

## Host Plant Effects on *Halyomorpha halys* (Hemiptera: Pentatomidae) Nymphal Development and Survivorship

Angelita L. Acebes-Doria,<sup>1,2</sup> Tracy C. Leskey,<sup>3</sup> and J. Christopher Bergh<sup>1</sup>

<sup>1</sup>Alson H. Smith Jr. Agricultural Research and Extension Center, Virginia Tech, Winchester, VA 22602 (aacebes@vt.edu; cbergh@vt.edu), <sup>2</sup>Corresponding author, e-mail: aacebes@vt.edu, and <sup>3</sup>USDA-ARS, Appalachian Fruit Research Station, 2217 Wiltshire Rd, Kearneysville, WV, 25430 (tracy.leskey@ars.usda.gov)

Received 14 December 2015; Accepted 20 February 2016

### Abstract

*Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) is a highly polyphagous invasive species and an important pest of orchard crops in the United States. In the Mid-Atlantic region, wild hosts of *H. halys* are common in woodlands that often border orchards, and *H. halys* movement from them into orchards poses ongoing management issues. To improve our understanding of host plant effects on *H. halys* populations at the orchard–woodland interface, nymphal survivorship, developmental duration, and adult fitness (size and fresh weight) on apple (*Malus domestica* Borkh.), peach (*Prunus persica* (L.) Batsch), Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle), and northern catalpa (*Catalpa speciosa* (Warder)) were examined in laboratory studies. Specifically, we investigated nymphal performance on the foliage and fruiting structures of those hosts and on single- versus mixed-host diets, as well as the effects of host phenology on their suitability. Nymphal performance was poor on a diet of foliage alone, regardless of host. When fruiting structures were combined with foliage, peach was highly suitable for nymphal development and survivorship, whereas apple, Tree of Heaven, and catalpa were less so, although nymphal survival on Tree of Heaven was much greater later in the season than earlier. Mixed-host diets yielded increased nymphal survivorship and decreased developmental duration compared with diets of suboptimal single hosts. Adult size and weight were generally greater when they developed from nymphs reared on mixed diets. The implications of our results to the dispersal behavior, establishment, and management of *H. halys* are discussed.

**Key words:** host plant suitability, brown marmorated stink bug, mixed diet, polyphagy, nymph

Plant species vary widely in their suitability as food for polyphagous insect herbivores (Scriber 1984) and can affect insect development and survival differently via their chemical (e.g., nutritional quality, allelochemicals) or physical (e.g., trichomes, tissue hardness) characteristics, which may vary with plant age and phenology (Bernays and Chapman 1994). Polyphagous insect herbivores may complete development on a single host, but their fitness is generally enhanced when they feed and develop on multiple plant species (Bernays et al. 1994, Hägele and Rowell-Rahier 1999, Miura and Ohsaki 2004). For example, the polyphagous hemipteran, *Bemisia tabaci* (Gennadius), exhibited higher survivorship and increased fecundity on a mixed diet of cotton, cucumber, tomato, cabbage, and kidney beans than on any of those plants alone (Zhang et al. 2014). Earlier studies found that fitness advantages of mixed diets were associated with nutritional complementarity and/or the dilution of allelochemicals (Bernays et al. 1994, Hägele and Rowell-Rahier 1999).

Research on the relative suitability of plant species to polyphagous insect pests that utilize both cultivated and wild hosts has important implications for understanding aspects of pest biology and ecology, such as their movement in the landscape, host use patterns,

and population dynamics, as well as the susceptibility of economic crops to attack (Panizzi 1997). Such studies have yielded beneficial information about basic pest biology, informed the development of ecologically based pest management options (Panizzi and Parra 2012), and are especially relevant to recently invasive economic pests, about which there are often important knowledge gaps regarding their biology and ecology in the invaded range. The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is a classic example of this.

*Halyomorpha halys* is an invasive pest from Asia that did not become a major pest until the late 2000s (Leskey et al. 2012a), following its initial detection in Allentown, PA, about a decade earlier (Hoebeke and Carter 2003). Since its widespread outbreak in the Mid-Atlantic region of the United States in 2010, *H. halys* has caused significant economic damage to various fruit, vegetable, and field crops (Rice et al. 2014). Its effects in Mid-Atlantic fruit orchards have been especially pronounced via reductions in fruit yield and quality and changed pest management practices (Leskey et al. 2012b) that have resulted in secondary pest outbreaks. *Halyomorpha halys* is reported to utilize well over 100 plant species

as feeding or reproductive hosts (Rice et al. 2014), many of which are deciduous trees that grow in forested areas that often border commercial orchards in this region (Bakken et al. 2015). The abundance of wild hosts in these woodlands, the development of large *H. halys* populations on some, and the high dispersal capacity of *H. halys* adults and nymphs (Lee et al. 2014, Wiman et al. 2014, Lee and Leskey 2015) combine to create pest pressure in commercial orchards through most or all of the fruiting period (Joseph et al. 2015). Moreover, Funayama (2006) showed that fitness of *H. halys* nymphs was positively affected when they developed on a mixed diet.

Investigation of the effects of different wild and cultivated host plants on *H. halys* development and survivorship in its invaded range should further our understanding of their relative contributions to local *H. halys* population densities and the risk to economic crops and may aid the development of ecologically based pest management tactics against this important pest. Here, we report laboratory experiments that examined the effects of selected wild and tree fruit hosts in Virginia on the survivorship and developmental duration of *H. halys* nymphs and aspects of adult fitness (size and fresh weight). Specifically, the suitability of apple (*Malus domestica* Borkh.), peach (*Prunus persica* (L.) Batsch), Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle), and northern catalpa (*Catalpa speciosa* (Warder)) was examined, focusing on vegetative and reproductive structures, the effects of single- versus mixed-host diets, and changes in host suitability during the growing season.

