ACQUIRED NATURAL ENEMIES OF THE WEED BIOLOGICAL CONTROL AGENT *OXYOPS VITIOSA* (COLEPOTERA: CURCULIONIDAE)

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ABSTRACT

The Australian curculionid *Oxyops vitiosa* Pascoe was introduced into Florida in 1997 as a biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.) S. T. Blake. Populations of the weevil increased rapidly and became widely distributed throughout much of the invasive tree's adventive distribution. In this study we ask if *O. vitiosa* has acquired natural enemies in Florida, how these enemies circumvent the protective terpenoid laden exudates on larvae, and what influence 1 of the most common natural enemies has on *O. vitiosa* population densities? Surveys of *O. vitiosa* populations and rearing of field-collected individuals resulted in no instances of parasitoids or pathogens exploiting weevil eggs or larvae. In contrast, 44 species of predatory arthropods were commonly associated (>5 individuals when pooled across all sites and sample dates) with *O. vitiosa*. Eleven predatory species were observed feeding on *O. vitiosa* during timed surveys, including 6 pentatomid species, 2 formicids and 3 arachnids. Species with mandibulate or chelicerate mouthparts fed on adult stages whereas pentatomids, with haustellate beaks, pierced larval exoskeletons thereby bypassing the protective larval coating. Observations of predation were rare, with only 8% of timed surveys resulting in 1 or more instances of attack. Feeding by the pentatomid *Podisus mucronatus* Uhler accounted for 76% of all recorded predation events. *Podisus mucronatus* numerically responded to fourth instars but no response was observed for other life stages. Damage to *M. quinquenervia* plants from feeding by *O. vitiosa*, however, was not influenced by *P. mucronatus* densities, indicating that predation does not alter plant suppression.

Key Words: biological control, biotic resistance, predation, *Oxyops vitiosa, Melaleuca Quinquenervia, Podisus mucronatus*

RESUMEN

El curculiónido australiano *Oxyops vitiosa* Pascoe fue introducido a la Florida en 1997 como un agente de control biológico para el árbol invasor, *Melaleuca quinquenervia* (Cav.) S. T. Blake. Poblaciones del gorgojo aumentaron rapidamente y se distribuyeron ampliamente por mucho de la distribución del árbol invasor adventivo. En este estudio, preguntamos si *O. vitiosa* han adquerido enemigos naturales en la Florida, como estos enemigos evitan las secreciones de turpenoides que protejen las larvas, y que influencia tiene uno de los enemigos naturles mas comunes sobre la densidad de la población de *O. vitiosa*? La inspección de la población de *O. vitiosa* y la cria de individuos recolectados en el campo resulto en no caso de parasitoides y patógenos usando los huevos o larvas de los gorgojos. En contraste, 44 especies de artrópodos depredadores fueron comúnmente asociadas (>5 individuos cuando se agregados por todos los sitios y fechas de muestreo) con *O. vitiosa*. Se observaron once especies de depredadores alimentándose sobre *O. vitiosa* durante los sondeos, incluyendo 6 especies de pentatómidos, 2 formícidos y 3 arácnidos. Especies con partes bucales mandíbuladas y queliceradas se alimentaron sobre los estadios adultos mientras que los pentatómidos, con su pico chupador, puncharon los exo-esqueletos de las larvas asi pasando el cubertura protectiva de las larvas. Observaciones de depredación fueron raras, con solamente 8% de los estudios que llevaron el tiempo resultaron en 1 ó más instancias de ataque. La alimentación del pentatómido *Podisus mucronatus* Uhler contó con 76% de los eventos de depredación registrados. *Podisus mucronatus* respondió numericamente al los instares de cuarto estadio pero ninguna respuesta fue observada en los otros estadios de vida. El daño a las plantas de *M. quinquenervia* debido a la alimentación por *O. vitiosa*, sin embargo, no fue influenciado por la densidad de *P. mucronatus*, que indica que la depredación no altera la supresión de la planta.

Acquisition of novel natural enemies may influence the successful establishment, spread, and impact of introduced weed biological control agents in their adventive range (Goeden & Louda 1976; Semple & Forno 1987; Simberloff 1989; Cornell & Hawkins 1993; Hill & Hulley 1995; McPartland & Nicholson 2003; Norman et al. 2009; Paynter et al. 2010). Of the arthropods introduced for control of invasive plants world wide, approximately 50% suffer sufficient mortality from higher trophic levels to significantly limit suppression of target weeds (Goeden & Louda 1976).

