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Diversity of stink bug (Hemiptera: Pentatomidae) egg parasitoids in woodland and crop habitats in southwest Georgia, USA

P. Glynn Tillman*

Abstract

Euschistus servus (Say), Chinavia hilaris (Say), and Nezara viridula (L.) (Hemiptera: Pentatomidae) are economic pests of row crops. They move within and between closely associated crop and non-crop habitats throughout the growing season in response to deteriorating suitability of their current host plants. This study was conducted to investigate parasitism of naturally occurring *C. hilaris* and *E. servus* eggs in woodland habitats and crops alongside these habitats in southwest Georgia, USA. Also, parasitism of sentinel eggs of *N. viridula* was examined in a woodland habitat. Ten species of parasitoids, including 7 scelionids, 2 eupelmids, and 1 encyrtid, parasitized *E. servus* eggs. *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae) was the most prevalent parasitoid of *E. servus* eggs in each of 3 habitats: woodlands, an early-season crop, and late-season crops. In woodlands, 27.9% of *E. servus* eggs were parasitized by *Anastatus reduvii* (Howard) and *A. mirabilis* (Walsh & Riley) (Hymenoptera: Eupelmidae). Four species of parasitoids, including 1 scelionid, 2 eupelmids, and 1 encyrtid, parasitized *C. hilaris* eggs. *Trissolcus edessae* Fouts (Hymenoptera: Scelionidae) was the most prevalent parasitoid of *C. hilaris* eggs in woodlands and the only parasitoid of *C. hilaris* eggs in late-season crops. In woodlands, 40.7% of *C. hilaris* eggs were parasitized by *A. reduvii* and *A. mirabilis*. In a woodland habitat, 6.6% of *N. viridula* sentinel eggs were parasitized by *A. reduvii* females, *Anastatus* males, and 1 encyrtid. *Anastatus* species were the only parasitoids that existed primarily in woodland habitats. In conclusion, a diversity of parasitoid species parasitizes native stink bug eggs in southwest Georgia, and species of parasitoids emerging from stink bug eggs can vary by habitat.

Key Words: Telenomus podisi; Trissolcus edessae; Anastatus reduvii; Anastatus mirabils

Resumen

Euschistus servus (Say), Chinavia hilaris (Say), y Nezara viridula (L.) (Hemiptera: Pentatomidae) son plagas económicas de los cultivos en hileras. Se mueven dentro y entre los hábitats agrícolas y no agrícolas estrechamente asociados en toda la temporada de crecimiento en respuesta al deterioro desarrollado por sus plantas hospederas actuales. Se realizó este estudio para investigar el parasitismo de huevos de C. hilaris y E. servus ocurriendo naturalmente en hábitats de bosques y cultivos junto a estos hábitats en el suroeste de Georgia, EE.UU. Además, se examinó el parasitismo de huevos de N. viridula centinelas en un hábitat boscoso. Diez especies de parasitoides, incluyendo 7 scelionidos, 2 eupelmidos y 1 encirtido, parasitaron los huevos de E. servus. Telenomus podisi Ashmead (Hymenoptera: Scelionidae) fue el parasitoide más frecuente de huevos de E. servus en cada uno de los 3 hábitats: bosques, un cultivo del principio de temporada, y los cultivos de final de temporada. En los bosques, el 27,9% de los huevos de E. servus fueron parasitados por Anastatus reduvii (Howard) y A. mirabilis (Walsh y Riley) (Hymenoptera: Eupelmidae). Cuatro especies de parasitoides, incluyendo 1 scelionido, 2 eupelmidos y 1 encirtido parasitaron huevos de C. hilaris. Trissolcus edessae Fouts (Hymenoptera: Scelionidae) fue el parasitoide más frecuente de huevos de C. hilaris en los bosques y la única parasitoide de C. hilaris en los cultivos de final de temporada. En los bosques, el 40,7% de los huevos de C. hilaris fueron parasitados por A. reduvii y A. mirabilis. En un hábitat boscoso, el 6,6% de los huevos centineles de N. viridula fueron parasitados por hembras de A. reduvii y machos de Anastatus y 1 encirtido. Las especies de Anastatus fueron los únicos parasitoides que existían principalmente en hábitats de bosques. En conclusión, una diversidad de especies de parasitoides nativos parasita los huevos de las chinches en el sudoeste de Georgia, y especies de parasitoides que emergen de los huevos de las chinches hediondas p

