

Video analysis to determine how habitat strata affects predator diversity and predation of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in a vineyard

Steven D. Frank^{a,*}, Stephen D. Wratten^b, Harpinder S. Sandhu^b, Paula M. Shrewsbury^a

^a University of Maryland, Department of Entomology, 4112 Plant Sciences Building, College Park, MD 20742, USA

^b National Centre for Advanced Bio-Protection Technologies, P.O. Box 84, Lincoln University, Canterbury, New Zealand

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Abstract

Preserving arthropod predator abundance and diversity in agricultural ecosystems may reduce pest populations and subsequent loss in yield. However, since natural enemy species vary in their impact on pest populations, it is crucial to identify which predators are effective at reducing pest abundance. Leafrollers spend part of their life on the ground and part in the canopy of vineyards. In this experiment, predation of tethered leafrollers on the ground and in the vine canopy was compared in a New Zealand vineyard. Leafrollers in each stratum were recorded using video equipment to identify predators that were consuming leafrollers. A separate experiment investigated the behavior of *Epiphyas postvittana* larvae when encountered by earwigs on vines or concealed within leaf shelters. Predation rates of leafrollers did not differ between the ground and canopy strata. However, predator activity, attack rate, and species richness were higher on the ground. Six predator taxa consumed leafrollers on the ground whereas only earwigs consumed leafrollers in the canopy. Earwigs were more active, and killed significantly more leafrollers in the canopy than on the ground, compensating for the relatively low activity and diversity of other predators in that stratum. This research demonstrates the value of video recording in biological control research, as it permits identification of the predators contributing to pest reduction. In addition, it highlights the need to understand the contributions of individual predator taxa to biological control to better conserve the ‘right diversity’ in agricultural systems and benefit from this ecosystem service.

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1. Introduction

Preserving and enhancing arthropod predator abundance and diversity in agricultural ecosystems can reduce pest populations, subsequent loss in yield, and the need for insecticide applications (Landis et al., 2000; Gurr et al., 2004). However, simply increasing predator abundance (Prasad and Snyder, 2004) or diversity (Snyder and Ives, 2001; Snyder and Wise, 2001; Wilby et al., 2005) does not always result in greater control of target pests. In addition,

since natural enemy species vary in their impact on pest populations, the identity of predators in an assemblage may have more influence on prey populations than species richness or abundance (Chalcraft and Reserits, 2003; Finke and Denno, 2005; Straub and Snyder, 2006). Therefore, in agro-ecosystems it is crucial to identify which predators consume focal pests so that efforts to enhance and preserve natural enemies can focus on the most important taxa. This targeted approach may lead to more efficient development of conservation biological control tactics and more effective pest control.

Leafroller (Lepidoptera: Tortricidae) larvae are important pests in commercial vineyards throughout the world. The light brown apple moth, *Epiphyas postvittana*

* Corresponding author. Fax: +1 301 314 9290.

E-mail address: sfrank@umd.edu (S.D. Frank).

(Walker), is a common leafroller species in New Zealand and Australian vineyards. This pest consumes grape leaves, flowers, and fruit. Leafroller feeding damage can predispose berries to bunch rot, *Botrytis cinerea* (Nair et al., 1988), while contaminated larvae can transmit this disease from one bunch to another (Bailey et al., 1997). Direct consumption of plant tissue and the subsequent infection by bunch rot can result in a lower grape yield and economic loss for growers (Lo and Murrell, 2000).

Leafroller pests of vineyards are generally managed with broad-spectrum insecticides such as organophosphates and carbamates which have detrimental effects on resident natural enemies and other non-target organisms (Epstein et al., 2000; Lo et al., 2000; Nagarkatti et al., 2002). In addition, some leafroller species, including *E. postvittana*, have begun to develop insecticide resistance (Suckling et al., 1984; Lo et al., 2000; Nagarkatti et al., 2002). For these reasons, there is increasing interest in attracting and conserving arthropod natural enemies in vineyards to help reduce leafroller abundance and damage.

