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Comparative Behavioral Studies of Indigenous Hemipteran Predators and Hymenopteran Parasites of the Green Cloverworm (Lepidoptera: Noctuidae)

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ABSTRACT: The green cloverworm, *Plathypena scabra* (F.), is an indigenous pest of soybean and other leguminous crops in the eastern United States. We have recently investigated the ecology and behavior of nabid predators of the green cloverworm, as well as the tactics used by four common hymenopteran parasites to overcome the defensive behavior of young green cloverworm caterpillars. Of the three dominant *Nabis* species in Kentucky agroecosystems, *Nabis roseipennis* Reuter is the most successful colonist of soybean fields. Our studies have determined the seasonal phenology, within-plant stratification, and predatory habits of these *Nabis* species, and we have demonstrated the impact of *N. roseipennis* on green cloverworm populations in the field. Three braconid primary parasites and an ichneumonid hyperparasite all must capture young green cloverworms in order to oviposit. Early instars of the green cloverworm usually respond to disturbance from other insects by dropping from the foliage and hanging on silk threads. Each of the four parasites uses a different tactic, or set of tactics, to overcome the caterpillar's defensive behavior. These studies illustrate that taxonomically closely related species, such as nabids, or members of the same ecological guild, such as parasites of young green cloverworm larvae, can exhibit striking behavioral differences. Comparative behavioral studies are an important step in determining the respective roles of these species in the natural biological control of the green cloverworm.

Certain hemipteran predators, notably species of *Nabis* and *Orius insidiosus* Say, are among the most abundant insect predators in soybean and other crops in the north central United States (Irwin and Shepard, 1980). Both *Nabis* and *Orius* species are thought to be important natural enemies of the green cloverworm, *Plathypena scabra* (F.), an indigenous pest of several leguminous crops (e.g., Pedigo et al., 1983). While *Orius* is represented by a single abundant species in the eastern United States, *Nabis* is represented by several species. Unfortunately, due to taxonomic difficulties, *Nabis* species have generally been lumped together in most studies of these predators in agroecosystems. Several years ago, our observations in soybean and alfalfa caused us to suspect that different nabid species had fundamentally different behaviors which could influence their potential impact on pest species.

In addition to presumed mortality from predators, green cloverworms are attacked by more than 50 species of parasitic Hymenoptera and Diptera (Harper et al., 1983). Different stages, such as eggs and larvae, are attacked by different species of parasites. Within the larval stage, small to medium sized larvae are attacked by different species (primarily hymenopterans) than those attacking medium to large larvae (primarily dipterans).

Here we focus on two lines of study which we have pursued regarding these natural enemies. First, we consider the comparative ecology and behavior of *Nabis*

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Table 1. Predicted number of generations per year in central Kentucky for three *Nabis* species based on developmental rate data collected in the laboratory under eight constant temperature regimes.

	N. americoferus	*N. roseipennis*	*N. rufusculus*
Calculated threshold temperature for total development	11.3°C	11.0°C	11.9°C
Mean thermal requirements for total development and pre-oviposition (DDC)[a]	497.4	610.4	597.7
Range of annual DDC accumulation above threshold for Jan.–Oct. in 1983–1986	1844–2047	1900–2100	1892–1933
Predicted number of generations per year	3	3	3

[a] Thermal requirement for pre-ovipositional period calculated by using threshold for total development and observed duration of pre-ovipositional period; DDC = degree days Celsius (Braman and Yeargan, 1988).

species. Then we discuss the behavior of a guild of hymenopteran parasites which attack small to medium sized green cloverworms.