The spider mite *Tetranychus lintearius* (Dufour), for example, was introduced into New Zealand, Australia, and the United States as a biological control agent of the invasive plant *Ulex europaeus* L. (Fabaceae) (Hill & Stone 1985; Hill et al. 1991). Although successfully established and widely distributed, mites in each country rarely sustained sufficient population densities to provide permanent control of the target weed (Rees & Hill 2001). Subsequent studies demonstrated that a complex of native and introduced predators suppressed *T. lintearius* populations and limited control of the invasive weed (Peterson 1993; Peterson et al. 1994; Pratt et al. 2003).

Considering the ecological risks (Carvalheiro et al. 2008) and expense of biological control, increased attention in the scientific literature has focused on predicting susceptibility of introduced biological control agents to natural enemies in the adventive range (Kuhlmann et al. 2006). Hill & Hulley (1995), for instance, demonstrated that variation in susceptibility of introduced herbivores to parasitoids is related, in part, to evolutionary strategies that render the prey less accessible, apparent, or palatable to the attacker. Along this continuum of use by natural enemies lie those species that are highly apparent yet experience relatively less attack due to the expression of chemical deterrents that render them less palatable or even toxic to prospective natural enemies. The introduced weevil *Oxyops vitiosa* Pascoe sequesters terpenoids from leaves of its host plant *Melaleuca quinquenervia* (Cav.) S. T. Blake and larvae excrete these compounds through their integument (Wheeler et al. 2002). The consumption and expression of these terpenoids repels the red imported fire ant (*Solenopsis invicta* Buren) and red wing blackbird (*Agelaius phoeniceus* L.) under controlled feeding tests (Wheeler et al. 2002). It remains unclear, however, if this acquired repellency confers protection from the suite of potential novel natural enemies that exist in the herbivore's adventive range.

Oxyops vitiosa is native to eastern Australia and is a specialist herbivore of the invasive tree *M. quinquenervia* (Balciunas et al. 1994). Based on its narrow host range, the weevil was permitted for release in Florida in 1997 and readily established in *M. quinquenervia* dominated habitats (Center et al. 2000; Pratt et al. 2003). Adult weevils feed on *M. quinquenervia* foliage whereas larvae consume only newly-developed leaves that are ephemerally produced in seasonal flushes at branch apices (Purcell & Balciunas 1994).

Following its introduction, *O. vitiosa* populations increased rapidly and became widely distributed throughout much of the invasive tree's geographic distribution in Florida (Pratt et al. 2003; Balentine et al. 2009). When considering the large densities of these herbivores in the environment, we questioned (1) whether *O. vitiosa* had acquired natural enemies in Florida, (2) how these enemies mitigated the defensive strategies of the herbivore, and (3) what impact the most abundant of these natural enemies has on *O. vitiosa* population densities?

Materials and Methods

Surveys for natural enemies associated with *O. vitiosa* were conducted at 4 locations in south Florida. Site 1 was located near Ft. Lauderdale, Broward Co., FL. The site was a 0.5-ha field consisting of 2- to 5-m tall trees occurring at a density of 21,560 trees/ha. In general, *M. quinquenervia* trees were growing in organically rich soils typical of reclaimed 'glades' systems. *Melaleuca quinquenervia* trees at site 2 occurred under a power line right of way near Weston, Broward Co., FL. Prior to 1997 land managers cut *M. quinquenervia* trees near their bases, resulting in multi-stemmed coppices. The study area was 0.5 ha and trees were 2-5 m tall, occurring at a density of 2,517 trees/ha. Site 3 was located near Estero, Collier Co., FL and consisted of an 8-ha area of drained wetland converted to pasture. To suppress *M. quinquenervia* growth, land managers mowed trees at 6-month intervals, resulting in coppices 0.5-2 m in height. These coppicing clumps formed a dense, nearly continuous canopy of leaves with 4,406 stumps/ha. In contrast to the previous sites, the soil type was primarily sand, consistent with an invaded pine flatwoods. Site 4 consisted of a 1-ha area within the historically mesic flatwoods of the Picayune Forest near Belle Meade, Collier Co., FL. A fire burned much of the *M. quinquenervia* dominated areas in 1998 resulting in recruitment of 129,393 trees/ha of primarily small 1-2 m tall saplings, with an occasional large, mature tree interspersed (Table 1).