## Materials and Methods

### Insects

Adult male and female *H. halys* collected from natural overwintering aggregations in northern Virginia in April 2012 and February 2013 were placed in black, plastic bags with crumpled newspaper and held in a dark room at 4°C at Virginia Tech's Alson H. Smith, Jr. Agricultural Research and Extension Center (AHSAREC), Winchester, VA. In mid-April of each year, ~30 male and ~30 female adults collected during the same year were placed in each of several 30.48-cm<sup>3</sup>, screened cages (BioQuip Products, Inc., Rancho Dominguez, CA) in a laboratory room at ~25°C, ~70% RH, and a photoperiod of 16:8 (L:D) h provided by overhead banks of 34-W fluorescent lights (Ace Hardware Corp., Oak Brook, IL). For the experiment that began in August 2013, fifth instars and adult *H. halys* were collected from the field in July and reared under the same conditions. Cages were provisioned regularly with popcorn kernels, barley, buckwheat, soybeans, dried figs, dry roasted, unsalted peanuts, sundried tomatoes, and water. Oviposition substrates in each cage included paper towel on the cage floor and three to four freshly excised compound leaves of Tree of Heaven in a water-filled vase. Egg masses produced between late May and early June and in early August were used in the early- and late-season experiments, respectively. *Halyomorpha halys* females most often deposit eggs in clutches of 28 (Nielsen et al. 2008). Egg masses (≤1-d-old) were removed *in situ*, held in groups of five in 100 by 15-mm petri dishes (Thermo Fisher Scientific Inc., Pittsburgh, PA) in the same room, and monitored daily for hatch. Those that hatched within a 5-d period and had ~28 first instars were assigned to the diet treatments. First-instar *H. halys* aggregate around and on the empty egg mass before dispersing (Taylor et al. 2014) and thus were easily transferred to cages as cohorts from each egg mass.

### Host Plant Sources

'Smoothie Golden' apple and 'Redhaven' peach trees growing at the AHSAREC were the sources of cultivated host plant material. These trees were treated with fungicides, but not insecticides, during the growing season. Northern catalpa (hereafter referred to as catalpa) and Tree of Heaven growing on or near the AHSAREC property were selected as the wild hosts, based primarily on their inclusion in the host list for *H. halys* (see StopBMSB.org) but also on reports by Bakken et al. (2015) and anecdotal observations of large populations of *H. halys* nymphs and adults on both species and the results of a census showing that Tree of Heaven was the most common deciduous tree species growing at the edge of woodlands adjacent to orchards in this region (Acebes-Doria, unpublished data). Like *H. halys*, Tree of Heaven is an invasive species from Asia (Kowarik and Säumel 2007) and catalpa is native to eastern North America (see <http://dendro.cnre.vt.edu>).

Freshly excised foliage and reproductive structures (flowers, fruit, or seed pods) of apples, peaches, Tree of Heaven, and catalpa were offered to nymphs. The reproductive structures used reflected the stage of development of each host plant in the field at the time each experiment was conducted. From early- to mid-June, immature apple and peach fruit (three to four per replicate) and foliage, Tree of Heaven flowers and foliage, and catalpa flowers and foliage were used. The volume of Tree of Heaven and catalpa flowers offered was comparable with the total volume of the apple and peach fruit offered. Later in the season,—one to two larger apple and peach fruit and foliage were offered. At that time, three catalpa seed pods (10.16–12.70 cm in length) and foliage and Tree of Heaven samaras and foliage were offered. The volume of seed pods and samaras offered was approximately the same as the other treatments.

The plant materials were washed thoroughly under running tap water to remove contaminants (e.g., fungicide residues, other arthropods, etc.). The foliage offered to nymphs included three terminal twigs of apples and peaches with—six to eight leaves (20.32–25.40 cm in length), two apical branches of catalpa with—two to three leaves (15.24–20.32 cm in length), and three compound leaves of Tree of Heaven (25.4–30.48 cm in length). All shoots offered, including those with flowers, samaras, or catalpa pods, were inserted into—two to four holes (8 mm diameter) in the plastic lid of plastic containers (8 cm height, 115 mm diameter) containing water, while peach and apple fruit were placed on the cage floor. All plant tissues were replaced—two to three times per week.

### Single-Host Diets

A completely randomized design with two factors, host plant species and plant tissue (foliage versus foliage plus reproductive structures), was used in an experiment between late May and early August 2012. Cohorts of first instars, each with ~28 individuals, were assigned individually to seven replicates of each diet treatment. Each cohort of first instars on the egg mass was placed on or near the plant material inside a 30.48 by 30.48 by 30.48-cm cage (BioQuip Products, Inc, Rancho Dominguez, CA) with ad libitum access to the food source and water. Water was provided in a plastic container with a cotton wick inserted through the lid. Cages were inspected daily for the presence of exuviae, which indicated the molt between instars, and the specific instars were identified following Hoebeke and Carter (2003). As well, the numbers of live and dead nymphs and live adults were recorded. Stage-specific survivorship and nymphal developmental period were recorded for each diet treatment.