Leafrollers spend much of their life inside shelters made by webbing leaves together with silk which may give protection from natural enemies. Leafrollers will leave their shelters to forage on nearby foliage, to search for a new shelter or pupation site, or to move from the foliage to fruit (MacLellan, 1973). Movement within the canopy may render them more vulnerable to predation than when they are in shelters. *E. postvittana* overwinters as larvae on the vineyard floor feeding on the vegetation there (Danthanarayana, 1975). Leafrollers on the vineyard floor may encounter a different assemblage of predators, relative to that of the canopy, which may differentially affect their survival. Late instar leafrollers and codling moth larvae in orchards suffer high levels of predation if they drop from the canopy or venture to the ground in search of pupation sites (Glenn and Milsom, 1978; Epstein et al., 2001). Research on the natural enemies and biological control of leafrollers in vineyards has been dominated by work on parasitoids (Danthanarayana, 1980a,b; Glenn et al., 1997; Berndt et al., 2002). However, little is known about the frequency or consequence of leafroller exposure to the predator fauna of vineyards or the behavior of leafrollers when they are encountered by a predator.

The objective of this study was to determine the identity, activity, and species richness of predators in the canopy and on the ground of a vineyard and their ability to successfully kill leafrollers. We use time-lapse video monitoring to test the hypothesis that predator activity and diversity will be greater on the vineyard floor than in the canopy. Based on this expectation our second hypothesis is that predation of sentinel leafrollers will be greater on the vineyard floor than canopy. Using information from the video recordings we also compare the rate of attack and successful predation of *E. postvittana* by the different predator taxa to identify the predators most important in reducing leafroller abundance. To further understand the

vulnerability of *E. postvittana*, we compare their escape and defensive behaviors while exposed on grape vines or concealed in leaf shelters. The use of time-lapse video in this research will increase our understanding of which predators contribute to leafroller predation and in which strata leafrollers are most susceptible. It will also demonstrate the value of video technologies to ecological study. Understanding the role of predator taxa in pest suppression increases our ability to benefit from this ecosystem service (Gurr et al., 2004).

2. Materials and methods

The study site was a 2 ha Riesling vineyard in the Horticultural Research Area of Lincoln University, Canterbury, New Zealand. Herbicide was applied periodically to reduce weeds beneath the vines and fungicide was applied to manage botrytis disease. However, no insecticide had been used in the 2004/2005 season. At the time of this experiment the vegetation beneath the vines was approximately 10 cm high and consisted primarily of white clover, *Trifolium repens* (L.). The area between vine rows was planted with orchard grass *Dactylis glomerata* (L.) mowed to 5 cm high. The entire vineyard was surrounded by a windbreak of *Populus* spp.

2.1. Predation of sentinel leafrollers

Sentinel leafroller larvae were used to evaluate ambient rates of predation in the canopy and floor of the vineyard. The experiment was conducted in a different area of the vineyard on each of five nights, between 11 and 20 January 2005. Each night was a replicate. On each night 20 fifth instar leafroller larvae (2 cm long) were positioned on the ground below the grape vines and 20 in the grape vine canopy (=2 treatments). Larvae were obtained from HortResearch, Auckland, New Zealand. All leafrollers were secured in their respective positions using size '0' insect pins (Frank and Shrewsbury 2004). Leafrollers were pinned through their penultimate abdominal segment. Preliminary trials ensured that *E. postvittana* larvae survived at least 12 h after pinning and that they did not escape from the pins.

On each night half of the length (i.e. from one end of the rows to the center) of two adjacent rows of vines was used in the experiment. Leafrollers in the ground treatment were pinned to the ground directly below the vines in both vine rows. Larvae in the vine treatment were pinned to the base of a leaf petiole 10–20 cm above a vine trunk in both vine rows. All larvae were at least 2 m apart. Leafrollers were placed in the vineyard at 18:00 h on each night. The following morning at 06:00 h, the leafrollers were counted and classified as either eaten or not eaten.

2.1.1. Statistical analysis

The number of leafrollers (of 20) eaten in each treatment per night (five replicates) was compared using a *t*-test.

2.2. Predator assemblages and activity

Leafroller larvae were monitored with video cameras to determine which predators were attacking and consuming the larvae in the canopy compared to the ground of the vineyard. The experiment was conducted on six nights between 15 and 26 January 2005. On each night, four larvae (two in the canopy and two on the ground) were monitored from 18:00 to 06:00 h. The cameras were Bishke CCD50 12P hi-resolution, monochrome, low-light surveillance cameras (Videotronic Uwe Bishke GMBH International, Neumünster, Germany) illuminated by infrared LED bulbs. Recordings were made on a Hitachi time-lapse video recorder (Model: VT-L1500E, Hitachi, Tokyo, Japan).