Palabras Clave: Telenomus podisi; Trissolcus edessae; Anastatus reduvii; Anastatus mirabils

Stink bugs (Hemiptera: Pentatomidae) are primary pests responsible for millions of dollars in losses and cost of control in row crops. For example, nearly 130,000 bales of cotton (*Gossypium hirsutum* L.; Malvales: Malvaceae) nationwide were estimated lost due to pest stink bug species in 2014 (Williams 2015). In southwest Georgia, USA, corn (*Zea mays* L.; Poales: Poaceae) is one of the first crops available to stink bugs for feeding and oviposition (Tillman 2011a). *Euschistus servus* (Say) and *Nezara viridula* (L.) are the predominant stink bug species in this crop. Generally, peanut (*Arachis hypogaea* L.; Fabales: Fabaceae) is the next crop in which these 2 stink bug species occur (Tillman 2008). Stink bugs

feed on vegetative parts of peanut plants (Tillman 2008) and thus are not considered economic pests. However, when *E. servus* and *N. viridula* inhabit peanut in peanut—cotton farmscapes, it leads to a negative impact on cotton because they develop on peanut and then disperse in cotton (Tillman et al. 2009). Both corn and peanut are unlikely hosts for *Chinavia hilaris* (Say) (Tillman 2013). Soybean (*Glycine max* [L.] Merr.; Fabales: Fabaceae) and cotton, though, are mid-to-late-season crops of *C. hilaris*, as well as *E. servus* and *N. viridula* (Bundy & McPherson 2000; Tillman et al. 2009). In cotton, stink bugs feed on developing seeds and lint, causing shedding of young bolls, yellowing of lint, reduction

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in yield, and transmission of a bacterial pathogen (Barbour et al. 1990; Medrano et al. 2009). In soybean, pod feeding by stink bugs results in reduction in oil content and yield (McPherson et al. 1995).

In farmscapes in the southeastern United States, numerous noncrop hosts of C. hilaris and E. servus, including black cherry (Prunus serotina Ehrh.; Rosales: Rosaceae), elderberry (Sambucus nigra subsp. canadensis [L.] R. Bolli; Dipsacales: Adoxaceae), and mimosa (Albizia julibrissin Durazz.; Fabales: Fabaceae), exist in woodlands bordering crops (Jones & Sullivan 1982; Tillman & Cottrell 2015). Black cherry is an early-season host plant; C. hilaris adults are present on trees from Apr until early Jul, and large nymphs occur on trees from late May through mid-Jul. Elderberry is an early-to-mid-season host plant; C. hilaris adults begin colonizing this shrub in mid-May, remaining on it through Jul. Large nymphs are then present on plants from mid-Jun through Jul. In mimosa, reproductive populations of C. hilaris are present from mid-Jul through Aug. Rattlebox (Sesbania punicea [Cav.] Benth.; Fabales: Fabaceae) is a newly discovered early-season host plant for C. hilaris (Tillman 2015). Except for occasionally developing on pokeweed (Phytolacca americana L.; Caryophyllales: Phytolaccaceae) in woodland borders near crops (Tillman et al. 2014), N. viridula has not been detected in woodland habitats in southwest Georgia.