Surveys were conducted monthly at each site from Nov 2000 through Jun 2001 and sampling occurred between 10 AM and 2 PM on days without precipitation. Sampling consisted of sweeping *M. quinquenervia* foliage, and occasionally trunks, with a 90-cm diameter sweep net. One sample consisted of 100 sweeps of the net in a sweeping motion of 180° with sweeps spaced ca. 1.0 m apart along a randomly selected 100-m transect. Four samples along separate transects were collected each month. The content of the net after 100 sweeps was emptied into a 4-liter sealable bag and frozen at minus 20 (±1) °C until processed. Arthropods were then separated from plant material, sorted by morphological types, and pinned or stored in 70% ethanol.

One limitation of our sweep sampling method included collecting arthropods that were not closely associated with *O. vitiosa*, but were transients, merely resting on the plant foliage or disturbed from understory vegetation while sampling. Additionally, this method was biased to-

TABLE 1. RESEARCH SITE DESCRIPTION AND SUMMARY OF SURVEYS CONDUCTED FOR *O. VITIOSA* IN SOUTH FLORIDA.

Site	GPS Coordinates		Surveys conducted[a]	Habitat	Hydro-period
1	N 26.05605	W -80.25168	1, 2, 3, 4	Swale	Short
2	N 26.03548	W -80.43495	1, 2, 3, 4	Swale	Medium
3	N 26.42550	W -81.81033	1, 2, 3, 4, 5	Mesic flatwoods	Short
4	N 26.10478	W -81.63392	1, 2, 3, 4	Mesic flatwoods	Short
5	N 26.46017	W -81.70186	4	Mesic flatwoods	Short
6	N 26.54698	W -81.79820	4	Wet flatwoods	Short
7	N 28.47323	W -81.33632	4	Upland lake	Long
8	N 25.71341	W -80.47949	4	Swale	Medium
9	N 25.81208	W -80.41780	4	Swale	Medium
10	N 26.16227	W -80.36269	4	Swale	Long

[a]1 = Arthropods associated with *O. vitiosa,* 2 = *O. vitiosa* population density, 3 = *O. vitiosa* egg parasitism, 4 = Entomopathogens of *O. vitiosa,* 5 = Impacts of *P. mucronatus* on *O. vitiosa* populations.

wards poor fliers. All study sites possessed smaller trees that facilitated sampling but may have biased collections to lower rather than higher canopy dwelling species. Therefore, caution should be used when drawing inferences from these data due to the unknown relationships between sampled arthropods and *O. vitiosa.* For this reason, a minimum of 2 observers also searched for direct predation or parasitism for 30 min/survey at each site monthly.

All specimens, except formicids, were submitted to and deposited at the Florida State Collection of Arthropods (FSCA, Division of Plant Industries, Gainesville, FL) for identification and incorporated into their taxonomic database (Costello et al. 2003). Most formicids were identified and retained by L. Davis of the Fire Ant Unit, Agricultural Research Service, USDA, Gainesville, FL. A few formicids were identified by M. Deyrup of the Archbold Biological Station, Lake Placid, FL. Several dipteran specimens were identified at the Systematic Entomology Laboratory, Agricultural Research Service, USDA, Beltsville, MD.

Population densities of *O. vitiosa* at sites 2 and 3 were monitored by delineating a 0.5-ha study site within the existing *M. quinquenervia* stands, respectively. Within these plots, transects were arranged in a grid pattern with 8 transects oriented east to west at 10-m intervals and points on each transect spaced 10 m apart. Beginning in Nov 2000 through Jun 2001, *M. quinquenervia* trees were sampled monthly at 20 randomly selected transect points. Plants at each sampling point were selected based on the quarter method of vegetation sampling (Smith 1966). The area was divided into 4 quarters at each sampling point based on the 4 cardinal directions. The nearest tree to the sample point in each quarter was examined to determine the number of *O. vitiosa* per plant. The ordered distance method was used to quantify weevil population densities over time at sites 1 and 4 (Krebs 1999). In total, 30 points were randomly selected at each sampling interval and the nearest tree to each point was inventoried. At all sites, *O. vitiosa* life stages were counted along with plant resource availability. Resource availability was assessed on a 5-point scale based on visual estimation of percentage of suitable foliage for feeding by *O. vitiosa*: 0 = no suitable foliage; 1 = less than 25%; 2 = 26 to 50%; 3 = 51 to 75%; 4 = 76 to 100%.

