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**Frequency, efficiency, and physical characteristics of predation by generalist predators
of brown marmorated stink bug (Hemiptera: Pentatomidae) eggs**

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Abstract

The native generalist predator community of *Halyomorpha halys*, an invasive species in the United States and Europe, has not been well defined to date. The aims of the current study were to determine whether generalist predators that are commonly found in mid-Atlantic orchards and vegetable crops are capable of feeding on *H. halys* eggs and, if so, to systematically characterize the appearance of feeding damage in order to link it to sentinel egg mass surveys. Over 25 field-collected and commercially available arthropod predator taxa, including adults and immatures, were evaluated as potential predators of *H. halys* eggs in laboratory trials, and a photographic library of egg mass damage was developed. In addition, over 400 sentinel egg masses were deployed in tree fruit and vegetable crops, and direct observations were made of predator taxa in situ. We found that the most frequent and efficient predators of *H. halys* eggs were katydids and ground beetles, and to a lesser extent earwigs, jumping spiders, and crickets. Egg damage for each taxon studied was ascribed to one of four egg damage syndromes: complete chewing, incomplete chewing, stylet sucking, and punctured sucking. The first two are caused by predators with chewing mouthparts and are differentiated by the presence of irregular chorion debris left behind in the case of incomplete chewing compared with nothing left behind or an entire segment of the egg mass completely removed for complete chewing. The latter two are caused by predators with piercing/sucking mouthparts or chelicerae and are separable by the presence of a feeding sheath for stylet sucking compared to a simple hole or slit in otherwise hollowed eggs for punctured sucking via chelicerae. Complete and incomplete chewing were the two feeding syndromes most frequently documented in the field and with the greatest number of eggs consumed per egg mass. Taxa evaluated in laboratory trials were reliably found in tree fruit

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38 and vegetable crops. Overall, our work contributes to the identification of key egg mass

39 predators of *H. halys* in specialty crop agroecosystems.

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42 *Keywords:* biological control; *Halyomorpha halys*; integrated pest management; handling

43 behavior; sentinel egg masses

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1. Introduction

Increasingly, generalist predators have been recognized as an important regulator of arthropod herbivores (e.g. Riechert and Lockley 1984, Riechert and Bishop 1990, Jones 1995, Symondson et al. 2002, Messelink et al. 2010). For example, 75% of studies that examined biological control by a generalist predator found reduced pest numbers in the presence of the predator (Symondson et al. 2002). Predators play an even larger role in the biological control of invasive species that may lack specialist predators in their introduced range (Chang and Kareiva 1999). However, it is often difficult to link mortality to specific predator groups.

The brown marmorated stink bug, *Halyomorpha halys* (Stål), is an invasive (Hoebeke and Carter 2003), highly polyphagous agricultural pest in the US (Leskey et al. 2012a), Europe, and elsewhere (Lee 2015). *Halyomorpha halys* feeds on more than 150 different plants (www.stopbmsb.org), with all major vegetable and fruit crops susceptible (Kuhar et al. 2012; Leskey et al. 2012b). Conventional *H. halys* management in the U.S. relies on high dosage applications of broad spectrum insecticides (Leskey & Hamilton 2011; Leskey et al. 2012b), a tactic that can disrupt effective biological control and integrated pest management programs aimed at controlling other pests. Since the introduction of *H. halys*, insecticide use has increased by up to 4-fold in some crops (Leskey et al. 2012b). Currently, conventional management practices for *H. halys* are not economically or ecologically sustainable for vegetable and fruit crops.

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71   There is a high level of interest among growers in alternative management strategies
72   for *H. halys* (Working Group Priorities, 2015). Control of *H. halys* offers the promise of
73   long-term regulation of the populations of this invasive species, while minimizing insecticide
74   input into agroecosystems (Messing and Wright, 2006). It is important to consider the
75   phenology of *H. halys* in determining which life stages may be vulnerable to attack by natural
76   enemies. *Halyomorpha halys* completes two full generations in some mid-Atlantic states
77   (e.g., West Virginia), with F₁ eggs initially appearing in agricultural systems in mid- to late-
78   May and F₂ eggs by late June to early July (Leskey et al. 2012c). Eggs of *H. halys* deposited
79   in agroecosystems develop in 5-6 d (Lee et al. 2013, Nielsen et al. 2008), during which they
80   are vulnerable to attack by natural enemies. Eggs are likely more vulnerable to generalist
81   predator attack than other life stages, because other *H. halys* life stages are highly mobile
82   (Lee and Leskey 2015; Lee et al. 2014).