Stink bugs move within and between closely associated crop and non-crop habitats throughout the growing season in response to deteriorating suitability of their current host plants (Velasco & Walter 1992; Panizzi 1997; Ehler 2000). Habitat edges include not only crop-to-crop interfaces but also woodland habitats next to crops. For C. hilaris, an edge effect in dispersal of adults was detected in cotton adjacent to woodlands (Tillman et al. 2014), indicating that the non-crop hosts in woodlands were sources of this stink bug in this crop. Spatiotemporal distribution of C. hilaris in cotton suggested that elderberry and mimosa were sources of this stink bug dispersing into this crop (Tillman & Cottrell 2015). Preliminary mark-recapture studies have shown that C. hilaris disperses from elderberry into cotton in mid Jul to early Aug (P. G. Tillman, unpublished). The timing of completion of development of C. hilaris on elderberry and the later appearance of this stink bug in adjacent soybean suggested that elderberry also was a source of this pest into this crop (Miner 1966; Jones & Sullivan 1982).

An understanding of natural biological control of stink bugs in both woodland habitats and crops is necessary for developing effective management strategies for these pests. Multiple studies have investigated parasitism of *E. servus*, *C. hilaris*, and *N. viridula* egg masses in crops (Schoene & Underhill 1933; Underhill 1934; Yeargan 1979; Orr et al. 1986; Jones et al. 1996; Koppel et al. 2009; Tillman 2010, 2011b), but data on parasitism of eggs of these stink bug species in woodlands are rare (Yeargan 1979; Koppel et al. 2009). Interestingly, stink bug egg parasitoids can disperse from crop to crop throughout the seasonal succession of crops in farmscapes composed of combinations of corn, peanut, and cotton to parasitize *E. servus* and *N. viridula* egg masses (Tillman 2011b). Considering the crop-to-crop dispersal of these stink bugs, their parasitoids are likely responding to host plant switching by their hosts.

However, very little is known as to whether parasitoids of stink bugs disperse from woodland habitats into crops. *Trissolcus japonicus* (Ashmead) (Hymenoptera: Scelionidae), an Asian egg parasitoid of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål), was discovered parasitizing *H. halys* in a woodland habitat in Beltsville, Maryland (Talamas et al. 2015a). In contrast, *H. halys* egg masses were not parasitized by this parasitoid in nearby soybean and an abandoned apple orchard. Information regarding stink bug egg parasitoids in woodland habitats and crops is crucial now in Georgia because reproductive populations of *H. halys* recently have been detected in the state (P. G. Tillman, unpublished). This study was conducted for 10 field

seasons to examine parasitism of naturally occurring *C. hilaris* and *E. servus* eggs in woodland habitats and crops alongside these habitats in southwest Georgia. Also, parasitism of sentinel eggs of *N. viridula* was examined in a woodland habitat.

Materials and Methods

STUDY SITES

This study was conducted from 2005 through 2015, excluding 2012. Over the 10 yr study, crop hosts and non-crop hosts in woodlands adjacent to these crops were sampled at 25 sites for parasitism of *E. servus* and *C. hilaris* egg masses. The same sites and crops could not be sampled each year of the study due to crop rotation practices and changes in grower collaborations. All sites were located near Mystic (31.6219444°N, 83.3355556°W) in Irwin County, Georgia, USA. During the study, non-crop host plants were sampled in 20 woodland habitats, and crop host plants were sampled in 21 corn and cotton fields, 15 peanut fields, and 2 soybean fields. Crop fields ranged in size from 9 to 36 ha. Crops were grown using University of Georgia Cooperative Extension recommended practices for corn (Lee 2012), peanut (Beasley 2012), cotton (Collins 2012), and soybean (Whitaker 2012).

INSECT SAMPLING

In woodland habitats, black cherry, rattlebox, elderberry, and mimosa were sampled for stink bug egg masses. For sampling on a black cherry tree, the foliage and fruiting structures of 3 limbs were thoroughly checked visually for stink bug egg masses. For rattlebox, elderberry, and mimosa, a whole plant, including foliage and fruiting structures, was examined for the presence of stink bug egg masses. When necessary, a 1.52-m-long cattle show stick with a small hook at the end was used to gently pull a limb or branch within reach to check for egg masses. All non-crop hosts in a woodland habitat were sampled weekly or bi-weekly. The development time of female stink bug egg parasitoids is approximately 2 wk, and females can oviposit from 3 to 7 wk (Yeargan 1980, 1982, 1983; Powell & Shepard 1982). Therefore, whether plants were sampled once or twice a week likely did not influence the estimated percentage of parasitism of egg masses.