A partial correlation analysis was used to identify those predators positively associated with *O. vitiosa* (PROC CORR), after controlling for the influence of site by the PARTIAL statement (SAS 1999). For all tests, a P-value <0.05 was considered significant evidence for association among predators and *O. vitiosa*. However, caution should be used when interpreting these data because association is not sufficient evidence to suggest that a trophic relationship exists among the species.

To determine if *O. vitiosa* had acquired egg or larval parasitoids in its adventive range, 50 eggs were collected at random from sites 1-4 at monthly intervals. Eggs were examined under a dissecting microscope (10-50X) to detect presence of larval exit holes indicating larval eclosion; eggs with exit holes were discarded. The remaining eggs were left attached to leaf material and placed in gelatin capsules. These capsules were transferred into a Petri dish (10 × 1.5 cm) that was then sealed with Parafilm to retain leaf moisture. Petri dishes were placed in an environmental chamber at 25 (±1) °C, with a photoperiod of 16:8 (L:D) and a relative humidity of 65% ± 10%. Hatching of eggs was monitored once a week. Eggs that did not hatch after 1 month were dissected.

To detect larval parasitoids, 50 third or fourth instars of *O. vitiosa* were reared to the pupal stage. Each larva was placed individually in 1 Petri dish (10 × 1.5 cm) with moistened filter paper and *M. quinquenervia* leaves. Petri dishes were sealed with Parafilm and kept in an environmental chamber under the same conditions as described earlier. Host leaves were replaced every

other day until the prepupal stage, when leaves were removed for the remainder of the study.

Surveys for entomopathogens of *O. vitiosa* were conducted at 10 sites between Jun 2003 and Jan 2004 (Table 1). Late instars and adults were collected, packaged in an ice-cooler, transported to the laboratory, and examined by USDA/ARS insect pathologists at the Center for Medical, Agricultural, and Veterinary Entomology, Gainesville, FL. All live individuals originating from the same location were homogenized in 3-5 mL of deionized water and a sample of the crude suspension was examined with a phase-contrast microscope to search for pathogens, such as microsporidia, fungal spores, or occluded viruses.

During initial surveys, the pentatomid bug *Podisus mucronatus* Uhler was commonly associated with *O. vitiosa* and observed feeding on larval stages of the biological control agent at each of the 4 study sites. Therefore, we quantified the population dynamics of *P. mucronatus* and *O. vitiosa* at site 3. Sampling was conducted as described earlier except 20 transects were oriented east to west at 20-m intervals with 9-10 points on each transect spaced 20 m apart. *Melaleuca quinquenervia* plants were sampled at 50 randomly selected transect points every 6 weeks (approximate generation time; Purcell & Balciunas 1994) beginning in Dec 2000 and continuing through Oct 2002. As before, the nearest plant to the sample point in each quadrant was examined to determine the number and life stage of each *O. vitiosa* and *P. mucronatus* individual. In addition to these data, we also noted the amount of damage due to herbivory, plant resource availability (as described earlier), and the number of dead larvae. Herbivory damage was assessed on a 5-point scale based on visual estimation of the percentage of suitable foliage destroyed by *O. vitiosa* feeding: 0 = no damage; 1 = less than 25% destroyed; 2 = 26 to 50%; 3 = 51 to 75%; 4= 76 to 100% destroyed. Linear regression was used to test for a numerical response of predators to life stages of *O. vitiosa* (n = 6), dead larvae, food availability, and herbivory damage (i.e., aggregation of predators to patches of high prey density; Schenk & Bacher 2002).

Results and Discussion

Biotic resistance describes the collective influence of parasitoides, predators, pathogens, and competitors on the establishment and proliferation of non-indigenous species, including introduced biological control agents (Simberloff & Von Holle 1999). Historically, native predators, parasitoids, and pathogens have interfered with half of the published case histories involving insect introductions for weed control (Goeden & Louda 1976). Considering this high rate of interference, we questioned if *O. vitiosa* had acquired natural enemies in its adventive range.