83   Native stink bug species in the US experience frequently experience high egg
84   parasitism and predation (e.g. Jones 1995, Tillman 2010, Tillman 2011, Yeargan 1979).
85   Important genera of parasitoids include *Trissolcus* spp., *Telenomus* spp., and *Ooencyrtus* spp,
86   and in which individuals may parasitize up to 100% of the eggs in an egg mass (Tillman
87   2010, Ehler 2002, Koppel 2009). In a laboratory evaluation of over 25 potential arthropod
88   predators of *Nezara viridula* (L.) eggs, only five species fed, including Chrysopidae and
89   *Geocoris* spp. (Ehler 2002). The same study found that Coccinellidae, Reduviidae, Nabidae,
90   and Araneae were frequent predators of nymphal *Nezara viridula*. Additionally, predation
91   rates ranged from 2.3-22.2 % for eggs of *Euschistus servus* (Say) and *Podisus maculiventris*
92   (Say) when surveyed in field and vegetable crops in Virginia (Koppel et al. 2009), but can be
93   significantly higher for certain pentatomids in corn (Tillman 2010, Tillman 2011).

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In its native range in Asia, *H. halys* experiences top-down pressure from its native natural enemies, including 14 species of parasitic Hymenoptera that attack the egg stage and predators in the families Anthocoridae, Asilidae, Canidae, Pentatomidae, Reduviidae and Thomisidae that attack various life stages (Lee et al. 2013). To some degree, all three stages of *H. halys* (i.e., eggs, nymphs and adults) are vulnerable to generalist predators. Jones (2013) found that the wheel bug, *Arilus cristatus* (Hemiptera: Reduviidae), was the most efficient predator of *H. halys* adults and nymphs. The same study found very low rates of predation in the laboratory by *Orius insidiosus* (Hemiptera: Anthocoridae), *Hippodamia convergens* (Coleoptera: Coccinellidae), and *Harmonia axyridis* (Coleoptera: Coccinellidae) on first instar *H. halys* nymphs. Based on field surveys, Rice et al. (2014) reported that predators in the families Araneae, Coccinellidae, Forficulidae, Anthocoridae, Geocoridae, Reduviidae, Mantidae, and Chrysopidae attack *H. halys* in North America. To date, specific information on potential *H. halys* egg predators in US agroecosystems has not been widely reported. Three predators commonly found in Canadian agroecosystems, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), *Coleomegilla maculata* (De Geer) (Coccinellidae), and *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), were shown to attack *H. halys* eggs in the laboratory (Abram et al. 2015). Another stink bug predator, the predatory digger wasp, *Astata occidentalis* (Hymenoptera: Sphecidae), is attracted to methyl (*E,E,Z*)-2,4,6-decatrienoate as a host-finding kairomone (Cottrell et al. 2014). This compound, in combination with the recently identified *H. halys* aggregation pheromone (Khrimian et al. 2014), is used to monitor *H. halys* through the growing season in the United States (Leskey et al. 2015a; Leskey et al. 2015b; Morrison et al. 2015a).

Recently, sentinel *H. halys* egg masses generated in the laboratory have been deployed in coordinated trials throughout the mid-Atlantic states to monitor parasitism and

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predation by native natural enemies. Lacking a viable seriological technique for detecting predation by specific taxa, egg predation has been typically characterized as “chewing” or “piercing/sucking” based on visual observations. However, during the course of these surveys, widespread and frequent unexplained loss and damage to egg masses have been commonly reported (Dieckhoff 2014). In cases where eggs were completely removed, they have typically been reported as “lost” (e.g. see Koppel et al. 2009), potentially deflating estimates of predation rates and assessment of control by natural enemies in the field. Whether this pattern is due to predation or abiotic factors (e.g. abrasion with neighboring leaves, and ablation by wind or rain) is unknown, as it is unclear whether predators are able to remove egg masses from sentinel cards.

The aim of our study was to conclusively establish which generalist predators potentially found in or near mid-Atlantic orchards and vegetable crops are capable of feeding on *H. halys* eggs and to systematically characterize the appearance of feeding damage to eggs attacked by specific native predator taxa. We exposed 11,800 *H. halys* eggs to generalist predators in 25 families in controlled laboratory trials and catalogued the resulting physical damage to the eggs via pre- and post-exposure microscopic photography. We also monitored research apple and peach orchards through beat sampling and vegetable crops on an organic farm through visual sampling to confirm the presence of our laboratory-tested predators in agroecosystems. Finally, we also deployed sentinel egg masses in orchard and field crop systems using a predator exclusion technique to link patterns of predator damage from the lab to the field and to distinguish between abiotic factors that could result in physical changes to the *H. halys* eggs and effects of predators.