Crop hosts, including corn, peanut, cotton, and soybean, were sampled weekly. Each crop was sampled from the onset of flowering to maturation of fruit. For the sampling of corn, cotton, or soybean, plants within a 1.83 m length of a row were visually checked for egg masses. In peanut, sweep nets (38 cm in diameter) were used to capture stink bugs. The canopy within a 7.31 m length of a row was swept once. Also, any egg masses observed on peanut during the sweeping were collected. Crop fields were sampled at each field edge and in the interior of the field. Based on previous studies on the spatiotemporal dynamics of stink bug populations in crops (Tillman et al. 2009, 2014; Tillman 2011a; Cottrell & Tillman 2015; Tillman & Cottrell 2015), field size should be considered in determining the appropriate number of samples obtained per field. Therefore, in the current study, the number of samples obtained per field varied by field size and ranged from 50 to 200 samples per field.

Nymphs of *N. viridula* were occasionally observed on pokeweed in a woodland habitat (Tillman et al. 2014), but egg masses were not detected on any plant species in this habitat during the study. Therefore, in 2014, laboratory-reared egg masses (less than 16 h old) of *N. viridula* were frozen in a freezer held at $-77~^{\circ}$ C and then placed as sentinels in the field (as described in Tillman 2008) to determine what, if any, species of parasitoids parasitized eggs of this stink bug in this habitat. In

total, 7 egg masses (1 egg mass per shrub) were hung on a branch of an elderberry shrub in a woodland habitat adjacent to a cotton field on 28 and 30 Jul and 4 Aug 2014. At the end of a 48 h exposure time, egg masses were collected from shrubs.

Naturally occurring and sentinel stink bug egg masses were brought to the laboratory and held for emergence of adult parasitoids. Gyron obesum Masner (Hymenoptera: Scelionidae) and Trissolcus species (Hymenoptera: Scelionidae) were identified using a key to Nearctic species of Trissolcus (Talamas et al. 2015b). The species of Anastatus (Hymenoptera: Eupelmidae) females were identified using a key to North American species of this genus (Burks 1967). Currently, a key to identify species of Anastatus males is not available; therefore, males were identified only to genus. Telenomus podisi Ashmead (Hymenoptera: Scelionidae) was identified using a key to species of Telenomus (Ashmead 1893). Also, Dr. Norman F. Johnson (Department of Evolution, Ecology and Organismal Biology, Ohio State University, Columbus, Ohio) identified some specimens of Trissolcus brochymenae (Ashmead), Trissolcus euschisti (Ashmead), Trissolcus thyantae Ashmead, Trissolcus basalis (Wollaston), T. podisi, and G. obesum. Voucher specimens of all insects were deposited in the United States Department of Agriculture, Agricultural Research Service, Crop Protection & Management Research Laboratory in Tifton, Georgia.

DATA ANALYSES

All data were analyzed using SAS statistical software (SAS Institute 2010). Chi-squared tests were used to compare frequencies of parasit-oid species parasitizing *E. servus* and *C. hilaris* egg masses in woodland and crop habitats (PROC FREQ). For parasitoids from *E. servus*, analyses were grouped by woodland habitats, an early-season crop, corn, and late-season crops including peanut, cotton, and soybean. For parasit-oids from *C. hilaris*, analyses were grouped by woodland habitats and 2 late-season crops (cotton and soybean). Parasitism rates of *E. servus* and *C. hilaris* eggs among the various habitat groups were analyzed us-

ing PROC ANOVA (P < 0.05). Means were separated using Tukey's honest significance difference (HSD) test (P < 0.05) when appropriate. Seasonal presence of parasitized stink bug egg masses was determined for the woodland habitat, the early-season crop, and late-season crops.