### Single- Versus Mixed-Host Diets Early and Late in the Growing Season

The onset of these experiments coincided with two key points in the seasonal phenology of *H. halys* populations in the Mid-Atlantic region. Peak emergence of *H. halys* adults from overwintering sites occurs between approximately mid-May and early June (Bergh and Leskey, unpublished data), and F<sub>1</sub> generation adults are estimated to be reproducing in early to mid-August based on degree-day accumulations (Leskey et al. 2012c; Bakken et al. 2015). Experiments initiated in late May (early season) and mid-August 2013 (late season) included the following treatments in a completely randomized design with host plant as the factor: 1) apple, 2) peach, 3) Tree of Heaven, 4) catalpa, 5) apple plus Tree of Heaven, 6) apple plus Tree of Heaven plus peach, and 7) apple plus Tree of Heaven plus peach plus catalpa. Host plants in the mixed diet treatments were provided all at once. Hereafter, we refer to the diet treatments that consisted of three or four hosts as the three-host and four-host diet, respectively. All treatments included foliage and fruiting structures and each treatment was replicated four times.

As in the previous experiment, cohorts of ~28 *H. halys* first instars on the egg mass were placed individually in 30.48 by 30.48 by 30.48-cm rearing cages provisioned ad libitum with the diet treatment and water. Cages were checked daily to monitor the development and survivorship of nymphs from each egg mass. Stage-specific survivorship and nymphal developmental duration were recorded for nymphs from each cohort. Within 48 h after molting to the adult stage, the fresh weight of all adults produced was measured (nearest 0.1 mg) using a digital scale (AB54-S Mettler Toledo, Columbus, OH) and their pronotum width was measured (nearest 0.01 mm) with a digital caliper (ROK International Industry Co., Ltd., Guangdong, China). Wild adult *H. halys* ( $n = 30$ ) collected from Tree of Heaven trees at the AHSAREC in early September 2013 also were weighed and measured for comparison with adults obtained from the late-season laboratory experiments.

### Data Analyses

All analyses were conducted using JMP® Pro version 11 (SAS Institute Inc., Cary, NC, 2007) and outcomes were considered significant at  $P < 0.05$ . Data that did not satisfy the assumptions of parametric tests were transformed using arcsine-square root for percentage data and  $\log(x+1)$  for nymphal developmental duration and the pronotum width and fresh weight. Two-way analysis of variance (ANOVA) was used to compare nymphal stage-specific survivorship and developmental duration among the diets that included foliage alone and foliage plus reproductive structures. One-way ANOVA was used to analyze the survivorship and developmental duration among the diets during the early- and late-season experiments. Student's *t*-test was used to compare nymphal survivorship between the early- and late-season experiments for each diet. One-way ANOVA was used to compare the effect of host plant diet on the fresh weight and pronotum width of the females and males that developed to the adult stage during the early- and late-season experiments, including measurements from the field-collected adult males and females, which were compared only with the adults reared from the late-season experiment. Student's *t*-test was used to compare the fresh weight and pronotum width, based on pooled data across all diet treatments. Multiple mean comparisons used Tukey's post hoc honestly significant difference test.

## Results

### Single-Host Diets

In this experiment,  $94.45 \pm 1.39\%$  of the eggs from each mass hatched. As first-instar *H. halys* do not feed on plant tissue, their survivorship was not significantly affected by diet treatment (Table 1). There were significant effects of host plant and the inclusion of reproductive structures on the survivorship of second through fifth instars (Table 1). In general, the percentage of nymphs that survived each of these instars was much higher on diets that combined foliage and reproductive structures than on foliage alone, although this effect was much less pronounced on Tree of Heaven, on which the fewest number of nymphs survived the second instar.

As the developmental duration of first instars was not significantly affected by diet treatment ( $F_{7, 48} = 0.30$ ,  $P = 0.95$ ), the duration between the second instar and adult eclosion was compared. Moreover, as diets of foliage alone yielded very few adults, developmental duration was analyzed only for treatments that included fruiting structures. Among those, the developmental duration varied significantly among the treatments (Table 1) and was shortest on Tree of Heaven and significantly shorter on peach than on apple or catalpa, which did not differ from each other.

### Single- Versus Mixed-Host Diets Early and Late in the Growing Season: Survivorship.

In this experiment,  $93.61 \pm 1.25\%$  of eggs from each mass hatched. As in the previous experiment, diet treatment had no effect on the survivorship of first instars during the early- or late-season experiments (Table 2). In the early-season study, there were numerical, but not statistically significant, diet effects on second-instar survivorship, with the lowest survivorship on apple. In the late-season study, apple also resulted in second-instar survivorship that was significantly or numerically lower than on the other diets, which did not differ.

The early- and late-season experiments yielded significant diet effects on survivorship during the third through fifth instars (Table 2). In the early-season study, highest nymphal survivorship through the fifth instar was on peach, apple plus Tree of Heaven, and the three- and four-host diets; the lowest survivorship was on apple, Tree of Heaven, and catalpa. In the late-season study, apple and catalpa again yielded the lowest survivorship through the fifth instar, whereas the other diets yielded  $>69\%$  survivorship. In both experiments, there was a pronounced decrease in survivorship on catalpa between the fourth and fifth instars that was not observed on the other diets.