2. Materials and methods

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2.1. Laboratory studies

Laboratory studies were performed in 2014 and 2015 at the USDA Appalachian Fruit Research Station (Kearneysville, WV, USA) and the Institute of Environmental and Physical Sciences, Shepherd University (Shepherdstown, WV, USA). From May-September of each year, predators were collected daily from local agricultural landscapes (minimally treated apple and peach orchards at the Appalachian Fruit Research Station and vegetable row crops under USDA-certified organic production at Redbud Farm, LLC, Inwood, WV) where *H. halys* is widespread and abundant (Leskey et al. 2015; Morrison et al. 2015). Most predators used in trials were collected by vacuum sampling vegetation (D-Vac, Bioquip Products, Inc., Rancho Dominguez, CA) or by hand collection and held individually in lidded small plastic containers (4 × 4 D:H) in the laboratory with a water wick at ~24°C, ~50% RH, 16:8 L:D photoperiod for 24 h after collection to induce starvation before testing. Additional predator groups not found in sufficient numbers in the field were obtained from commercial biological control supply companies where possible and held under identical conditions (Table 1). After the 24-h starvation period with a wick containing water, individual predators were provided a single *H. halys* egg mass (median of 28 eggs per mass: Nielsen et al. 2008) affixed to the bottom of a deep petri dish (19 × 2.5 cm D:H) with permanent 12.7 mm (width) double-sided tape (Scotch, St. Paul, MN) and held for 48 h at 25±0.1°C, 50±10% RH and 16:8 L:D photoperiod. Egg masses were 24-48 h old, generated by laboratory colonies at the Appalachian Fruit Research Station (AFRS, Kearneysville, WV) or the Beneficial Insect Laboratory (Trenton, NJ) and shipped overnight. When fresh egg masses were not available, frozen egg masses collected from the AFRS colony (< 2 weeks old) were used. A paper disc marked with a central transect with the four cardinal directions was affixed to the underside of a petri dish with double-sided tape, such that the egg mass was oriented centrally over the

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four quadrants. Photographs (SMZ1500, Nikon Instruments, Inc., Melville, NY; light source: A20500, Schott-Fostec, LLC., Auburn, NY) of each egg masses were systematically taken (Paxcam ARC, Villa Park, IL) with a total of 5 images (1 central view of complete egg mass at 20X and 1 view of each quadrant at 50X plus a zoomed-in central view) before predator exposure. Starved predators collected from the field and obtained through commercial suppliers were introduced into petri dishes and left for 48 h. At the conclusion of a trial, the predator was removed and preserved in 75% (v/v) ethanol. Eggs were photographed at the end of the trial according to the same protocol described above. Physical changes in the eggs before and after predator exposure were noted. The number of eggs damaged was recorded, and percent predation per egg mass was calculated. A minimum of 10 replicates was performed with predators available via biological control suppliers (Table 1), though not every instar was tested; replication for taxa collected in the field ranged from 3-20, depending on availability.

For those taxa that consistently fed on *H. halys* eggs in laboratory trials, videography (Entovision, EIS-1030-AAD, GT Vision, LLC) was performed on at least one additional *H. halys* egg mass, to document specific feeding and handling behaviors. The photographs of attacked eggs were analyzed and grouped according to four feeding syndromes that were consistently observed based on egg damage and handling behavior from the videography: punctured sucking, stylet sucking, incomplete chewing, and complete chewing (Table 2). This is a new extension of already existing terminology for egg damage (Yeargan 1979, Tillman 2011).

The number of individuals in a taxon feeding on *H. halys* egg masses was calculated. The taxa that fed on eggs of *H. halys* were analyzed for differences in frequency of attack by a predator taxa (% of egg masses attacked) and predator efficiency (% of eggs consumed in

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an egg mass) using a generalized linear model (GLM) with a binomial distribution and a logit link function. Categorical variables included in the model were predator taxon, feeding guild (“chewing” or “piercing/sucking”), predator life stage (adult, nymph, or larva), and condition of the egg mass (fresh or frozen). Overdispersion was assessed and not found to be an issue with the model. A log-likelihood test was conducted based on a chi-square distribution to evaluate the significance of the explanatory variables, comparing the full model to a reduced model without the variable of interest. When the GLM produced significant results, Tukey’s HSD was used for pairwise comparisons (for this and all other tests $\alpha = 0.05$). All statistical tests were performed using R Software unless otherwise specified (R Core Development Team, 2015).

2.2. Sentinel Egg Mass Studies

Field studies were conducted in research orchards at the Appalachian Fruit Research Station (AFRS: 39°21'43.73"N; 77°53'16.90"W) and organic vegetable plots at Redbud Farm (39°23'37.01"N; 78° 4'34.67"W) in 2015. Egg masses of *H. halys* (either fresh or frozen from colony, as above) were prepared for deployment as sentinels by affixing with double-sided tape to a piece of index card (7.5 × 6.5 cm L:W) marked with two intersecting transects containing four cardinal directions (as above) and sample identification information. Tape was used to ensure that sentinel egg mass deployments were comparable with prior work for *H. halys* (Jones et al. 2014). A total of 16-24 egg masses per crop and sampling period (depending on availability from colony production) was placed in the field between June to September 2015. Sentinel egg masses were deployed at AFRS on 14 Jul and 19 Aug 2015, and at Redbud Farm on 4 Jul, 18 Jul, 23 Jul, 6 Aug, 19 Aug, 28 Aug, and 5 Sep 2015. Sentinel egg masses were deployed in apple (*Malus domestica* Borkh) on perimeter and