Results

Ten species of parasitoids parasitized naturally occurring egg masses of E. servus (Table 1). These included 7 scelionids, 2 eupelmids, and 1 encyrtid. Telenomus podisi was the most prevalent parasitoid of E. servus eggs in each of the 3 habitats, i.e., woodland, early-season corn, and late-season crops including peanut, cotton, and soybean. In corn, the percentage of eggs parasitized by male Anastatus adults was very low, and these eggs were found on the outermost row of corn in close association with a woodland habitat. Anastatus species did not parasitize E. servus eggs in late-season crops. However, in woodland habitats, 27.9% of the eggs were parasitized by Anastatus species, including Anastatus reduvii (Howard) and A. mirabilis (Walsh & Riley) females and Anastatus males. Less than 10% of the eggs were parasitized by any other parasitoid species for each of the 3 habitats. Trissolcus edessae Fouts parasitized E. servus eggs only in the woodland habitat and late-season crops. Trissolcus basalis and G. obesum attacked E. servus eggs only in crops.

Four species of parasitoids parasitized naturally occurring egg masses of *C. hilaris* (Table 2). These included 1 scelionid, 2 eupelmids, and 1 encyrtid. *Trissolcus edessae* was the most prevalent parasitoid of *C. hilaris* eggs in woodland habitats and the only parasitoid attacking *C. hilaris* eggs in late-season crops. Egg masses of *C. hilaris* were not detected in peanut. For corn, the only *C. hilaris* egg mass detected was parasitized by *T. basalis* in a location where *N. viridula* egg masses were present. In woodland habitats, 40.7% of the *C. hilaris* eggs were parasitized by *Anastatus*, including *A. reduvii* and *A. mirabilis* females and *Anastatus* males.

Table 1. Occurrence of stink bug egg parasitoid species attacking *Euschistus servus* in woodland habitats, an early-season (ES) crop, and late-season (LS) crops in Irwin County, Georgia, over a 10 yr period.

Parasitoid	Parasitoid species frequency (%)							
	Woodland ^a (44/827) ^d	ES crop ^b (210/4583) ^d	LS crops ^c (62/1237) ^d	χ²	df	Р		
Telenomus podisi	53.1	92.3	80.2					
Anastatus (♂)	15.0	0.7	_					
Anastatus reduvii (♀)	12.1	_	_					
Trissolcus brochymenae	8.6	4.1	6.6					
Ooencyrtus sp.	4.2	1.1	1.1					
Trissolcus euschisti	2.8	0.1	0.7					
Trissolcus edessae	2.1	_	1.0					
Trissolcus thyantae	1.3	0.6	4.0					
Anastatus mirabilis (♂)	0.8	_	_					
Trissolcus basalis	_	0.8	4.1					
Gyron obesum	_	0.3	2.3					
Frequency comparisons:								
Woodland: all species				1,625.4	8	0.0001		
Woodland: T. podisi vs. all Anastatus				65.6	1	0.0001		
ES crop: all species				26,722.1	7	0.0001		
LS crops: all species				5,211.4	7	0.0001		

^aBlack cherry, elderberry.

bCorn.

^{&#}x27;Peanut, cotton, soybean.

^dTotal number of parasitized egg masses per total number of parasitized eggs from which adult parasitoids emerged.

Table 2. Occurrence of stink bug egg parasitoid species attacking *Chinavia hilaris* in woodland habitats and late-season (LS) crops in Irwin County, Georgia, over a 10 yr period.

	Parasitoid species frequency (%)					
Parasitoid	Woodland ^a (49/1298) ^c	LS crops ^b (12/391) ^c	χ²	df	Р	
Trissolcus edessae	53.3	100				
Anastatus (♂)	25.4	_				
Anastatus reduvii (♀)	13.9	_				
Ooencyrtus sp.	6.0	_				
Anastatus mirabilis ($ \circ $)	1.4	_				
Frequency comparisons:						
Woodland: all species			1,115.6	4	0.0001	
Woodland: T. edessae vs. all Anastatus			22.0	1	0.0001	

^aBlack cherry, rattlebox, elderberry, mimosa.