The cameras were positioned approximately 10 cm above larvae that were on the ground. Those in the canopy were recorded from a horizontal perspective with the lens 10 cm away. The cameras monitored an area approximately 10 cm in diameter (the 'arena') at the center of which was the leafroller. From the recordings, each time a predator entered the arena the species (or morphospecies), the time it entered and left the arena, and attacks on *E. postvittana* were recorded. This provided two measurements of predator activity: (1) the number of times a predator entered the arena (= visits); and (2) the duration of the visit (= time). Predator attacks were classified as either unsuccessful (i.e. the leafroller was attacked but not killed) or successful (i.e. attack resulted in the death of the leafroller). Species richness, used to compare predator assemblages in each stratum, was calculated as the mean number of species (morphospecies) that entered the arena each night.

2.2.1. Statistical analysis

Twelve leafrollers on the ground and 10 in the canopy were monitored by video. Many of the predators were occasional or appeared in only one of the two habitat strata and earwigs were most common. Therefore, separate *t*-tests were used to compare total (all predators combined) predator visits between the ground and canopy as well as European earwig, *Forficula auricularia* (L.) (Dermaptera: Forficulidae), visits between the strata. The other measure of activity, time, was analyzed the same way. Each monitored larva was a replicate.

Analysis of attack data was conducted by χ^2 -squared tests. The first test compared the number of visits and the number of attacks by each predator taxon using a 2 (visits and attacks) by 5 (five predator taxa) contingency table. This analysis included visits prior to leafroller consumption, after which predators did not have an option to attack. The second χ^2 -squared test compared the number of attacks and the number of successful attacks by each predator taxon in a 2 (attacks and successful attacks) by 5 (five predator taxa) contingency table. If the 2 × 5 table was significant ($P < 0.05$), pairwise comparisons were made between predator taxa using 2 × 2 contingency tables. A

t-test was used to compare species richness (average number of predator taxa that visited the arena per night) between the ground and canopy strata.

2.3. Leafroller response to earwigs

The European earwig was the most common predator species recorded in the canopy. Therefore, an experiment was designed to determine how leafrollers respond when encountered by an earwig while exposed on a leaf or vine or concealed in a shelter. This experiment was conducted over 4 days using a potted grapevine that was 80 cm tall. The first day of the experiment 12 leafrollers were released onto the plant and allowed 30 min to settle on the leaves and vines. After 30 min, leafrollers had dispersed throughout the plant but had not constructed shelters (= exposed treatment). An adult earwig was released at the base of the plant and allowed to search until it encountered a leafroller exposed on a leaf or vine. The immediate response of the leafroller was recorded and the earwig was removed from the plant. This process was repeated 12 times with different earwigs (alternating male and female) on the first day of the experiment. By the following day, most of the leafrollers had constructed shelters (= shelter treatment). An earwig was released as before and allowed to search until it encountered a leafroller in a shelter; the immediate behavior of the leafroller was recorded. This was repeated nine times then all leafrollers were removed from the plant. The following day the same 2-day protocol was repeated. Thirteen more observations were made of leafrollers on vines and leaves (total $n = 25$) while seven more were made of leafrollers in shelters (total $n = 15$). Leafroller response was recorded in one of two broad categories, escape or defense. Within these broad categories two escape and two defense behaviors were identified that were specific to larvae exposed on leaves and vines or those concealed in shelters. Leafrollers on vines dropped with a silk thread that kept them attached to the plant (escape), dropped without a thread and landed on the soil (escape), remained still as the earwig investigated (defense), or thrashed violently to deter the earwig (defense). Leafrollers in shelters dropped without a thread (escape), exited the shelter (escape), remained still (defense), or thrashed violently within the shelter (defense).

2.3.1. Statistical analysis

The number of times larvae exhibited escape and defense behavior while exposed and in shelters was compared by χ^2 -squared test using 2 (exposed and shelter) × 2 (escape and defense) contingency tables. The number of times the different responses were exhibited by leafrollers within the exposed or shelter group were compared separately by χ^2 -squared tests using 4 (four responses) × 2 (present or absent) contingency tables. If the 4 × 2 table was significant ($P < 0.05$), pairwise comparisons were conducted using 2 × 2 contingency tables.

3. Results

3.1. Predation of sentinel leafrollers

The mean number of leafrollers (\pm SE) consumed each night on the ground (10.6 ± 1.0) and in the canopy (12.6 ± 1.5) were not significantly different ($t = 1.10$; $df = 8$; $P > 0.05$).