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interior trees, as well as on randomly selected plants on the interior of corn (*Zea mays* L.), pepper (*Capsicum annuum* L. var. Aristotle), sunflower (*Helianthus* sp.) and sorghum (*Sorghum bicolor* Moench) rows. The sampled crop areas ranged from 0.01 to 3.8 ha plots. Egg masses were attached to the host plant by stapling the index card directly to the abaxial aspect of a randomly selected leaf. The sentinel egg masses on four randomly selected plants per sample period were designated as ‘controls’ and were covered with predator exclusion cages. The exclusion cages consisted of a cylindrical supported sleeve constructed of 3 x 3 mm black vinyl mesh covered by a white polyester bag with 1 x 1 mm mesh (REI Company, Kent, WA). The cage was sealed at the proximal end after vigorously agitating the terminal vegetation to remove any predators present. The external sleeve was positioned a minimum of 8 cm from the sentinel egg mass, creating sufficient space to prevent piercing/sucking insects from accessing *H. halys* eggs from the cage exterior. Photography (as previously described) was performed before deployment and repeated after deployment for 48 h in the field. The images captured before and after field exposure were compared to determine the effects of abiotic factors on egg mass physical characteristics (caged egg masses) compared with the effects of predators (uncaged egg masses). The number of egg masses attacked by predators (e.g. frequency) and the percent egg predation per egg mass (e.g. efficiency) was calculated. In addition, predator damage was attributed to the appropriate feeding syndrome (for written definitions, see Table 2; for visual definitions, see Fig. 4). Differences in the attack frequency (number of egg masses attacked) and efficiency (number of eggs consumed in a mass) were analyzed with a GLM using the crop habitat (apple, corn, pepper, sunflower, and sorghum), predation syndrome (complete chewing, stylet sucking, incomplete chewing, or punctured sucking), condition of egg mass (fresh or frozen), and treatment (openly accessible or enclosed in mesh netting) as categorical variables to understand the effect on the

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number of eggs damaged in a sentinel egg mass. In addition, the interaction between crop and feeding syndrome was included. A binomial distribution was used for the model with a logit link function. Overdispersion in the model was not an issue, so no scaling factor was required. P-values were calculated with a log-likelihood test based on a chi-squared distribution comparing the full model to a reduced model lacking the variable of interest. Upon a significant result from the ANOVA, pairwise comparisons were conducted with Tukey's HSD.

2.3 Field Observation of Predators in Fruit

To confirm that predators tested in the laboratory trials described above could potentially be found in fruit agroecosystems, predator counts on fruit host plants were also done to document those predator taxa present in the crops where sentinel *H. halys* were deployed, and neighboring fields. In apple (3.8 ha) and peach (2.8 ha: *Prunus persica* [L.]) research plots at AFRS (same coordinates as sentinel egg mass study), a total of 12 trees were randomly selected at the beginning of the round of sampling, and these were spaced throughout the two orchard blocks. A total of 5 large limbs/day and tree were strongly tapped over a beating sheet between 29 Jul – 7 Aug 2015. Sampling occurred on a total of 9 d spread over 2 weeks, and took place at identical apple trees on which the sentinel egg masses were deployed. Predator sampling always took place in the late morning and early afternoon, as this has been when the natural enemy community is typically most active (Dondale et al. 1972). The number of individuals that landed on beat sheets belonging to major predator taxa were recorded. An ANOVA was performed that used the crop (peach or apple) and predator family as explanatory variables. Additionally, the interaction term between the two explanatory variables was also included in the model. Inspection of the residuals indicated

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that the data did not fulfill the assumptions of a normal distribution, so they were log transformed to correct the issue. Log transformed data fulfilled the assumptions of normality. Upon a significant result from the ANOVA, Tukey's HSD was used for pairwise comparisons.

2.4 Field Observation of Predators in Vegetables

A total of 20 randomly selected interior plants per plot and crop were sampled during each sentinel deployment period (4, 18 and 23 July, 6, 19 and 28 Aug, and 5 Sept 2015) in corn, pepper, sunflower, okra (*Abelmoschus esculentus* Moench), tomato, and sorghum (plots ranging from 0.01 – 0.23 ha) at Redbud Farm (same coordinates as above) by visually examining the entire plant for a period of 1 min, during which the number of predators/plant was recorded. The predator counts were grouped in aggregate across vegetable crops for the analysis. An ANOVA was performed as described above, using the predator family as the categorical explanatory variable. Because inspection of residuals revealed deviance from the assumptions of normality, the data were log transformed. Upon a significant result from the ANOVA, Tukey's HSD was used for pairwise comparisons.

3. Results

3.1. Laboratory studies

Overall, we tested 455 predators (Supplementary Table 1), representing 25 taxa that were found on 19 different hosts or habitats (Supplemental Fig. S2) over two years. While the majority of predators were found directly on agricultural crops, many were present in grassy field margins and on non-crop species or in agricultural structures also utilized by *H. halys* (Supplemental Fig. S2). The predators most frequently observed feeding on *H. halys*