In a woodland habitat, *A. reduvii* females, *Anastatus* males, and *Ooencyrtus* sp. (Hymenoptera: Encyrtidae) emerged from *N. viridula* sentinel egg masses. Overall, 6.6% of the eggs were parasitized.

Percentage of parasitism per egg mass was significantly influenced by habitat for *E. servus* (F = 28.19, df = 2, P = 0.0001) and *C. hilaris* (F = 11.41, df = 1, P = 0.001). Percentage of parasitism of *E. servus* eggs was higher in the early-season crop than in the other 2 habitats (Table 3). Percentage of parasitism was lowest for the woodland habitat. Percentage of parasitism of *C. hilaris* eggs was higher in woodland habitats than in late-season crops. Interestingly, in general terms, percentage of parasitism was similar for both *E. servus* and *C. hilaris* in woodlands.

In general, the first parasitoids of stink bug eggs for the season were present in an early-season crop, corn, in late May (Table 4). In this crop, egg masses of E. servus, but not C. hilaris, were detected (Tables 1 and 2). Most of the species that parasitized E. servus eggs over all habitats emerged from eggs in corn. However, T. edessae did not parasitize E. servus eggs, and male Anastatus rarely parasitized them in this crop. Parasitization of E. servus eggs continued in corn through Jul. By early Jun, parasitoids began parasitizing both E. servus and C. hilaris egg masses in woodland habitats (Table 4). Except for T. basalis and G. obesum, all parasitoid species attacking E. servus in corn were present in woodland habitats, but none of the Trissolcus species that parasitized E. servus eggs in corn emerged from C. hilaris eggs in woodlands (Tables 1 and 2). Each of the 2 Anastatus species and T. edessae also parasitized E. servus, as well as C. hilaris, in woodlands. Parasitized E. servus and C. hilaris egg masses were detected in woodlands through early Aug (Table 4). From 1 Aug through early Oct, parasitoids emerged from both E. servus and C. hilaris eggs in late-season crops. Except for Anastatus species, species present in corn and woodland habitats par-

Table 3. Mean $(\pm$ SE) percentage of parasitism per egg mass (n) for naturally occurring egg masses of *Euschistus servus* and *Chinavia hilaris* in woodland and crop habitats in Irwin County, Georgia, over a 10 yr period.

Species	Habitat	n	Mean
E. servus	woodland	129	46.4 ± 4.1 c
	early-season crop	271	80.0 ± 2.3 a
	late-season crops	90	66.7 ± 4.8 b
C. hilaris	woodland	77	45.5 ± 5.0 a
	late-season crops	55	20.5 ± 5.2 b

Means by parasitoid species followed by a different letter indicate significant differences (Tukey's HSD test, P < 0.05).

asitized *E. servus* eggs in these crops (Tables 1 and 2). Only *T. edessae* parasitized *C. hilaris* eggs in cotton and soybean.

Discussion

In southwest Georgia, E. servus and C. hilaris populations can begin developing on host plants in woodlands early in the season. For C. hilaris, diversity of egg parasitoids was greater and percentage of parasitism was higher in woodland habitats compared with those observed in crops. Of the 4 species of parasitoids of C. hilaris in woodlands, T. edessae and Anastatus species were the prevalent species. Anastatus species existed primarily in woodland habitats, and, thus, they may have a preference for woody trees and shrubs. Similarly, T. euschisti parasitized Podisus maculiventris (Say) (Hemiptera: Pentatomidae) eggs only on a woody non-crop host, hackberry (Celtis occidentalis L.; Rosales: Cannabaceae), when sentinel eggs were placed in both hackberry and alfalfa (Medicago sativa L.; Fabales: Fabaceae) (Okuda & Yeargan 1988). Parasitization of a couple of *E. servus* egg masses by *Anastatus* males in corn was likely due to their close proximity to a woodland habitat. Trissolcus edessae, though, apparently dispersed from woodland habitats into late-season crops. In contrast to C. hilaris, diversity of parasitoids of E. servus eggs was broad, 7 to 8 species per habitat, although not all parasitoid species were present in each habitat. Trissolcus edessae parasitized E. servus eggs only in woodlands and late-season crops (i.e., cotton and soybean), habitats in which C. hilaris reproduced on hosts. Again, this parasitoid species likely dispersed from woodland habitats into these late-season crops. Trissolcus brochymenae, T. euschisti, T. thyantae, T. podisi, and Ooencyrtus sp. attacking E. servus in corn and