Between the early- and late-season experiments, nymphal survival to the adult stage increased from 20 to 72% on Tree of Heaven ( $t = 6.32$ ,  $df = 6$ ,  $P = 0.001$ ); survivorship to the adult stage on the other diets did not differ significantly between early- and late-season studies (apple:  $t = 2.34$ ,  $df = 6$ ,  $P = 0.06$ ; peach:  $t = -2.19$ ,  $df = 6$ ,  $P = 0.07$ ; catalpa:  $t = 0.66$ ,  $df = 6$ ,  $P = 0.54$ ; apple plus Tree of Heaven:  $t = 0.79$ ,  $df = 6$ ,  $P = 0.46$ ; three-host diet:  $t = -1.06$ ,  $df = 6$ ,  $P = 0.33$ ; and four-host diet:  $t = 0.09$ ,  $df = 6$ ,  $P = 0.93$ ).

### Single- Versus Mixed-Host Diets Early and Late in the Growing Season: Developmental Duration and Adult Size and Fresh Weight

There was no effect of diet on the developmental duration of first instars (Table 3). Significant diet treatment effects on the developmental duration of second, fourth, and fifth instars were recorded during

**Table 1.** Stage-specific survivorship and developmental duration of *H. halys* nymphs reared on single-host plant diets consisting of foliage or foliage plus reproductive structures, 2012

Diet treatment (N) <sup>a</sup>	Mean ± SE percent survivorship <sup>b</sup>					Mean ± SE duration (days) from second instar to adult eclosion (N) <sup>c</sup>
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	
Foliage alone						
Apple (195)	100.00 ± 0.00a	0.00 ± 0.00d	0.00 ± 0.00c	0.00 ± 0.00d	0.00 ± 0.00c	
Peach (188)	97.38 ± 1.29a	1.74 ± 1.22d	0.55 ± 0.55c	0.55 ± 0.55d	0.55 ± 0.55c	86.98 (1)
Catalpa (199)	99.49 ± 1.29a	7.85 ± 4.05cd	7.32 ± 4.10bc	5.26 ± 0.55cd	0.00 ± 0.00c	
Tree of Heaven (199)	98.92 ± 0.70a	9.02 ± 2.63bcd	7.96 ± 2.32bc	7.43 ± 2.99bcd	5.84 ± 1.96bc	76.39 ± 4.37 (11)
Foliage plus fruit						
Apple (186)	97.45 ± 1.69a	29.27 ± 8.92bc	27.54 ± 8.15b	26.70 ± 8.26b	16.25 ± 5.39b	77.06 ± 5.67a (28)
Peach (187)	100.00 ± 0.00a	86.53 ± 2.75a	83.73 ± 4.85a	79.65 ± 6.50a	72.49 ± 8.12a	52.87 ± 2.37b (135)
Catalpa (192)	96.97 ± 1.43a	33.22 ± 8.76b	21.90 ± 5.44b	15.11 ± 2.87bc	7.12 ± 3.35bc	72.89 ± 3.49a (11)
Tree of Heaven (196)	100.00 ± 0.00a	13.27 ± 7.66bcd	11.93 ± 6.81bc	11.93 ± 6.81bcd	11.42 ± 6.89bc	36.49 ± 2.40c (20)
One-way ANOVA						
Two-way ANOVA	$F_{7,48} = 1.79$ $P = 0.112$	$F_{7,48} = 22.66$ $P < 0.0001$	$F_{7,48} = 25.49$ $P < 0.0001$	$F_{7,48} = 24.66$ $P < 0.0001$	$F_{7,48} = 25.75$ $P < 0.0001$	$F_{3,19} = 23.15$ $P < 0.0001$

<sup>a</sup> Total number of first instars at the outset of the experiment.

<sup>b</sup> Stage-specific survivorship was computed as the number of surviving individuals in a specific stage/initial no. of individuals × 100.

<sup>c</sup> Total number of nymphs that developed to the adult stage. The developmental duration of the plant feeding stages of nymphs (second through fifth instars) was compared only among diets that included foliage plus fruit.

Means with the same letters under the same column are not significantly different at  $\alpha = 0.05$ .

**Table 2.** Stage-specific survivorship of *H. halys* nymphs reared on single- and mixed-host plant diets in experiments beginning in May (early season) and mid-August (late season) 2013