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egg masses were Tettigonnidae (82%), Carabidae (80%), Salticidae (46%), Dermaptera (35%), and Gryllidae (29%; Fig. 1a). Egg predation varied significantly among taxa (GLM: $\chi^2 = 37.09$; $df = 23$, 421; $P = 0.0001$; Fig. 1b; Supplemental Supplemental Fig. S2), with the Tettigoniidae, Carabidae, Gryllidae, Dermaptera, and Salticidae significantly more efficient than other taxa (Tukey's HSD test; Fig. 1b). Coccinellidae were not a substantive source of predation for *H. halys* eggs, despite seven species being tested (Supplementary Supplemental Fig. S2; Fig. 1b). Predator efficiency depended on both the predator's mouthpart morphology ($\chi^2 = 6.86$; $df = 1$, 421; $P < 0.001$) and its behavior in handling the egg mass (as determined via videography), with chewing predators being 4x more efficient than piercing/sucking predators (Fig. 2A). Ontogeny also significantly affected predator efficiency ($\chi^2 = 43.81$; $df = 2$, 421; $P < 0.0001$), with adults being over 4x more efficient than larval or nymphal stages (Fig. 3). The condition of the egg mass (frozen or fresh) did not significantly affect predation ($\chi^2 = 0.0027$; $df = 1$, 421; $P = 0.958$).

Eggs exhibited characteristic damage patterns or syndromes depending on mouthpart morphology and feeding behavior. Overall, we identified four syndromes of egg damage: complete chewing, stylet sucking, incomplete chewing, and punctured sucking (see Table I for a breakdown of predator taxa by syndromes). For instance, some chewing insects such as the Dermaptera consumed from the top of the egg mass, leaving edges with characteristic irregularly serrated appearance and chorion debris in the vicinity of the egg mass (Fig. 4). The Tettigoniidae typically chewed through everything, leaving only remnants of the egg chorion and the leaf substrate (Fig. 4). In contrast, the Salticidae grasped the entire egg mass and inserted their chelicerae, apparently sucking out the internal contents of the individual eggs in the egg mass (Fig. 4). This feeding style left two characteristic punctures that may be visible from the top or sides of the individual egg (Fig. 4). Predatory Hemiptera, on the other

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hand, left behind feeding sheaths on the surfaces of the eggs, and consequently were

categorized as stylet sucking (Fig. 4, Table 2).

3.2. Sentinel Egg Mass Studies

The effects of abiotic factors were readily distinguished from those of predators in the field. The egg masses exposed only to abiotic factors (caged controls) sometimes appeared sunken after field exposure (Fig. 5), but this physical change to the eggs was easily distinguished from damage caused by both chewing and piercing/sucking predators. Among the four feeding syndromes identified in laboratory trials, the majority (37%) of egg predation in the field was consistent with the physical attributes of Tettigoniidae predation (e.g. complete chewing), in which the entire egg mass is chewed from the substrate, and there is often chewing damage on the sentinel card itself in the vicinity of the egg mass during the insect's 'handling' phase. Stylet sucking damage was also frequent in the field (35% of all eggs), and to a lesser extent incomplete chewing damage (24%), and punctured sucking damage (4%). Overall, most predation could be attributed to predators that had chewing mouthparts (Fig. 2B, Tukey's HSD).

A total of 209 sentinel egg masses containing 5,559 *H. halys* eggs were deployed in seven different crops. Our overall model significantly explained 53% (Adj. R^2) of the variation in the predation of *H. halys* egg masses (GLM: $\chi^2 = 3680.3$; $df = 30, 179$; $P < 0.0001$). The sentinel egg masses protected by exclusion cages did not experience any predation, whereas over 24.3% of egg masses without cages were attacked by predators ($\chi^2 = 480.5$; $df = 2, 179$; $P < 0.0001$ Fig. 6). On average, $9.12 \pm 1.8\%$ of eggs were missing per mass as compared with caged egg masses that experienced no predation Fig. 6. In addition, the crop in which the sentinel egg mass was placed significantly affected the level of

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predation ($\chi^2 = 1092.9$; $df = 6, 179$; $P < 0.0001$; Fig. 6). The greatest overall level of predation was found in apple ($5.4 \pm 1.9\%$), followed by sorghum and okra, which had 81% and 63% as much predation relative to apple. The crops with the lowest amount of predation were pepper and corn with 21% and 3% of eggs eaten per mass, respectively, compared with apple.

Certain damage syndromes resulted in significantly greater or fewer numbers of eggs removed per egg mass across all crops ($\chi^2 = 2094$; $df = 3, 179$; $P < 0.0001$; Fig. 6).

Specifically, punctured sucking resulted in the lowest numbers of eggs consumed (only 0.08% of an egg mass) across crops. By contrast, stylet sucking, incomplete chewing, and complete chewing resulted in 10, 12, and 69 times higher percentages of eggs consumed, respectively, compared with punctured sucking overall. In all crops where sentinel egg masses were deployed, complete chewing resulted in the most egg damage (Fig. 7, Tukey's HSD). The damage from the other syndromes was partially modulated by the crop in which the sentinel egg mass was deployed (crop $\times$ damage syndrome interaction: $\chi^2 = 25.1$; $df = 18, 179$; $P < 0.0001$). Whether the sentinel egg mass was frozen or fresh did not significantly impact the efficiency of predation ($\chi^2 = 1.8$; $df = 1, 179$; $P = 0.068$).