Table 4. Seasonal presence of parasitized stink bug egg masses in an early-season (ES) crop, woodland habitats, and late-season (LS) crops in Irwin County, Georgia, over a 10 yr period.

Habitat	May	Jun	Jul	Aug	Sep	Oct
ES crop ^a						
Woodland⁵						
LS crops ^c						

^aCorr

^bCotton, soybean.

Total number of parasitized egg masses per total number of parasitized eggs from which adult parasitoids emerged.

^bBlack cherry, rattlebox, elderberry, mimosa.

Peanut, cotton, soybean.

woodland habitats likely dispersed from these habitats into late-season crops, whereas *T. basalis* and *G. obesum* dispersed from corn into these late-season crops.

Even though T. brochymenae, T. euschisti, T. edessae, T. thyantae, Ooencyrtus sp., T. basalis, and G. obesum parasitize Euschistus species, including E. servus, as in the current study, T. podisi is the predominant egg parasitoid of Euschistus species in crops or cropping systems (Yeargan 1979; Orr et al. 1986; Koppel et al. 2009; Tillman 2010, 2011b). Percentage of parasitism of eggs by T. podisi ranges from 70 to 100% for Euschistus species, 1 to 65% for C. hilaris, and 0 to 20% for N. viridula when Euschistus species coexist with one or both of the other two stink bugs species. Thus, T. podisi also tends to prefer egg masses of Euschistus species to those of C. hilaris and N. viridula. In the current study, C. hilaris eggs were not parasitized by T. podisi in woodlands or late-season crops. However, this egg parasitoid was previously recovered from this stink bug species in soybean (Yeargan 1979; Orr et al. 1986). Javahery (1990) also recovered a single T. podisi from a C. hilaris egg mass found on buckthorn (Rhamnus catharticus L.; Rosales: Rhamnaceae). This is the first report on parasitism of E. servus eggs in woodland habitats.

Based on the results of the current study and previous studies, overall percentage of parasitism of C. hilaris eggs ranged from 16 to 49% in crops (Yeargan 1979; Orr et al. 1986; Jones et al. 1996; Koppel et al. 2009). As in the current study, Jones et al. (1996) recovered only T. edessae from C. hilaris in soybean, even though these authors reported that T. basalis, T. euschisti, and T. podisi were also present in the crop. They also mentioned that T. edessae was the only parasitoid that emerged from C. hilaris egg masses collected from various host plants in a variety of habitats, but no information was provided on the species of host plants or habitats studied. The prevalent egg parasitoids of C. hilaris recovered by Orr et al. (1986) in soybean were T. edessae and T. euschisti. One C. hilaris egg mass was parasitized by Trissolcus cristatus Johnson. Koppel et al. (2009) recovered T. edessae, T. euschisti, and T. basalis from 6 C. hilaris egg masses in crops and basswood trees. Yeargan (1979) reported that T. podisi and T. euschisti emerged from 16 C. hilaris egg masses collected from soybean. Even though the current information on parasitism of C. hilaris eggs varies by study, T. edessae was recovered from eggs of this stink bug in 4 of the 5 studies. Except for the current study, parasitism of C. hilaris was studied primarily in crops. Because host plants of C. hilaris exist in woodlands, an investigation of parasitism within and between woodlands and crops is essential to our understanding of natural biological control of C. hilaris.

