \pm SE)¹

Parasitoid treatment	Trial 1 ²	Trial 2 ³
Detached cocoons with no stilt bugs (control)	22.9 \pm 8.0 a	9.2 \pm 2.5 a
Attached cocoons with stilt bugs	64.6 \pm 6.9 b	72.9 \pm 5.6 b
Detached cocoons with stilt bugs	96.6 \pm 2.0 c	95.6 \pm 95.6 c

¹Data (percent survival) were analyzed by ANOVA and means were separated by Waller-Duncan K-ratio *t*-tests ($k = 100$, $df = 11$); means followed by a different letter differ significantly ($P < 0.05$).

²Each replicate contained 8 to 24 cocoons, $n = 36$.

³Each replicate contained 20 cocoons per replicate, $n = 36$.

contained ten cocoons and ten eggs and those with bugs contained ten bugs.

Results

Our observations of feeding by spined stilt bugs on pupae of *C. congregata* in the field were confirmed by closer examination of adults and late-instar nymphs feeding on parasitoid pupae under a dissecting microscope. Feeding was indicated by three specific observations: (1) stylet penetration through parasitoid cocoons, (2) stationary positioning of stylets, and (3) abdominal swelling of stilt bugs with inserted stylets (Elsey, 1972b). Results of Experiment 1 (Table 1) demonstrate that stilt bug feeding resulted in significant mortality to both detached (ca. 96%) and attached parasitoid pupae (ca. 69%), compared to the control (ca. 16%). However, mortality of parasitoids within attached cocoons was significantly lower than parasitoids within detached cocoons, demonstrating that attachment to the host larva confers at least some protection against predation by *J. wickhami*.

Predation by stilt bugs significantly reduced the survival of parasitoid pupae in no-choice laboratory experiments (Experiment 2, Table 2). Although mortality of parasitoid pupae among the four ages tested did not differ significantly, orthogonal contrasts with pooled data (0 and 1-day-old pupae vs. 2 and 3-day-old pupae) suggest that younger pupae were more vulner-

Table 2. Effect of predation by the stilt bug, *Jalysus wickhami*, on survival of *Cotesia congregata* (mean percent mortality \pm SE)

Age of <i>C. congregata</i>	Stilt bugs present	Stilt bugs absent
<i>Experiment 2</i> ¹		
0-Day-old	61.0 \pm 11.1	3.0 \pm 2.0
1-Day-old	65.0 \pm 11.5	11.0 \pm 3.7
2-Day-old	50.0 \pm 12.6	3.0 \pm 2.0
3-Day-old	14.0 \pm 14.4	3.0 \pm 1.0
<i>Experiment 3</i> ²		
0-Day-old	64.0 \pm 6.1	3.7 \pm 1.2
3-Day-old	38.3 \pm 5.3	2.2 \pm 0.6

¹Data (percent survival) were analyzed by ANOVA and means were compared by orthogonal contrasts, $n = 40$. Contrasts for 0 + 1-day-old pupae vs. 2 + 3-day-old pupae, $P = 0.0841$. Contrasts for stilt bug treatments 0 vs. 1-day-old, 0 vs. 2-day-old, and 0 vs. 3-day-old pupae, $P \geq 0.1890$. Contrasts for stilt bugs vs. no stilt bugs in each age class, $P \leq 0.0008$.

²Data (percent survival) were analyzed by ANOVA and means were compared by orthogonal contrasts, $n = 520$. Contrasts for stilt bug treatments, 0 vs. 3-day-old pupae, $P < 0.01$. Contrasts for stilt bugs vs. no stilt bugs in each age class, $P < 0.01$. Contrasts for no stilt bugs, 0 vs. 3-day-old pupae, $P < 0.01$.

able and/or acceptable than older ones ($P=0.08$; Table 2). This trend was confirmed by the results of Experiment 3 (Table 2).

In combination experiments involving the four ages of parasitoid pupae and two age classes of hornworm eggs, acceptability (as measured by resulting mortality) of parasitoid pupae was not affected by the presence or age of hornworm eggs offered to stilt bugs at the same time (Experiment 4, Table 3). Mortality of hornworm eggs was not affected by the age of hornworm eggs, nor by the age of pupal parasitoids available to stilt bugs. Because assumptions for parametric analysis of the entire data set could not be met, data were pooled within prey treatments and analyzed with a separate one-way ANOVA. As indicated in no-choice situations (Experiments 2, 3, Table 2), younger (0 and 1-day-old) parasitoid pupae were more vulnerable than older (2 and 3-day-old) parasitoid pupae.