3.3. Field Observation of Predators in Fruit and Vegetables

Overall, 363 predators representing 22 taxa were observed on 16 sampling days from July to September 2015 in 8 tree fruit and vegetable crops. Half, or a total of 11, of these same taxa were also tested during laboratory trials for predation of *H. halys* egg masses. The overall model explaining the abundance of predators in tree fruit was significant (ANOVA: $F = 21.1$; $df = 43, 173$; $P < 0.0001$). There was a significant difference in the abundance of various natural enemy taxa in tree fruit ($F = 37.4$; $df = 21, 173$; $P < 0.0001$; Fig. 7, top and

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middle panel). The two most abundant predator families regardless of tree fruit crop were Salticidae and Thomisidae. These two families were 67 and 57 times greater in abundance in apple, and 40 and 13 times greater in abundance in peach than the least abundant taxon (Fig. 7, top panel). In apple, the three least abundant taxa were Dermaptera, Syrphidae, and Hemerobiidae (Fig. 7, Tukey's HSD). In peach, the least abundant taxa were Vespidae and Dermaptera. Within tree fruit, the crop species significantly affected the abundance of predators found ($F = 23.6$; $df = 1, 173$; $P < 0.0001$; Fig. 7). In particular, there were almost three times as many predators in apple than there were in peach. Eleven taxa found in apple orchards and eight found in peach are confirmed predators of *H. halys* egg masses from the laboratory trials. There was also a significant interaction between tree fruit crop type and predator family ($F = 4.68$; $df = 21, 173$; $P < 0.0001$).

In vegetable crops, there was a significant difference in the abundance of predator taxa ($F = 13.3$; $df = 10, 130$; $P < 0.0001$; Fig. 7, bottom panel). The Coccinelidae were by far the most abundant family of predators in vegetable crops, followed by Anthocoridae, Dolichopodidae and Pentatomidae (Fig. 7). Six of the predator taxa found in vegetable crops were also documented to feed on eggs of *H. halys* in the laboratory (Fig. 7). Importantly, the Tettigoniidae were also found in the vegetable crops. The crop species did not significantly affect the number of predators present ($F = 1.10$; $df = 5, 130$; $P = 0.153$), though there was a significant interaction between the crop species and predator taxa on abundance of individuals ($F = 3.24$; $df = 50, 130$; $P < 0.0001$). Numerically, sorghum had the greatest abundance of predators with 0.5 ± 0.2 (mean $\pm$ SE) predators per plant. This was followed in decreasing order by corn, peppers, and okra, which had 80%, 35%, and 10% the abundance of predators compared to sorghum, respectively.

4. Discussion

Our studies provide the first in-depth examination of a large variety of specific generalist predator taxa found in agroecosystems of the mid-Atlantic U.S. involved in *H. halys* egg predation and indicate that some groups, such as the Tettigoniidae and Carabidae (*Harpalus spp.*), are capable of consuming a considerable number of *H. halys* eggs. While Carabidae are known to be important predators in many agroecosystems (Lövei and Sunderland 1996), including tree fruit orchards (Epstein et al. 2001), the finding that Tettigoniidae will readily consume *H. halys* egg masses is more surprising. However, omnivory is widespread and relatively common among the tettigoniids (Gwynne 2008), which may take advantage of protein-rich food sources. Both *Concocephalus strictus* and many *Orchelimum spp.* fit into this category, and we found that both readily eat *H. halys* eggs. Moreover, certain tettigoniids are exclusively predaceous or have a preference for carnivory, including *Atlanticus testaceus* (Gangwere 1967), which was also found in agroecosystems of our study.

To a lesser extent, we have also shown that Salticidae, Dermaptera, and Gryllidae will feed on *H. halys* egg masses, though they fed on fewer eggs per mass and did not attack as frequently. However, Salticidae (jumping spiders), in particular, were the dominant group in the tree fruit orchards sampled, suggesting that even if only a few of those individuals eat some of the eggs in a particular mass, this may still represent a significant amount of predation. Salticidae are well-known for their behavioral flexibility and conditional predatory strategies, including the use of trial-and-error learning (Jackson and Pollard 1996). Indeed, we observed salticids removing egg masses that were affixed with double-sided tape from surfaces, carrying them around, inverting the egg masses, and inserting their chelicerae to consume the contents. Interestingly, the “punctured sucking” syndrome, which is at least

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partly caused by jumping spiders, was only represented in the apple and not in the other crops, suggesting that while jumping spiders may be abundant in the environment and especially in the diversified farm where sentinel eggs were deployed (Sunderland and Samu 2000), they may prefer alternative prey.

The remaining taxa that were field-collected and tested in the laboratory did not contribute significantly to the mortality of *H. halys* eggs. Importantly, this includes all the Coccinellidae species (seven total) we tested. While coccinellids have been demonstrated to be important for the mortality of soft-bodied insects, such as aphids (Rutledge et al. 2004), they do not seem to contribute significantly to predation of *H. halys* eggs.