We observed no instances of parasitoids (egg and larval) or pathogens exploiting *O. vitiosa*. Of the 1138 *O. vitiosa* eggs collected from the study sites (Table 1), 782 hatched and developed normally while the remaining 356 did not hatch. Of the 1266 fourth-instars collected from study sties, 913 survived to become adults. Dissection of both unhatched eggs and dead larvae yielded no evidence that mortality was due to parasitism. Similarly, no pathogens were found in the late instars and adults collected from sampled sties (Table 1). These results indicate that despite the herbivore's high population densities and large geographic distribution (Pratt et al. 2003; Balentine et al. 2009), native parasitoids and pathogens have failed to exploit these lifestages of *O. vitiosa*.

One explanation for the lack of *O. vitiosa* parasitization may be that native parasitoids require more than the 4 years allotted in this study to adjust behaviorally and physiologically to exploit the new host as well as produce sufficient densities to be discovered through our sampling protocols. In contrast, Hill & Hulley (1995) determined that 16 of the 40 established weed biological control agents in South Africa had acquired native parasitoids within 3 years of release. Similarly, the biological control agent *Neomusotima conspurcatalis* Warren acquired a suite of parasitoids within months of its release in *Lygodium microphyllum* (Cav.)-dominated habitats of Florida (Kula et al. 2010). These and other examples of rapid parasitoid acquisition by biological control agents (Carvalheiro et al. 2008; Paynter et al. 2010) suggest that the timing of our study was not premature but that future parasitoid (or pathogen) surveys may yield new discoveries as the region continues to recruit exotic species (Klassen et al. 2002; Dobbs & Brodel 2004; Childers & Rodrigues 2005).

Surveys of *O. vitiosa* populations resulted in the collection of 154 species of predatory arthropods, yet only 44 had an overall abundance greater than 5 individuals when pooled across all sites and dates (Table 2). Species positively correlated with *O. vitiosa* (all stages) included the salticid *Eris flava* (Peckham & Peckham), the crab spiders *Misumenops bellulus* (Banks) and *Misumenops* sp., and the pentatomid bug *Podisus mucronatus* Uhler (Table 2). Although these data indicate that predators are associated with the introduced herbivore, direct observation of predation provides conclusive evidence of these novel trophic interactions. Eleven predatory species were observed feeding on *O. vitiosa* during timed surveys, including 6 pentatomid species (*Euthyrhynchus floridanus* (L.), *P. mucronatus* (Say), *Podisus jole* (Stal), *Podisus maculiventris* (Say), *Podisus sagitta* (F.), *Stiretrus anchorago* (F.)), 2 formicids (*Pseudomyrmex gracilis* (F.), *Solenopsis invicta*) and 3 arachnids (*Peucetia viridans* (Hentz), *Latrodectus mactans* (F.), *Latrodectus geometri-*

TABLE 2. THE ABUNDANCE OF PREDACEOUS ARTHROPODS COLLECTED FROM THE INVASIVE TREE *MELALEUCA QUINQUENERVIA* AND THEIR CORRELATION WITH THE INTRODUCED BIOLOGICAL CONTROL AGENT *OXYOPS VITIOSA*.