Diet treatment (N) <sup>a</sup>	Mean ± SE percent survivorship <sup>b</sup>				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Early season					
Apple (120)	92.86 ± 6.01a	34.72 ± 23.61a	15.03 ± 8.92c	14.36 ± 8.43b	8.21 ± 5.16b
Peach (115)	98.21 ± 1.03a	91.38 ± 5.36a	88.79 ± 5.87a	87.90 ± 5.34a	86.18 ± 5.95a
Catalpa (103)	99.00 ± 1.00a	91.73 ± 3.25a	81.53 ± 2.79a	74.22 ± 5.66a	9.77 ± 1.93b
ToH <sup>c</sup> (109)	99.11 ± 0.89a	60.71 ± 22.73a	26.30 ± 4.58bc	22.04 ± 3.35b	20.18 ± 2.29b
Apple + ToH <sup>c</sup> (110)	100.00 ± 0.00a	73.50 ± 11.16a	70.72 ± 10.34ab	70.05 ± 10.29a	68.27 ± 10.37a
Three-host <sup>d</sup> (113)	100.00 ± 0.00a	95.60 ± 0.91a	94.67 ± 1.80a	92.06 ± 1.66a	89.41 ± 1.99a
Four-host <sup>e</sup> (114)	97.12 ± 2.88a	89.73 ± 9.12a	86.02 ± 9.52a	82.92 ± 10.51a	80.77 ± 11.53a
One-way ANOVA	$F_{6,21} = 0.89$ $P = 0.522$	$F_{6,21} = 2.02$ $P = 0.108$	$F_{6,21} = 14.23$ $P < 0.0001$	$F_{6,21} = 13.87$ $P < 0.0001$	$F_{6,21} = 21.72$ $P < 0.0001$
Late season					
Apple (112)	99.11 ± 0.89a	53.08 ± 11.67b	48.26 ± 13.96b	39.52 ± 9.45b	26.26 ± 9.55bc
Peach (104)	99.17 ± 0.83a	90.30 ± 1.77a	87.73 ± 0.91ab	82.29 ± 2.18a	69.74 ± 4.55ab
Catalpa (82)	97.29 ± 0.90a	77.03 ± 3.47ab	67.04 ± 4.02ab	48.00 ± 2.97ab	13.64 ± 5.57c
ToH <sup>c</sup> (105)	99.11 ± 0.89a	89.74 ± 7.90a	87.93 ± 7.45a	83.26 ± 7.17a	72.04 ± 7.88ab
Apple + ToH <sup>c</sup> (106)	99.11 ± 0.89a	96.42 ± 2.07a	92.91 ± 3.15a	87.24 ± 4.25a	77.78 ± 6.26a
Three-host <sup>d</sup> (100)	97.11 ± 1.90a	83.33 ± 11.77ab	75.59 ± 16.87ab	72.83 ± 18.49ab	70.48 ± 17.71ab
Four-host <sup>e</sup> (104)	97.76 ± 1.33a	95.40 ± 1.78a	90.74 ± 1.07ab	83.83 ± 2.36a	81.81 ± 3.16a
One-way ANOVA	$F_{6,21} = 0.61$ $P = 0.717$	$F_{6,21} = 4.41$ $P = 0.005$	$F_{6,21} = 3.45$ $P = 0.016$	$F_{6,21} = 4.68$ $P = 0.004$	$F_{6,21} = 8.44$ $P < 0.0001$

<sup>a</sup> Total number of first instars at the outset of the experiment.

<sup>b</sup> Stage-specific survivorship was computed as the number of surviving individuals in a specific stage/initial no. of individuals × 100.

<sup>c</sup> ToH denotes Tree of Heaven.

<sup>d</sup> The three-host diet consisted of the foliage and fruiting structures of apple, ToH, and peach.

<sup>e</sup> The four-host diet consisted of the foliage and fruiting structures of apple, ToH, peach, and catalpa.

Means with the same letters under the same column and in the same experiment are not significantly different at  $\alpha = 0.05$ .

the early-season experiment, while in the late-season study, there were significant effects on second, third, and fifth instars. In the early season, total developmental period was significantly shorter on peach and the three- and four-host diets than on apple or catalpa, with intermediate durations on the others. The late-season study

yielded similar results, with significantly shorter total developmental duration on peach, Tree of Heaven, and the four-host diet than on apple or catalpa, with intermediate periods among the other diets.

Based on pooled data across all diet treatments, mean adult pronotum width was significantly greater for females ( $7.95 \pm 0.02$  SE

**Table 3.** Stage-specific stadia and developmental duration (mean days  $\pm$  SE) of *H. halys* nymphs on single- and mixed-host plant diets during the early- and late-season experiments, 2013