3.2. Predator assemblages and activity

A total of 12 leafrollers were video recorded on the ground of which 7 (58%) were consumed. Ten leafrollers were recorded in the canopy of which 6 (60%) were consumed.

3.2.1. Predator activity

A total of 12 predator taxa were identified through video monitoring of the prey arenas (Table 1). Ants were responsible for killing one larva. During this single predation event, ants made 50 visits per hour to the arena which resulted in 212:57:00 (h:min:s) of activity. This value accounted for 85% of the total 249:51:49 (h:min:s) of predator activity recorded during all monitoring of ground predators. This one event overwhelmed the results of all other analyses of predator activity data, obscuring the contributions of other taxa. Therefore, the ant activity data from this predation event were removed from the analysis of predator activity. All other ant activity was included in the analysis (Table 1).

The mean number of visits by predators to prey arenas on the ground per night was significantly higher than in the canopy ($t = 4.18$; $df = 20$; $P = 0.0005$) (Fig. 1). Likewise, the mean total predator seconds spent in prey arenas per night in the ground arenas was significantly higher than those spent in the canopy ($t = 4.50$; $df = 20$; $P = 0.0002$) (Fig. 1). Analysis of earwig data revealed opposite trends. The mean number of earwig visits per night in the canopy

was significantly higher than on the ground ($t = 2.21$; $df = 20$; $P = 0.038$) (Fig. 1). The mean number of seconds spent per night by earwigs was also significantly higher in the canopy than on the ground ($t = 3.05$; $df = 20$; $P = 0.0064$) (Fig. 1).

3.2.2. Predator attacks

Predators that attacked very few times or never had a successful attack were not included in these analyses. As

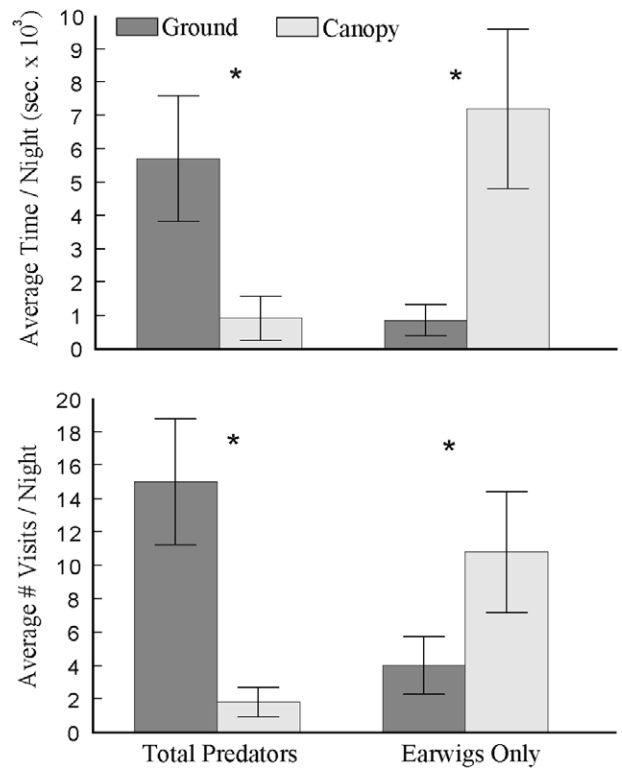


Fig. 1. The average number of seconds spent in, and number of visits to arenas by all predators combined (not including earwigs) and by earwigs each night. *Indicates significant difference ($P < 0.05$) between habitat strata.

Table 1

Summary of the duration and number of visits by predator taxa observed in video-monitored leafroller arenas on the vineyard floor and canopy