Nabid Predators

Species of Nabidae commonly associated with field crops differ in their geographic distributions within the United States. *Nabis americoferus* (Carayon) is prevalent throughout the northern half of the United States from coast to coast (Harris, 1928), while the morphologically similar *Nabis alternatus* Parshley is distributed over the western United States, primarily west of the Mississippi River. Common southern nabid species include *Nabis capsiformis* (Germar), *Hoplistocelis deceptivus* (Harris) and *Hoplistocelis sordidus* (Reuter) (Harris, 1928; Hormchan et al., 1976; Elvin and Sloderbeck, 1984). In the southeast *Nabis roseipennis* Reuter comprises a large percentage of the multi-species complex in soybean (e.g., Turnipseed, 1974). This species also is found throughout the eastern United States from the east coast to the Mississippi River and in the northwest from British Columbia and Alberta to Colorado (Slater and Barankowski, 1978). While *Nabis rufusculus* Reuter and *Nabis kalmii* Reuter have been reported to have northern versus southern distributions, respectively, they may, in fact, represent a single species (Harris, 1928; Mitri, 1960). *Nabis americoferus, N. roseipennis* and *N. rufusculus* are the three most abundant nabid species in alfalfa and soybean in Kentucky (Braman, 1987).

Seasonal synchrony between the multi-species *Nabis* complex and peak green cloverworm populations was observed in soybean in Kentucky (Raney and Yeargan, 1977), suggesting a potential role of one or more species as natural control agents of this pest. Laboratory derived data for developmental rates of *N. americoferus, N. roseipennis,* and *N. rufusculus* under eight constant and two fluctuating temperature regimes provided the basis for our prediction that these species could each complete as many as three generations per year in central Kentucky (Table 1) (Braman et al., 1984; Braman and Yeargan, 1988). Subsequent sampling in alfalfa (a full season habitat) and soybean revealed that at least three generations are produced in alfalfa, while only one generation is produced in soybean (Braman, 1987).

Sampling *Nabis* species with a sweep net in soybean and alfalfa proved to be

Table 2. Mean number of green cloverworm larvae (GCW) recovered from plots which had received varying densities of third instar *N. roseipennis* nymphs during a 2 year investigation in soybean.

Number of nabids per plot	Mean ± SE number of GCW recovered per plot (1985)	Mean ± SE number of GCW recovered per plot (1986)
0	1.8 ± 0.4a	104.7 ± 18.9ab
5		119.0 ± 35.3a
10	0.8 ± 0.4ab	136.7 ± 31.7a
15		92.8 ± 27.8ab
20	0.4 ± 0.2b	62.2 ± 13.1b
25		58.2 ± 8.9b

ANOVA followed by LSD; numbers within a column followed by the same letter are not significantly different, $P > 0.05$.

unsatisfactory because certain species, and certain stages of all species, were more effectively sampled with a suction sampler in alfalfa and a shake cloth in soybean. This differential capture with the sweep net indicated a possible difference in the vertical stratification among species within the alfalfa and soybean habitats (Braman, 1987). A series of direct visual observations in soybean allowed us to clarify the habitat segregation in that crop (Braman and Yeargan, 1989). Observations of 581 nabids revealed that *N. americoferus* adults were located high in the soybean canopy (upper one-third), while adults of the other two species, and nymphs of all three species, tended to be located lower on the plant (primarily in the middle one-third). In all cases there was vertical separation between adults and immatures of the same species and sometimes between early (first to third) and late (fourth and fifth) instars of a given species. We found that the within-plant distribution of *N. roseipennis* nymphs, in particular, overlaps that of green cloverworm eggs and small larvae on soybean (Pedigo et al., 1973). Of the 581 nabids observed, 40 had prey items when they were sighted. The wide variety of prey (at least 11 different species, including the green cloverworm) confirmed the generalist nature of nabid predation, but also demonstrated that nabids feed on green cloverworm larvae in soybean fields.

Isenhour and Yeargan (1982) discovered fewer than expected (based on adult abundance) *N. americoferus* eggs in soybean when compared to numbers of naturally oviposited *N. roseipennis* eggs. These findings suggested that there might be differential success among nabid species reproducing in the soybean habitat. Further studies showed that, of the three common species in Kentucky, *N. roseipennis* consistently (for 3 years) produced the greatest nymphal populations in that crop (Braman, 1987).