Diet treatment (N) <sup>a</sup>	Mean $\pm$ SE developmental duration (days)					Mean $\pm$ SE duration (days) from second instar to adult eclosion (N) <sup>b</sup>
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	
<b>Early season</b>						
Apple (120)	5.25 $\pm$ 0.48a	17.98 $\pm$ 0.09a	20.12 $\pm$ 1.26a	33.48 $\pm$ 3.77a	44.71 $\pm$ 1.46ab	91.79 $\pm$ 2.62a (10)
Peach (115)	5.26 $\pm$ 0.25a	13.26 $\pm$ 0.50bc	13.07 $\pm$ 0.71a	17.61 $\pm$ 1.14b	24.66 $\pm$ 2.06bc	53.45 $\pm$ 2.70c (99)
Catalpa (103)	5.15 $\pm$ 0.25a	13.09 $\pm$ 1.32c	18.94 $\pm$ 6.11a	28.46 $\pm$ 3.67ab	51.25 $\pm$ 8.71a	77.48 $\pm$ 8.66ab (10)
ToH <sup>c</sup> (109)	5.32 $\pm$ 0.23a	16.07 $\pm$ 0.82ab	20.13 $\pm$ 2.82a	22.90 $\pm$ 3.25ab	19.00 $\pm$ 3.56c	58.68 $\pm$ 4.98bc (22)
Apple + ToH <sup>c</sup> (110)	5.19 $\pm$ 0.27a	17.02 $\pm$ 0.86a	18.98 $\pm$ 1.73a	23.51 $\pm$ 1.49ab	23.31 $\pm$ 1.74c	62.59 $\pm$ 3.80abc (75)
Three-host <sup>d</sup> (113)	5.20 $\pm$ 0.27a	13.23 $\pm$ 0.62c	14.27 $\pm$ 1.00a	18.64 $\pm$ 1.59b	19.34 $\pm$ 0.71c	49.23 $\pm$ 2.80c (101)
Four-host <sup>e</sup> (114)	5.19 $\pm$ 0.36a	12.99 $\pm$ 1.13c	14.03 $\pm$ 1.17a	19.84 $\pm$ 2.15ab	23.54 $\pm$ 1.56c	52.85 $\pm$ 2.56c (96)
One-way ANOVA	$F_{6,21} = 0.03$ $P = 0.999$	$F_{6,19} = 4.04$ $P = 0.009$	$F_{6,19} = 1.45$ $P = 0.246$	$F_{6,19} = 3.92$ $P = 0.010$	$F_{6,19} = 10.69$ $P < 0.0001$	$F_{6,19} = 7.43$ $P = 0.0003$
<b>Late season</b>						
Apple (112)	4.82 $\pm$ 0.72a	22.39 $\pm$ 1.08ab	22.73 $\pm$ 0.70a	30.85 $\pm$ 2.05a	53.91 $\pm$ 4.31ab	105.21 $\pm$ 3.53a (32)
Peach (104)	5.90 $\pm$ 0.53a	16.89 $\pm$ 1.05ab	17.32 $\pm$ 0.33ab	20.65 $\pm$ 1.28a	27.96 $\pm$ 2.09c	63.58 $\pm$ 2.94c (68)
Catalpa (82)	5.72 $\pm$ 0.32a	22.33 $\pm$ 0.56ab	22.80 $\pm$ 1.85a	28.59 $\pm$ 3.69a	61.72 $\pm$ 6.45a	100.79 $\pm$ 4.46ab (12)
ToH <sup>c</sup> (105)	5.32 $\pm$ 0.27a	15.11 $\pm$ 2.60b	14.17 $\pm$ 2.43b	18.76 $\pm$ 3.97a	32.22 $\pm$ 6.53c	62.12 $\pm$ 11.92c (82)
Apple + ToH <sup>c</sup> (106)	5.24 $\pm$ 0.19a	18.61 $\pm$ 2.01ab	18.01 $\pm$ 2.50ab	25.59 $\pm$ 2.80a	41.33 $\pm$ 3.72abc	71.58 $\pm$ 4.14bc (85)
Three-host <sup>d</sup> (100)	5.58 $\pm$ 0.28a	23.21 $\pm$ 2.80a	19.42 $\pm$ 1.15ab	25.64 $\pm$ 1.99a	34.36 $\pm$ 4.00bc	68.03 $\pm$ 1.97bc (73)
Four-host <sup>d</sup> (104)	5.75 $\pm$ 0.28a	18.59 $\pm$ 0.69ab	19.70 $\pm$ 0.15ab	25.21 $\pm$ 2.51a	31.15 $\pm$ 2.81c	65.64 $\pm$ 1.45c (84)
One-way ANOVA	$F_{6,21} = 0.95$ $P = 0.482$	$F_{6,21} = 3.23$ $P = 0.021$	$F_{6,21} = 3.86$ $P = 0.009$	$F_{6,21} = 2.32$ $P = 0.071$	$F_{6,20} = 5.87$ $P = 0.001$	$F_{6,20} = 7.23$ $P = 0.0003$

<sup>a</sup> Total number of first instars at the outset of the experiment.

<sup>b</sup> Total number of nymphs that developed to the adult stage. Second through fifth instars are the plant-feeding stages of juvenile *H. halys*.

<sup>c</sup> ToH denotes Tree of Heaven.

<sup>d</sup> The three-host diet consisted of the foliage and fruiting structures of apple, ToH, and peach.

<sup>e</sup> The four-host diet consisted of the foliage and fruiting structures of apple, ToH, peach, and catalpa.

Means with the same letters under the same column and in the same experiment are not significantly different at  $\alpha = 0.05$ .

mm) than males (7.17  $\pm$  0.02 SE mm;  $t = -26.18$ ,  $df = 878$ ,  $P < 0.0001$ ) and females were significantly heavier (109.37  $\pm$  1.10 SE mg) than males (87.48  $\pm$  0.86 SE mg;  $t = -15.61$ ,  $df = 878$ ,  $P < 0.0001$ ). Diets that yielded fewer than three adult males or females were excluded from statistical comparisons. In both the early- and late-season experiments, the fresh weight and pronotum width of both sexes varied significantly among diets (Table 4). In the early season, Tree of Heaven and apple plus Tree of Heaven yielded females that were heaviest and had the largest pronotum width, while apple yielded the lightest and smallest females. The heaviest and largest males also were recorded from Tree of Heaven and apple plus Tree of Heaven, while the lightest and smallest males were from catalpa and apple. In the late-season study, the heaviest females and males were recorded from peach, although the three- and four-host diets also produced relatively heavy individuals of both sexes (Table 4). As in the early-season experiment, females and males from apple and catalpa were the lightest. The three- and four-host diets produced females with the largest pronotum width and smallest females were from catalpa and apple, while male pronotum width was largest from the four-host diet and smallest from apple. Field-collected females and males had statistically or numerically comparable fresh weights and pronotum widths to those from the three- and four-host diet treatments during the late-season experiment (Table 4).

## Discussion

The survivorship and developmental duration of laboratory-reared *H. halys* nymphs were significantly affected by host plant tissue,

host plant species, host phenology, and diet mixing. Like other pentatomid species, such as the southern green stink bug, *Nezara viridula* (L.), and the Neotropical brown stink bug, *Euschistus heros* (F.) (Panizzi 2000), *H. halys* nymphs have been known to feed on nonreproductive parts of plants such as the stem (Martinson et al. 2013) and foliage (Hoebeke and Carter 2003). For all plants examined, we found that diets consisting only of stems and foliage were unsuitable, and that most nymphs did not survive the second instar on them.