Predator taxa	Predator activity on the ground				Predator activity in the canopy			
	Time ^a	(%)	Visits ^b	(%)	Time	(%)	Visits	(%)
Formicidae	16:09:38	(42.6)	168	(42.5)	00:00:00	(0.0)	0	(0.0)
Forficulidae	02:47:46	(7.4)	48	(12.2)	20:00:02	(88.9)	108	(85.7)
Opilioniidae	03:09:00	(8.3)	43	(10.9)	00:00:00	(0.0)	0	(0.0)
Araneae	04:56:54	(13.0)	28	(7.1)	02:24:27	(10.7)	12	(9.5)
Tricladida	04:38:37	(12.2)	16	(4.1)	00:00:00	(0.0)	0	(0.0)
Pulmonata	04:22:55	(11.5)	40	(10.1)	00:00:00	(0.0)	0	(0.0)
Hemerobiidae	00:31:33	(1.4)	30	(7.6)	00:06:03	(0.4)	6	(4.8)
Chilopoda	00:05:15	(0.2)	9	(2.3)	00:00:00	(0.0)	0	(0.0)
Coccinellidae	00:03:49	(0.2)	3	(0.8)	00:00:00	(0.0)	0	(0.0)
Staphylinidae	00:08:20	(0.4)	4	(1.0)	00:00:00	(0.0)	0	(0.0)
Carabidae	00:07:02	(0.3)	3	(0.8)	00:00:00	(0.0)	0	(0.0)
Acari	00:57:36	(2.5)	3	(0.8)	00:00:00	(0.0)	0	(0.0)
Total	37:58:25	(100.0)	395	(100.0)	22:30:32	(100.0)	126	(100.0)

^a Total amount of time (h:min:s) spent in leafroller arenas by each predator taxon in the ground and canopy habitat strata (sum of all nights of video).

^b Total number of visits to leafroller arenas by each predator taxon in the ground and canopy habitat strata (sum of all nights of video).

indicated above ants were also not included. There was a significant difference in the frequency of visits relative to attacks by the six predator taxa overall and between individual pairs of taxa (Table 2). There was a significant difference in the frequency of attacks relative to successful attacks overall but not between pairs of taxa (Table 2).

As earwigs were the only predator that attacked and killed leafrollers in the canopy the above analyses were not conducted. However, earwig attacks on the ground and in the canopy were compared to determine if there was a difference in the attack number or successful attacks by this predator between the two strata. Earwigs attacked more per visit in the canopy than on the ground ($\chi^2 = 14.41$, $P = 0.001$) although the number of successful attacks did not differ ($\chi^2 = 0.124$, $P = 0.335$) (Fig. 2). In addition, earwigs were responsible for all six of the leafrollers killed in the canopy which is significantly greater than the frequency of

Table 2

The number of visits, total attacks, and successful attacks by common vineyard predators of leafrollers on the ground

Predator taxa	Visits	Total attacks		Successful attacks	
		#	% ^a	#	% ^b
Forficulidae	32	8	25.0b	2	25.0a
Opilionidae	29	14	48.3ab	1	7.1a
Araneae	23	4	17.4c	1	25.0a
Tricladida	11	9	81.8a	2	22.2a
Pulmonata	22	6	27.3b	0	0.0a
Formicidae	363	— ^c	—	1	—
χ^2 , P		3.10, 0.013		17.95, <0.001	

Taxa with different letters in the % column were not significantly different ($P < 0.05$) in pairwise comparisons.

^a Percentage of visits in which an attack occurred (# attacks/# visits \times 100%).

^b Percentage of attacks which resulted in a successful attack (# successful attacks/# attacks \times 100%).

^c Attack data was not calculated for Formicidae because they attacked in large groups (see text).

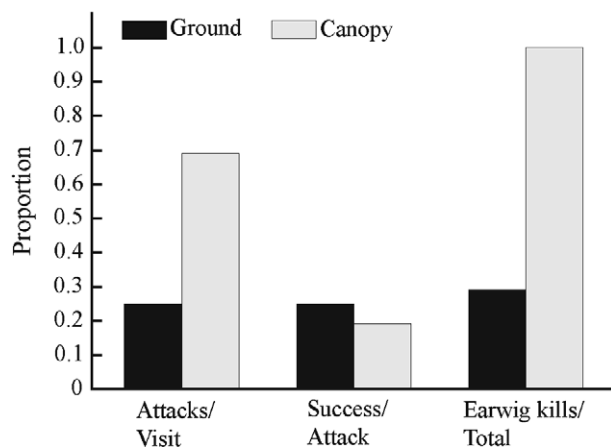


Fig. 2. Proportion of earwig visits that resulted in attacks (attacks/visit), percent of earwig attacks that were successful (success/attack), and percent of total leafrollers killed that were killed by earwigs (earwig kills/total) on the vineyard floor and canopy.

kills by earwigs on the ground ($\chi^2 = 6.96$, $P = 0.016$) (Fig. 2).