We found that there were stage-specific differences in predation of *H. halys* eggs. For example, adult predators were much more efficient in consuming a greater percentage of eggs in a mass than were immature stages. This finding concurs with other studies indicating that late instar and adult predators are more efficient at killing prey than younger stages (De Clercq et al. 2003). Moreover, we found that some immature predators consuming *H. halys* eggs did not do so as adults. This was notably true for Cantharidae larvae. Differential predation of *H. halys* eggs based on life stage has also been found for *C. carnea*, *C. maculata* (De Geer) (Coccinellidae), and *P. maculiventris* (Say) in the laboratory, with the most and least eggs consumed by late instar and second instar *C. carnea*, respectively (Abram et al. 2015). In addition, stage-dependent predation has also been found on native stink bugs for a variety of taxa, ranging from Reduviidae and Nabidae to Coccinellidae, with these taxa preferentially eating nymphs compared to eggs (Ehler 2002). Shifts in the diets and niches of holometabolous insects from one life stage to another is quite common, and prior research has shown that this can lead to the coexistence of predators within the environment (Loreau and Ebenhoh 1994).

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We have established a pattern of egg mass damage, which we define as four damage syndromes. This categorization is an extension of the already existing dichotomy between chewing damage and sucking/piercing damage present in the literature (e.g. Yeargan 1979, Tillman 2011). By far the most prevalent categories for both laboratory and field studies were the complete and incomplete chewing syndromes. In fact, for field-deployed *H. halys* egg masses, significantly higher percentages of attacked eggs exhibited the complete chewing syndrome relative to other damage syndromes in apple, sorghum, tomato, and pepper. Although we cannot directly attribute egg predation observed in the field to a particular predator taxon, taken together, the results of our laboratory and field studies suggest that chewing predators such as the Tettigoniidae could play a major role in *H. halys* egg predation in these systems. But, based on prior literature (e.g. Rice et al. 2014), and the observed high populations throughout the mid-Atlantic US, baseline levels of biological control by native natural enemies have to date been insufficient to suppress *H. halys* below economic thresholds (e.g. Leskey et al. 2012b). For native stink bugs, Yeargan (1979) found that chewing predators destroyed more eggs for four pentatomid species than sucking predators in soybean. In addition, Jones (1995) found that that an average of 31% of *Nezara viridula* (L.) sentinel egg masses placed in or near macadamia nut orchards in Hawaii were destroyed by predators, suggesting that chewing predators may be a large source of mortality across pentatomid taxa.

Furthermore, our results suggest that a portion of the missing egg masses and unresolved damage to recovered egg masses in previous field sentinel surveys may be the result of native predators that are fully consuming eggs of *H. halys*. In particular, feeding by the Tettigoniidae during laboratory trials commonly resulted in complete removal of both the *H. halys* egg mass and the substrate (plant matter or mesh from colony) on which the eggs

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454 had been deposited, with only the double-sided tape remaining on the petri dish. Field-
455 deployed sentinel egg masses in this condition would typically be considered 'lost' due to
456 wind or abrasion, deflating estimates of predation on *H. halys*. This may also help explain
457 sentinel eggs that were lost without a trace in prior studies for native stink bugs, including for
458 a study where 5.4-8.0% of 239 egg masses were missing upon retrieval (Yeargan 1979).
459 Moreover, we are now able to distinguish between sunken eggs due to abiotic factors and
460 damage to eggs as a result of feeding by predators, which seem to be clearly separate from
461 each other. The damage syndromes for egg masses we have laid out here is an extension of
462 the existing dichotomy used to categorize predator damage to eggs.,

463   These feeding syndromes may be more broadly applicable to other species of insects
464 than simply stink bugs. For example, these categories may be useful for any group of insects
465 with stationary and robust hosts affixed to substrates such as cocoons/pupae, eggs, and aphid
466 mummies (e.g. Brodeur and Rosenheim, 2000). There may be some limitations as well, for
467 example, if the complete chewing syndrome is common across these other groups of insects,
468 then these syndromes may be most useful in conjunction with sentinel eggs or prey where a
469 known group of individuals is present. In this case it may be less useful in naturally-laid egg
470 masses or among naturally occurring hosts, because it would be nearly impossible to evaluate
471 how many individuals (if any) were present initially on the substrate. Some of these aspects
472 should be explored in future studies to evaluate the generality and applicability of these
473 syndromes to naturally-occurring hosts.

474   In addition to demonstrating damage caused by specific taxa in the laboratory and
475 categorizing the types of damage, we have provided evidence that the taxa are likely found in
476 or near tree fruit and vegetable agroecosystems in the current study's location. It may be
477 useful for follow-up studies to use these feeding syndromes to understand how predation

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changes across the phenology of a crop. While the current level of biological control provided by natural enemies is insufficient to regulate *H. halys* populations below economic thresholds, knowing the identity of the most effective native predators provides a foundation for future conservation biological control efforts.

The use of habitat management or alternative tactics may enhance conservation biological control. Some of these strategies include the use of trap cropping with sunflowers (Soergel et al. 2016), border sprays (Blaauw et al. 2015), attract-and-kill (Morrison et al. 2015b), and threshold-based sprays (Short et al. 2016). Ultimately, tactics that conserve native natural enemies may be a promising means of potentially bolstering biological control of *H. halys* in agricultural systems.