Martinson et al. (2015) showed that the presence of fruit on ornamental trees in a nursery strongly influenced the abundance of *H. halys* nymphs and adults and that fruit removal had a profound negative effect on *H. halys* counts. Complementing their results, we found that combining foliage and fruiting structures of peach dramatically increased *H. halys* nymphal survivorship and reduced their developmental duration compared with foliage alone. For apple and catalpa, we also showed that fruiting structures and foliage only led to marginal improvements in nymphal survivorship both early and late in the season. Tree of Heaven foliage plus samaras produced the same result early in the season, but nymphal survivorship on that diet increased in the late-season study.

With regard to the cultivated plant species offered as single-host diets that combined foliage and fruit, the relatively poor suitability of apple for *H. halys* nymphs concurs with Funayama (2002), who reported that nymphs reared on apple had low survivorship and developed poorly. In our study, we consistently found that nymphal survivorship was higher and their developmental duration was shorter on peach than on apple, indicating a clear difference in the suitability of these two economically important hosts for nymphal

**Table 4.** Mean  $\pm$  SE fresh weights (mg) and pronotum widths (mm) of  $\leq$ 2-d-old *H. halys* adults reared on different diets during the early- and late-season experiments, and adults collected from the field in early-September 2013

Diet treatment	Females			Males		
	N	Weight (mg)	Pronotum width (mm)	N	Weight (mg)	Pronotum width (mm)
Early season						
Apple	3	70.53 $\pm$ 7.76d	6.98 $\pm$ 0.34d	7	67.44 $\pm$ 5.91c	6.62 $\pm$ 0.10c
Peach	51	111.84 $\pm$ 2.50c	7.72 $\pm$ 0.04c	48	96.87 $\pm$ 1.66ab	7.11 $\pm$ 0.04b
Catalpa	2	97.00 $\pm$ 22.20*	7.67 $\pm$ 0.53*	8	59.44 $\pm$ 4.10c	6.60 $\pm$ 0.11c
ToH <sup>d</sup>	7	138.04 $\pm$ 4.41a	8.50 $\pm$ 0.09a	15	107.47 $\pm$ 2.66a	7.55 $\pm$ 0.05a
Apple + ToH <sup>a</sup>	33	132.38 $\pm$ 3.25a	8.39 $\pm$ 0.06a	42	102.80 $\pm$ 1.70a	7.47 $\pm$ 0.04a
Three-host <sup>b</sup>	55	121.11 $\pm$ 2.02bc	8.09 $\pm$ 0.04b	46	93.21 $\pm$ 1.96b	7.20 $\pm$ 0.05b
Four-host <sup>c</sup>	50	118.04 $\pm$ 2.27c	8.04 $\pm$ 0.04b	46	96.62 $\pm$ 2.07ab	7.27 $\pm$ 0.04b
One-way ANOVA		$F_{5,193} = 13.32$ $P < 0.0001$	$F_{5,193} = 28.23$ $P < 0.0001$		$F_{6,205} = 28.84$ $P < 0.0001$	$F_{6,205} = 20.93$ $P < 0.0001$
Late season						
Apple	15	77.20 $\pm$ 2.27de	7.14 $\pm$ 0.10d	17	62.32 $\pm$ 2.30d	6.48 $\pm$ 0.09d
Peach	42	112.07 $\pm$ 2.90a	7.93 $\pm$ 0.06bc	26	85.96 $\pm$ 2.50ab	7.12 $\pm$ 0.04bc
Catalpa	10	67.85 $\pm$ 4.28e	6.92 $\pm$ 0.11d	2	66.45 $\pm$ 1.25*	6.64 $\pm$ 0.12*
ToH <sup>d</sup>	43	93.43 $\pm$ 3.37cd	7.75 $\pm$ 0.08c	39	75.50 $\pm$ 2.22bc	7.16 $\pm$ 0.08abc
Apple + ToH <sup>a</sup>	41	98.61 $\pm$ 3.79bc	7.79 $\pm$ 0.06c	44	73.93 $\pm$ 2.05cd	6.96 $\pm$ 0.06c
Three-host <sup>b</sup>	31	104.46 $\pm$ 2.67abc	8.11 $\pm$ 0.06ab	42	83.62 $\pm$ 1.54b	7.19 $\pm$ 0.04ab
Four-host <sup>c</sup>	48	106.85 $\pm$ 2.22ab	8.19 $\pm$ 0.04a	36	83.43 $\pm$ 1.99bc	7.37 $\pm$ 0.04ab
Field-collected (Sept. 2013)	15	121.90 $\pm$ 8.23a	8.30 $\pm$ 0.13a	15	98.72 $\pm$ 8.35a	7.47 $\pm$ 0.11a
One-way ANOVA		$F_{7,237} = 13.08$ $P < 0.0001$	$F_{7,237} = 26.41$ $P < 0.0001$		$F_{6,212} = 11.83$ $P < 0.0001$	$F_{6,212} = 17.32$ $P < 0.0001$

<sup>a</sup> ToH denotes Tree of Heaven.

<sup>b</sup> The three-host diet consisted of the foliage and fruiting structures of apple, ToH, and peach.

<sup>c</sup> The four-host diet consisted of the foliage and fruiting structures of apple, ToH, peach, and catalpa.

\*Treatment excluded from analyses due to sample size.