Discussion

Adults and nymphs of the spined stilt bug, *J. wickhami*, feed on pupae of *C. congregata*, a major parasitoid of

Table 3. Effects of predation by the spined stilt bug, *Jalysus wickhami*, on four pupal age classes of *Cotesia congregata* offered in choice tests with one of two age classes of eggs of *Manduca sexta* (mean percent mortality \pm SE)

Age of Prey	Parasitoid Pupae ¹	Hornworm Eggs ²
0-Day-old	67.0 \pm 9.5 a	43.2 \pm 4.0
1-Day-old	63.0 \pm 10.6 a	----- ³
2-Day-old	33.0 \pm 8.4 b	32.7 \pm 2.5
3-Day-old	23.0 \pm 3.7 b	----- ³

¹Data (percent survival) were pooled over ages of hornworm eggs and then analyzed by ANOVA; means were separated by Walter-Duncan K-ratio t tests ($k = 100$, $df = 11$, $n = 80$). Means separated by different letters differ significantly ($P < 0.05$).

²Data (percent survival) were pooled over ages of parasitoid pupae and then analyzed by ANOVA; survival of hornworm eggs was not affected by their age ($P \geq 0.05$, $n = 80$).

³Not tested.

M. sexta on tobacco; as a result of this feeding, the parasitoid suffers significant mortality (Experiment 1). Because the spined stilt bug and parasitoid both utilize *M. sexta*, spined stilt bug feeding on *C. congregata* is an example of asymmetric intraguild predation (Polis et al., 1989). To our knowledge, this is the first documented case of direct intraguild predation involving an insect predator and parasitoid in an agricultural system.

Although both attached and detached pupae of *C. congregata* suffered significant mortality as a result of feeding by adults of *J. wickhami*, mortality of attached pupae (69%) was significantly lower than that of detached pupae (96%) (Table 1). These results support our original hypothesis, based on field observations, that mortality related to stilt bug feeding on *C. congregata* would differ between attached and detached pupal parasitoids. Our results also support the recent and more general hypothesis that continued association of parasitoids with their hosts confers protection against predation (Brodeur & Vet, 1994).

Our observation of hornworm larvae in the field and laboratory suggest that lower mortality of attached pupae is most likely due to the direct defensive behavior of the host. For example, 5th instar hornworm larvae jerk their heads backwards and 'spit' at tachinids attempting to larviposit; head-jerking intensifies into 'twisting', i.e. rapid head-jerking from side-to-side, in response to being removed from the plant. In the laboratory, 2nd, 3rd, and 4th instars display similar behaviors in response to attempted parasitization by *C. congregata* and can sometimes cause serious injury to a parasitoid by capturing it in their mandibles and fling-

ing it several centimeters away (Kester, unpublished). Host-attached parasitoids may also benefit more indirectly from the ability of mobile hosts to evade or move away from predators like stilt bugs.

Attachment to the host may be particularly important for prepupal parasitoids because of their vulnerability to predators and hyperparasitoids. Our results demonstrate that prepupal parasitoids (0 - 1-day-old pupae) suffered greater mortality as a result of predation by stilt bugs than older ones (2 - 3-day-old pupae) that had probably pupated (Table 2). Most likely, prepupal parasitoids suffered greater mortality because they were more easily penetrated and fed on by stilt bugs. Prepupae of *C. congregata* are also attacked by several species of hyperparasitoids (McNeil & Rabb, 1973), but whether attachment to the host also offers protection against hyperparasitism remains to be seen.

Competition between *J. wickhami* and *C. congregata* may occur coincidentally, i.e., 'exploitive competition' (Polis et al., 1989), as stilt bug populations increase over the season (Elsey & Stinner, 1971) and parasitoid pupae become increasingly abundant. However, parasitoid pupae were at least as acceptable as hornworm eggs, a highly acceptable prey for *J. wickhami* (Elsey, 1973), in that mortality of pupal parasitoids was similar in no-choice and combination tests with hornworms eggs (Experiments 3, 4; Tables 2, 3). Also pupae of *C. congregata* are also as nutritious as hornworm eggs for *J. wickhami* (Jackson & Kester, 1996). The relatively high acceptability of pupae of *C. congregata* and their relatively high nutritive value, suggest that they may be an important food source for *J. wickhami*. This may be especially true late in the season when parasitism rates of *M. sexta* by *C. congregata* can reach 90–100% and very few lepidopteran eggs are available (Lawson, 1959; Kester & Barbosa, 1991a). Since *C. congregata* diapauses in the prepupal stage, (Rabb & Thurston, 1974) it will be most abundant for an extended period of time at its most vulnerable stage to predation by the pre-diapausing adults of *J. wickhami*. Thus, intraguild predation by *J. wickhami* on *C. congregata* may impact on both stilt bug and parasitoid populations, although this remains to be tested in the field.

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