		Site Abundance				Partial Correlation	
Family	Species	1	2	3	4	PCC	*P*-value
Alydidae	*Hyalymenus* sp. *A*	1	12	0	0	-0.23098	0.2112
Anyphaenidae	*Hibana* sp.	0	0	0	9	0.04519	0.8093
	Hibana sp.	4	0	1	2	-0.06653	0.7222
Araneidae	*Acacesia hamata* (Hentz)	15	14	2	2	0.15511	0.4047
	Eriophora ravilla (C.L. Koch)	5	1	0	1	-0.08230	0.6599
	Neoscona sp.	27	15	2	0	-0.08867	0.6353
	Neoscona arabesca (Walckenaer)	6	0	0	0	-0.13606	0.4655
Cixiidae	*Bothriocera* sp.	0	6	0	0	-0.11674	0.5317
Clubionidae	*Clubiona* sp.	0	6	0	5	0.01856	0.9211
Formicidae	*Camponotus planatus* (Roger)	75	46	2	0	0.05757	0.7584
	Camponotus floridanus (Buckley)	14	0	0	2	0.09479	0.6120
	Dolichoderus pustulatus Mayr	6	0	0	0	-0.14389	0.4400
	Paratrechina longicornis (Latreille) *	85	102	0	4	-0.14078	0.4500
	Paratrechina guatemalensis (Forel) *	16	2	0	6	-0.08637	0.6441
	Pseudomyrmex pallidus (F. Smith) *	15	11	0	0	-0.13190	0.4794
	Pseudomyrmex gracilis (Fabricius)	2	1	0	6	-0.17915	0.3349
	Solenopsis invicta Buren	8	16	16	64	0.02664	0.8869
Lycosidae	*Pardosa* sp.	1	0	16	0	0.33110	0.0688
	Pirata sp.	18	2	27	22	0.33916	0.0620
Lygaeidae	*Oedancala crassimana* (Fabricius)	13	2	8	0	0.33885	0.0622
	Paromius longulus (Dallas)	7	4	1	0	0.06829	0.7151
Membracidae	*Spissistilus festinus* (Say)	0	0	7	0	0.29864	0.1027
Mimetidae	*Mimetus* sp.	1	0	2	16	0.07110	0.7039
Miridae	*Taylorilygus pallidulus* (Blanchard)	2	2	4	0	0.31276	0.0867
Miturgidae	*Cheiracanthium inclusum* (Hentz)	96	140	10	16	-0.01003	0.9573
Oxyopidae	*Peucetia viridans* (Hentz)	137	9	11	4	0.06787	0.7168
Pentatomidae	*Podisus mucronatus* Uhler	6	1	98	4	0.52700	0.0023
Pisauridae	*Pisaurina* sp.	7	5	0	0	0.13199	0.4791
Reduviidae	*Zelus longipes* Linnaeus	25	0	0	1	-0.05046	0.7875
Salticidae	*Eris flava* (Peckham & Peckham)	4	5	16	9	0.36503	0.0435
	Hentzia palmarum (Hentz)	72	45	10	55	0.00540	0.9770
	Pelegrina galathea (Walckenaer)	12	5	14	0	0.18343	0.3233
	Phidippus sp.	0	1	0	5	-0.14807	0.4267
	Thiodina peurpera (Hentz)	0	19	0	0	-0.13863	0.4570
Scelionidae	*Trissolcus* sp.	0	8	0	0	-0.10483	0.5746
Tetragnathidae	*Tetragnatha* sp.	33	8	5	1	0.11216	0.5480
Theridiidae	*Anelosimus studiosus* (Hentz)	67	0	3	0	0.08956	0.6318
	Chrysso pulcherrima (Mello-Leitao)	1	0	1	4	0.26530	0.1492
	Theridion glaucescens (Becker)	12	0	0	1	0.13018	0.4852
	Theridion flavonotatum (Becker)	24	0	0	2	-0.01400	0.9404
Thomisidae	*Misumenops* sp.	2	3	5	4	0.30519	0.0950
	Misumenops bellulus (Banks)	26	37	27	15	0.35739	0.0484
	Misumenops sp.	10	0	29	2	0.39715	0.0269
	Tmarus sp.	2	0	1	52	-0.24154	0.1905

cus C.L. Koch). The formicids and arachnids were observed feeding exclusively on adult weevils whereas the pentatomids attacked larvae of *O. vitiosa*; *E. floridanus* was the only species observed exploiting all active stages of the introduced herbivore. Observing predation was rare, with only 8% of timed surveys resulting in 1 or more instances of attack. Feeding by *P. mucronatus* accounted for 76% of all recorded predation events and the remaining species each represented <5% of the events, respectively.

Ecological theory suggests that host range expansion is influenced in part by host phylogeny, with close relatives more readily adopted than distant ones (Paynter et al. 2010). Therefore, an alternative explanation for the lack of acquired

parasitoids and pathogens may be due to the paucity of closely related species in the biological control agent's adventive range. The Australian weevil *O. vitiosa* belongs to the tribe Goniopterini, which has no representatives in the New World (Alonso-Zarazaga & Lyal 1999). Similarly, invasion by *M. quinquenervia* markedly alters community structure in ways that are likely to repel habitat specialists. Therefore, the aquisition of parasitoids will likely require evolutionary rather than ecological time scales (Hill & Hulley 1995).