Trissolcus basalis tends to prefer *N. viridula* eggs over those of other stink bug species (Yeargan 1979; Orr et al. 1986; Jones et al. 1996; Koppel et al. 2009; Tillman 2010, 2011b). This may explain why levels of parasitism of *E. servus* by *T. basalis* were so low and only a single *C. hilaris* egg was parasitized by this parasitoid.

Anastatus species, including the two recovered in woodland habitats in the current study, A. reduvii and A. mirabilis, as well as Anastatus pearsalli Ashmead, have been reported as egg parasitoids of C. hilaris (Schoene & Underhill 1933; Underhill 1934; Yeargan 1979). Anastatus species have not been previously reported as egg parasitoids of E. servus, which may be due to the lack of studies on parasitism of E. servus eggs in woodland habitats. In the current study, N. viridula eggs were not detected in woodlands even though nymphs have occasionally been reported on black cherry and pokeweed (Jones & Sullivan 1982; Tillman et al. 2014). Anastatus species, though, have previously been reported to parasitize eggs of N. viridula (Jones 1988). However, Hokyo & Kiritani (1966) reported that Anastatus females could only be produced by host eggs larger than those of N. viridula. The current sentinel egg study revealed that Anastatus females can develop

in sentinel eggs of *N. viridula*. The emergence of *Anastatus* females from sentinel eggs of *N. viridula* in a woodland habitat could be due to a preference of *Anastatus* for woody trees and shrubs or may be due to the association of elderberry where *Anastatus* species parasitize *E. servus* and *C. hilaris* eggs.

A few reports exist regarding naturally occurring parasitoids of *E. servus* and *C. hilaris* eggs on woody plant species. *Euschistus* sp. eggs were parasitized by *T. euschisti* on sassafras (*Sassafras albidum* [Nutt.] Nees; Lauracea) (Yeargan 1979). *Chinavia hilaris* eggs were parasitized by *T. basalis* and *T. edessae* (35.2 and 20.7% parasitism of eggs, respectively) on basswood (*Tilia americana* L.; Malvales: Malvaceae) (Koppel et al. 2009) and by *A. pearsalli* on maple (*Acer* sp.; Sapindales: Sapindaceae) (Yeargan 1979).

Except for *A. pearsalli* and *Telenomus utahensis* Ashmead, parasitoid species that emerged from *E. servus* and *C. hilaris* egg masses in woodland habitats in southwest Georgia are reported to parasitize *H. halys* egg masses in crops in Delaware, Maryland, Virginia, and Pennsylvania (Rice et al. 2014). As in the current study for native species of stink bugs, species of parasitoids emerging from *H. halys* eggs can vary by habitat.

Certainly, conservation of the diverse species of parasitoids of stink bug eggs in woodland habitats has the potential to enhance natural biological control of stink bugs in agricultural ecosystems. The importance of nectar provision on parasitoid fitness has been demonstrated for various hymenopteran parasitoid species (Berndt & Wratten 2005; Araj et al. 2006). For *T. podisi*, incorporating buckwheat in soybean increased parasitism of *E. servus* egg masses in adjacent cotton (Tillman et al. 2015). Nectar provision along woodland field edges could provide a food source not only to parasitoids while in woodland habitats, but also as they disperse from woodlands into crops. *Anastatus* species were the most prevalent parasitoids emerging from naturally occurring eggs of *H. halys* in ornamental nurseries in Maryland (Jones et al. 2014). Providing nectar to *Anastatus* species near woodlands in Georgia is one of many management strategies available for managing this invasive pest in the state.

In conclusion, a diversity of parasitoid species parasitizes eggs of native stink bugs in southwest Georgia, and parasitoid species emerging from stink bugs eggs can vary by habitat. Spatial and temporal composition of host plants in various habitats also can influence species of parasitoids attacking stink bug species. Therefore, parasitism of stink bug eggs should be studied in the context of the ecosystem in which stink bug species and their parasitoids are reproducing.

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