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Table 1. Commercial insect sources used for laboratory trials at the Applachian Fruit Research Station in 2014 and 2015.

Species	Source	Life Stage	No. Tested	Holding Conditions
<i>Zelus renardii</i>	Arbico Organics ^a	1st instar	25	tested within 3 d after emergence and held with water wick
<i>Chrysoperla rufilabris</i>	Arbico Organics	1st instar	10	tested after 1 d emergence and held with water wick
<i>Podisus maculiventris</i>	Green Methods ^b	1st instar	20	held individually for 24 h with water wick
<i>Podisus maculiventris</i>	Green Methods	2nd instar	9	provided soybean leaves and carrots and tested after 24 h starvation period
<i>Podisus maculiventris</i>	Green Methods	3rd instar	11	provided soybean leaves and carrots and tested after 24 h starvation period
<i>Podisus maculiventris</i>	Green Methods	4th instar	2	provided soybean leaves and carrots and tested after 24 h starvation period
<i>Podisus maculiventris</i>	Green Methods	5th instar	2	provided soybean leaves and carrots and tested after 24 h starvation period
<i>Cryptolaemus montrouzieri</i>	Arbico Organics	adult	23	held with diet prior to 24 h starvation
<i>Hippodamia convergens</i>	Arbico Organics	adults	20	tested upon arrival
<i>Orius insidiosus</i>	Arbico Organics	adult	35	held without food and with water wick at ~8C and tested within 2 d of arrival

^a Oro Valley, AZ, USA^b Redding, CA, USA

Table 2. Predators observed feeding on *Halyomorpha halys* eggs in laboratory study performed in 2014-2015, with individual taxa grouped by characteristic feeding syndrome (replication in parenthesis)

Feeding Syndrome	Taxon (No. Tested)
Complete Chewing <i>Partial or full removal of individual eggs and accompanying substrate</i>	Gryllidae <i>Oecanthus spp.</i> (6) Tettigoniidae <i>Atlanticus testaceus</i> (3) <i>Conocephalus strictus</i> (13) <i>Orchelimum spp.</i> (2)
Incomplete Chewing <i>Remnants composed of irregular pieces of egg chorion often with outline of original mass remaining</i>	Coccinellidae <i>Coleomegilla maculata</i> (28) <i>Harmonia axyridis</i> (29) Carabidae <i>Harpalus spp.</i> (8) Dermaptera <i>Forficulidae spp.</i> (22)
Stylet Sucking <i>Eggs hollowed out with feeding sheath remaining</i>	Anthocoridae <i>Orius insidiosus</i> (38) Pentatomidae <i>Podisus maculiventris</i> (44)
Punctured Sucking <i>Eggs hollowed out with puncture wounds in top or side of egg</i>	Salticidae (28)

Figure Captions

Fig. 1. The A) frequency with which *H. halys* egg masses are attacked, and the B) efficiency in consuming eggs (including any predator individual consuming one or more eggs per mass) from field-collected predator taxa in laboratory trials after a 24 h starvation period. Predators were collected from Jefferson and Berkeley Co., WV. Numbers above each bar in (A) represent the total number of predators tested belonging to each taxon. Bars in (B) with shared letters are not significantly different from each other (Tukey's HSD, $\alpha = 0.05$). Error bars represent standard errors.

Fig. 2 The efficiency of predators based on their mouthpart morphology for A) field-collected predators brought to the laboratory and tested with fresh or frozen *H. halys* egg masses, or B) sentinel egg masses deployed in the field in apple, corn, peppers, sunflower, and sorghum during 2015 near Inwood and Kearneysville, WV. Error bars represent standard errors. Bars with shared letters are not significantly different from each other (Tukey's HSD, $\alpha = 0.05$).

Fig. 3 The effect of developmental stage on predator efficiency in attacking eggs of *H. halys* in laboratory trials with field-collected predators in 2014 and 2015 in Jefferson and Berkeley County, WV. Only predator taxa where experiments included both immature stages and adults were included for this comparison.

Fig. 4 Representative habitus images of predator damage syndromes found on sentinel egg masses in the field (left), and corresponding documented predator feeding, which caused similar patterns of damage in laboratory trials (right). Abbreviations: PT = pre-trial photo.

Fig. 5 Habitus images of a representative frozen sentinel egg mass enclosed in a mesh to exclude predators showing the effects of abiotic influences, which are distinctive from those of predator-induced damage.

Fig. 6. The percent of eggs consumed by predators from *H. halys* sentinel egg masses deployed in apple, okra, pepper, sweet corn, sunflower, sorghum, tomato, or across all crops, depending on the feeding damage syndrome. Bars represent standard errors, and bars that share lower case letters are not significantly different from each other (Tukey's HSD, $\alpha = 0.05$).

Fig. 7. Predators observed in apple (A), peach (B) and vegetable crops (C) via beat sheet sampling (apples and peaches) or whole-plant visual observation (vegetable crops) on 20 plants/d. Bars represent standard errors, and arrows indicate confirmed *H. halys* egg mass predator taxa from lab studies.

Figure 1

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Figure 2

Figure 3

Figure 4

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Figure 5