3.2.3. Predator species richness

Species richness was significantly higher on the ground (5.8 ± 0.9) than in the canopy (1.8 ± 0.3) ($t = 6.61$; $df = 20$; $P < 0.001$).

3.3. Leafroller response to earwigs

Escape and defense behavior was used by 22 (88%) and 3 (12%) leafrollers, respectively, when exposed on vines. This was significantly different from leafrollers in shelters of which 7 (47%) used escape and 8 (53%) used defensive behaviors ($\chi^2 = 8.03$, $P = 0.006$). When larvae were exposed on vines larvae dropped from the vine with or without a silk. The leafrollers that exhibited defensive behavior thrashed violently to ward off attack or remained still as the earwig investigated (Fig. 3). There were

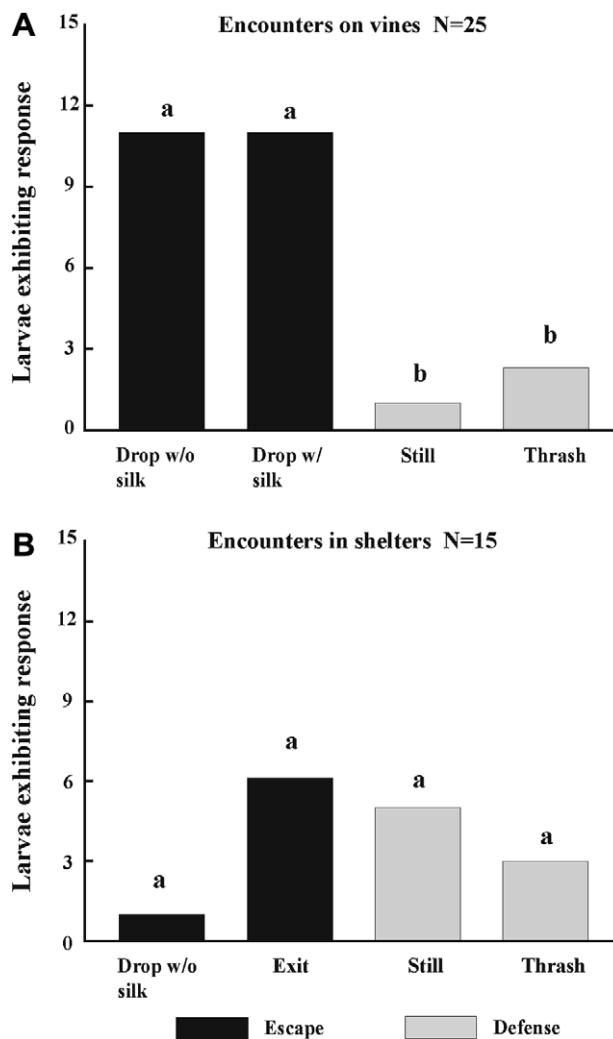


Fig. 3. The number of leafrollers that exhibited escape and defensive responses during encounters with earwigs while exposed on vines (A) or concealed in leaf shelters (B). Bars with different letters are significantly different at ($P < 0.05$).

significant differences in the frequency of these four behaviors within the exposed treatment overall ($\chi^2 = 14.52$, $P = 0.002$) and as determined by pairwise χ^2 -square tests (Fig. 3). When larvae were in shelters, escape behavior consisted of exiting the shelter or dropping (Fig. 3). Defensive behaviors were either thrashing violently or remaining still within the shelter (Fig. 3). There was no significant difference in the number of leafrollers using each of these behaviors ($\chi^2 = 3.93$, $P = 0.27$) (Fig. 3).

4. Discussion

The study vineyard had an active and relatively diverse predator community that could likely exert significant pressure on natural populations of leafrollers. The overall predation rate of leafrollers on the ground and in the canopy was 50–60% per night. This does not support our hypothesis that predation would differ between the canopy and the ground. The similarity in predation rate is interesting in light of the differences in predator diversity and activity between the ground and canopy. Predator species richness was 4 times greater on the ground than in the canopy. Predator activity, as indicated by time spent and the number of visits to prey arenas, was also higher on the ground than in the canopy.

Larvae in this experiment were pinned and could not exhibit their full repertoire of defensive behaviors such as the ability to escape. Therefore pinned leafrollers may be more susceptible to attack in general and to predator taxa that would not normally attack unpinned leafrollers. However given this, pinned leafrollers could still perform the thrashing defensive behavior that was observed in laboratory experiments and has been described by MacLellan (1973). This behavior was observed in video recordings to successfully drive off predators on many occasions and accounts for the low percentage of successful attacks by predators. This suggests that although pinning larvae may somewhat exaggerate predation rates and should be taken into consideration, results of these studies can still be used to make valid inferences on predator activity and predation.