Acceptability of various stages and instars of the green cloverworm and consumption rates by different aged *N. americoferus* and *N. roseipennis* in the laboratory (Sloderbeck and Yeargan, 1983) revealed how readily either of these nabids would prey on *P. scabra* in a petri dish arena. Consumption rates were similar for these two species suggesting that both showed potential as predators of this pest in the field. Because *N. roseipennis* was shown to be the most successful colonist of soybean in central Kentucky, this species was chosen for further study of its impact on green cloverworm eggs and larvae in the field. Studies were conducted in uncaged plots on soybean to determine the effects of different densities of *N. roseipennis* nymphs on resultant levels of green cloverworm larvae under conditions that closely resembled natural field conditions. Known numbers of *N. roseipennis* nymphs were introduced into small plots in which caged green cloverworm moths had recently oviposited. Cages were removed prior to the introduction of nabid nymphs, which were confined within the plots with barriers at ground level; flying insects could enter and leave the plots during the experiments, each of which lasted several days. During the course of the experiments, nabids initially had access to green cloverworm eggs and subsequently any larvae which hatched from those eggs. We demonstrated that *N. roseipennis,* when present in sufficient numbers at the appropriate time, is capable of causing a significant reduction in green cloverworm populations (Table 2), even when in the presence of alternative prey and other natural enemies (Braman and Yeargan, 1989).

Hymenopteran Parasites

The composition of the parasite fauna attacking the green cloverworm is well known (Harper et al., 1983; Daigle et al., 1988). The biology of a few of the more common species has been studied in the laboratory (Lentz and Pedigo, 1974; Kunnalaca and Mueller, 1979; Yeargan and Braman, 1986). Three braconid species, *Cotesia marginiventris* (Cresson), *Diolcogaster facetosa* (Weed), and *Rogas nolophanae* Ashmead, frequently oviposit in small to medium larvae (primarily instars 1 to 3) of the green cloverworm in Kentucky. In turn, all three of these braconids are hyperparasitized by an ichneumonid, *Mesochorus discitergus* Say; this hyperparasite must capture green cloverworms in order to place its eggs inside the developing primary parasite. Thus, all four species must overcome any defensive behavior of the caterpillars.

Green cloverworm larvae often respond to disturbance from other insects by dropping from the foliage. Young larvae usually drop on silken threads and remain suspended from the foliage; older larvae also may drop from foliage, but often do so without a thread (Yeargan and Braman, 1986).

We observed the behavior of the four above-mentioned parasite species to determine how they capture green cloverworm larvae. Caterpillars of the appropriate instars were placed on whole, potted soybean plants inside clear plastic cages; parasites were subsequently introduced and various components of their behavior were recorded.

The smallest of the primary parasites is *C. marginiventris,* and it primarily attacks first instars (Kunnalaca and Mueller, 1979). In our 91 observations, this species captured the host before it dropped in approximately half the cases; when larvae dropped on threads, the parasites immediately dove after them and were successful in capturing approximately 73% of the larvae.

Slightly larger larvae (primarily second and third instars) are captured by *D. facetosa,* but it rarely catches a larva before the caterpillar drops from the foliage. This parasite appears to have one consistent behavioral tactic for capturing green cloverworm larvae which drop from foliage on threads; namely, it slides slowly, head first, down the thread toward the suspended larva (Yeargan and Braman, 1986). Oviposition may occur while hanging on the thread, or both the host and parasite may tumble to the substrate below where oviposition then occurs.

The third primary parasite, *R. nolophanae,* usually attacks third instars, although second and fourth instars are occasionally attacked (Lentz and Pedigo,

Table 3. Tactics used by the hyperparasite *M. discitergus* to capture second, third, and fourth instar green cloverworm (GCW) larvae on soybean plants.

	Percent of total responses for each GCW instar			
GCW instar (*n*)	Captured GCW on leaf	Hoisted GCW by reeling in thread[a]	Combined reeling and walking down thread	Walked down thread[b]
Second (29)	6.9	65.5	27.6	0.0
Third (25)	40.0	16.0	36.0	8.0
Fourth (54)	44.4	1.9	18.5	35.2

[a] Parasite hung from leaf edge while reeling.
[b] Parasite walked down to caterpillar without reeling thread.