With the exception of *E. floridanus*, the exclusive use of adult versus larval prey observed herein may be explained by mouthpart morphologies and the antipredatory activity of the viscous coating that covers immature stages of *O. vitiosa* (Purcell & Balciunas 1994). Larvae of the introduced weevil sequester terpenoids from *M. quinquenervia* leaves and excrete these compounds through their integument (Wheeler et al. 2003). This larval coating has been shown to repel the red imported fire ant (*S. invicta*) and likely confers protection against other mandibulate predators (Wheeler et al. 2002). However, adults and pupae lack the coating and are susceptible to predation by a range of predator types. The larval coating does not confer protection against pentatomid species observed herein. The haustellate mouthparts of pentatomid species pierce the larval integument and largely bypass the terpenoid-laden coating to access the internal contents of the larval prey. Yet, mouthpart type alone does not facilitate exploitation of the abundant novel resource as other predators with haustellate mouthparts (i.e., *Zelus longipes* L.) occurred at the study sites but were not common or observed directly feeding on *O. vitiosa* larvae.

Increased densities of *O. vitiosa* eggs, early instars, and adults did not influence patch colonization by *P. mucronatus* (Table 3). A numerical response by *P. mucronatus* was observed, however, on plants harboring fourth instars (Table 3), indicating a preference for larger larval stages of the introduced weevil. These findings are consistent with Hawkins et al. (1997), who reported that insect predation is higher in late developmental stages due, in part, to resource concentration and handling time. Not surprisingly, a positive relationship between *P. mucronatus* and larval corpses also was observed.

TABLE 3. LINEAR REGRESSION OF *PODSUS MUCRONATUS* DENSITIES ON *OXYOPS VITIOSA* STAGE SPECIFIC DENSITIES, PLANT QUALITY, AND FOLIAGE AVAILABILITY.

Life stage	df	Estimate	*t*-value	Pr > *t*
Egg	1	-0.00097	-0.29	0.7752
1st instar	1	-0.00185	-0.24	0.8075
2nd instar	1	0.01394	1.66	0.0966
3rd instar	1	0.01175	1.27	0.2025
4th instar	1	0.0251	2.88	0.004
Adults	1	0.00818	1.06	0.2874
Dead	1	0.13755	16.16	<.0001
Damage	1	-0.00265	-1.31	0.1893
Plant foliage	1	-0.00176	-0.94	0.3462

While it is clear that *P. mucronatus* attacks *O. vitiosa* larvae and numerically responds to the single most damaging stage of the herbivore, does this predation disrupt biological control of *M. quinquenervia*? We hypothesized that increases in *P. mucronatus* densities results in concomitant increases in predation and ultimately decreases in plant damage caused by *O. vitiosa*. Damage levels observed herein, however, were not influenced by *P. mucronatus* densities (Table 3), indicating that predation does not alter plant suppression within the sampled patch. Similarly, the amount of plant resource availability for consumption by *O. vitiosa* does not vary based on predator loads, which suggest that predation does not result in a corresponding increase in undamaged plant material (Table 3). These results are supported by independent studies that also were conducted at site 3 and reported marked reductions in *M. quinqueneriva* growth and survival despite the presence of these predators (Center et al. 2000; Pratt et al. 2002; Pratt et al. 2004). The limited influence of *P. mucronatus* on *O. vitiosa* population growth and herbivory is likely related to low predation rates (mean = 9.5%, SE = 0.5).

The introduction of *O. vitiosa* has resulted in marked reductions in growth and survivorship of the invasive tree *M. quinqueneriva* (Pratt et al. 2003, 2005; Rayamajhi et al. 2008; Tipping et al. 2008, 2009; Balentine et al. 2009), with no direct non-target impacts to plant species in the weevil's adventive range (Pratt et al. 2009). The acquisition of higher trophic levels by *O. vitiosa*, however, suggests that indirect effects of apparent competition may exist as predators are subsidized by the introduced weevil and their resultant increased population densities may exert asymmetrical predation on their historical prey species (Carvalheiro et al. 2008). In the absence of pre-introduction food web analyses, it remains unclear how the exploitation of *O. vitiosa* by native predators affects apparent competition on shared prey densities. The limited predation by generalists suggests that the strength of apparent competition is weak but additional research is needed to quantify interactions among introduced and native prey species as mitigated by common predators.

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