The most effective predator, in terms of total leafroller predation, was earwigs, which spent 10-fold more time in the canopy arenas than in arenas on the ground. It appears the greater activity and efficiency of earwigs compensated for the lower activity and diversity of other predator taxa in the canopy relative to the ground, which resulted in similar rates of predation between the strata. Furthermore, although predator diversity was greater on the ground, three predator taxa—earwigs, spiders, and flatworms—accounted for 72% of leafroller predation there. High predation rates by a few taxa may partially explain why greater predator diversity did not result in higher levels of predation overall. These results suggest that predator identity may be more important than overall predator diversity in regulating herbivore populations in this system. This is similar to research in other agricultural systems where increasing species richness did not increase predation of pest species. For example, Straub and Snyder (2006) similarly demonstrated that aphid suppression was

greatest in the presence of predators with the highest consumption rates rather than in the presence of a diverse predator assemblage.

Although *E. postvittana* spend time in shelters, they frequently leave shelters to feed on nearby foliage, to find a new shelter or pupation site, or in response to predators invading their current shelter increasing their exposure to natural enemies (MacLellan, 1973). Additionally, field observations have found earwigs within leafroller shelters actively feeding on larvae (Danthanarayana, 1983). Our studies found that earwigs frequently encountered and attacked exposed leafrollers in the canopy and in 25% of attacks the leafroller was killed. However, our studies used pinned larvae which were restricted in their ability to drop from the canopy as seen in the laboratory study. As leafrollers escape by dropping, they often remain on a silk within the canopy until danger has passed. Therefore the use of pinned larvae in this study may have overestimated the impact of earwigs as canopy predators. However, if leafrollers drop to the ground, they are exposed to the diverse and active predator assemblage on the ground, from which they may be less able to escape. This suggests predation on the ground may be greater than in the canopy for unpinned leafrollers. Similar interactive effects between canopy and ground foraging predators have been demonstrated in alfalfa as coccinellid predators elicit a dropping response in aphids which were then consumed by ground dwelling carabid beetles (Losey and Denno, 1998). Similarly, late instar leafrollers and codling moth larvae in orchards suffered high levels of predation if they dropped from the canopy or ventured down in search of pupation sites (Glenn and Milsom, 1978; Epstein et al., 2001). Predator avoidance behavior such as dropping from vines can also reduce herbivore feeding efficiency and damage (Beckerman et al., 1997; Schmitz, 1998).

Evaluation of the predator species which contribute to pest reduction can be evaluated using many methods. The use of pitfall traps, sticky cards, or related collection techniques provide data on the potential predators present and, if accompanied by laboratory feeding trials, which ones may consume the pest in question. The use of sentinel prey items in the field can provide evidence of predation rate *in situ* but still leaves unanswered questions regarding the predator taxa responsible (e.g. Frank and Shrewsbury, 2004a). Advances in molecular and serological techniques can determine which predator taxa have consumed a particular pest species. However, these techniques can be expensive, time consuming, and do not address the frequency of predation, the quantity eaten or account for scavenging and secondary predation (Symondson, 2002). In the current research, time-lapse video equipment was used to monitor continuously sentinel prey items overnight and enabled quantification of predation events. Similar video technology has been used to identify the predators associated with agricultural field margins (Merfield et al. 2004).

The use of video to monitor leafroller prey resulted in observations and conclusions that would not be attainable

from unmonitored or sporadically monitored sentinel prey experiments. Video monitoring provided positive identification of predators that encountered the leafrollers and which ones were responsible for leafroller predation on the ground and in the canopy. This kind of information allows for the development of conservation biological control techniques directed at specific predatory taxa that consume focal pest species. *A priori* identification of important predators could reduce the research time and resources required to develop effective conservation biological control techniques to be implemented by producers.

This study fulfilled the first step in the development of biological control protocols in which we evaluated the ambient level of control by predators and identified which taxa are potentially important. Future research should determine how these and other predators affect the growth of natural leafroller populations. In addition, research should address whether vineyard habitat may be altered to attract and conserve greater populations of earwigs, spiders, and flatworms shown to successfully kill *E. postvittana*.

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