1974). It sometimes captures green cloverworms on the foliage, but frequently (27 of 47 observed encounters) the larvae drop as the parasite approaches. When that occurs, the parasite may dive immediately toward the suspended larva (approximately one-third of the time) or alternatively it may wait motionlessly in a head-downward position near the thread. After a variable period of waiting, which may last up to 10 minutes, the parasite usually dives toward the larva; about half of those dives are successful in capturing the host. In one case out of 46, the parasite remained in its head-downward position until the caterpillar ascended the thread and then captured it on the leaf.

The hyperparasite, *M. discitergus,* utilizes all three of the above-mentioned primary parasites as hosts. Since the primary parasites attack different instars of the green cloverworm, the hyperparasite must capture several different sizes of caterpillars. We determined the tactics it uses to capture second, third, and fourth instar green cloverworms.

To capture second instar caterpillars, the hyperparasite most frequently hung by its hind tarsi from the edge of the leaf from which the caterpillar was suspended and used its front and middle legs to reel in the caterpillar by pulling upward on the caterpillar's silk thread (Yeargan and Braman, 1989). As green cloverworm larvae get larger, higher percentages are captured on the foliage (Table 3). Another tactic used by the hyperparasite is a combination of walking partway down the thread and reeling the caterpillar up the rest of the way. Finally, the hyperparasite sometimes walks all the way down the thread to the suspended caterpillar. These last two tactics are used more frequently to capture third and fourth instars than to capture second instars (Table 3).

Thus, each of the four species of parasites uses a different tactic, or set of tactics, to overcome the defensive behavior of the green cloverworm. Furthermore, the hyperparasite, *M. discitergus,* uses several tactics which vary with the instar of green cloverworm which it is trying to capture.

What have we learned from these comparative behavioral studies of nabids and parasites? Despite their appearance, all nabids are not created equal. By undertanding seasonal phenology of the pest and nabid species in Kentucky, their respective distributions within plants, and the field biology of each nabid species, we now know which species is most relevant to natural control of the green cloverworm (and possibly other pests) in soybean, namely *N. roseipennis.* Furthermore, we have demonstrated the impact of *N. roseipennis* in the field, indicating that conservation of this predator is a valid objective in natural biological control of green cloverworms.

Doutt (1959) proposed a widely cited classification of the steps involved in host selection by parasitic insects. These steps are 1) host habitat finding, 2) host finding, 3) host acceptance, and 4) host suitability. Vinson (1975) added a fifth step which he termed host regulation. This scheme implies that when a parasite finds a host, it immediately begins to examine the host to determine its acceptability. Before a parasite can examine an active green cloverworm, however, it must first capture it. The defensive response of green cloverworm larvae must be overcome before a parasite can proceed from step 2 to step 3.

Doutt's (1959) classification of the behavior of host selection by parasites was an effort to explain in stepwise fashion why, in nature, a parasite attacks only a fraction of the host species that appear to be available to it. In certain instances the defensive behavior of potential hosts, and a parasite's ability or lack of ability to overcome that behavior, may further explain a given parasite's success or failure in exploiting a particular host species. We have shown that four species of parasites have behavioral adaptations which permit them to overcome the presumed defensive behavior of the green cloverworm.

While the green cloverworm and its parasites represent an indigenous and presumably coevolved system, our results suggest that this aspect of parasite behavior has implications for the success or failure of certain parasites imported for biological control. This could be particularly important in cases of classical biological control involving active stages of target hosts which are not conspecific with the host from which the parasites were reared in the country of origin.

Numerous questions remain about the green cloverworm and its predators and parasites. For example, how can nabid density be incorporated into pest management decisions? What is the role of other predators, such as *O. insidiosus,* in the natural control of the green cloverworm? In addition to conservation of these predators and parasites, is it possible to augment their impact?

The predatory and parasitic insect fauna associated with most crops in the United States has been thoroughly described. The roles of these natural enemies in pest suppression, however, are poorly understood. In some IPM programs, scouts sample for beneficial insects, but there is little basis for utilizing the data which are gathered. Ostlie and Pedigo (1987) recently addressed this issue by using pest survivorship estimates based on life table studies. If we are to successfully incorporate natural enemies into pest management decisions, comparative behavioral and ecological studies are needed to identify which beneficial insects are most relevant and to understand their potential roles in pest population suppression. Even in closely related groups, significant behavioral and ecological diversity exists.

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