Means with the same letters under the same column and in the same category are not significantly different at  $\alpha = 0.05$ .

development. The high suitability of peach for nymphal development and survival conforms to field observations that peach can support large *H. halys* populations from late May through harvest (Nielsen and Hamilton 2009) and often incurs higher levels of injury early in the growing season than apple (Leskey et al. 2012b, Joseph et al. 2015). While apples can sustain substantial injury from *H. halys* (Nielsen and Hamilton 2009, Leskey et al. 2012b, Joseph et al. 2015), this may be associated more with transient visits and feeding bouts by adults and nymphs than by resident populations; Morrison III et al. (2015) used harmonic radar to show that tagged *H. halys* adults remained on apple trees for only  $\sim$ 3.5 h.

A survey of 78 species of native and invasive trees and herbaceous shrubs in urban, rural, and forested areas in the eastern United States by Bakken et al. (2015) revealed that catalpa and Tree of Heaven were among the species that consistently yielded comparatively high counts of *H. halys* adults and nymphs. In China, Tree of Heaven is considered a preferred host of *H. halys* (reviewed in Lee et al. 2013). A possible explanation for the relatively poor performance of *H. halys* nymphs on catalpa and Tree of Heaven, discussed earlier, is that members of the Simaroubaceae (e.g., Tree of Heaven) and Bignoniaceae (e.g., catalpa) produce secondary metabolites with insecticidal properties (Tsao et al. 2002, De Feo et al. 2009, Castillo and Rossini 2010). The pronounced reduction in survivorship between the fourth and fifth instars of nymphs reared on catalpa may have been associated with the cumulative effects of these allelochemicals during their development. As well, the marked seasonal difference in the suitability of Tree of Heaven for nymphal survival may have been due to seasonal variation in allelochemical concentration and/or increasing nutritional value of the maturing samaras.

Diet mixing was clearly beneficial to the survivorship of *H. halys* nymphs. Funayama (2006) reported similar results when carrots were added to a peanut and soybean diet for *H. halys* nymphs; indeed, mixed diets for rearing *H. halys* have been universally adopted (Medal et al. 2012, Leskey and Hamilton 2014). In the early-season study in 2013, the diet that combined apple and Tree of Heaven, both of which were suboptimal as single hosts, yielded improved nymphal survivorship through the fifth instar, although this effect was not found for the same diet in the late-season study, perhaps due to the apparently increased suitability of Tree of Heaven. Nymphs of the polyphagous grasshopper, *Parapodisma subastrictis* (Huang), reared on diets of two, four, and six suboptimal hosts also showed higher survivorship compared with those on a diet of a single suboptimal host (Miura and Ohsaki 2004). The survivorship of *P. subastrictis* nymphs reared on all mixed diets of suboptimal hosts was statistically equivalent to that on single diets of the superior hosts, as was the case for *H. halys* reared on mixed diets of suboptimal hosts versus those on peach alone.

Overall, total developmental durations from the second through fifth instars were considerably longer than reported from *H. halys* rearing studies under similar environmental conditions by Nielsen et al. (2008) and Medal et al. (2012). Both previous studies used a bean, peanut, corn, and carrot diet, resulting in 34-d and 37-d developmental durations from the second through fifth instars, respectively. The underlying reasons for the differences between the present and previous experiments are unknown, but may be associated with differences in the nutritional quality of the diets used.

Previous studies on *N. viridula* showed that adult size was positively correlated with longevity, female fecundity (McLain et al. 1990), and winter survival (Todd 1989). Moreover, studies on *N.*

*viridula* (Kester and Smith 1984) and *B. tabaci* (Zhang et al. 2014) found that nymphs reared on mixed diets produced longer-lived adults and more fecund females. These results suggest that the larger and heavier adult *H. halys* from nymphs reared on suitable diets, whether of single or mixed hosts, may also have improved longevity and fecundity. The size and weight of adults from nymphs reared on mixed diets in the late-season study in 2014 did not differ significantly from field-collected adults in September 2013, which had likely also developed from nymphs that had fed on a range of host plants. As well, Todd's (1989) finding of higher overwintering survivorship in larger than smaller *N. viridula* adults suggests that the bigger and heavier *H. halys* adults from nymphs reared on mixed diets or peach later in the season also may be better able to overwinter successfully.

Further investigation of the mechanisms behind the relative suitability of the different host plants in our study and the benefits of diet mixing on *H. halys* development and survival may further improve our understanding of its host-utilization at the orchard–woodland interface. Toward the end, Acebes-Doria (unpublished data) quantified the nutrient content in the adults from this study that had developed from nymphs reared on the different diets, revealing new information about host plant effects on *H. halys* nutrition.

Despite the reports (Bakken et al. 2015) and observations of Tree of Heaven and catalpa supporting large populations of *H. halys* in the eastern United States, our results suggest that *H. halys* nymphs may need to disperse from these trees during their development to find and feed on other plants. In the laboratory, Lee et al. (2014) demonstrated that *H. halys* nymphs can walk up to 41 m in 1 h and up to 8 m in 15 min on smooth horizontal and vertical surfaces, respectively. In a follow-up field experiment using pheromone-baited traps near a woodlot, Lee et al. (2014) found that marked nymphs walked over 20 m on a mowed grassy lawn within 4–5 h. Acebes-Doria et al. (2016) captured *H. halys* nymphs in traps designed to monitor their upward and downward movement on tree trunks. Results from Tree of Heaven revealed that second through fifth instars were captured walking up and down tree trunks, but that more nymphs were captured while walking up than down, leading them to speculate that nymphs may also disperse from the tree canopy by dropping (Acebes-Doria et al. 2016). Follow-up field studies using trunk traps have also examined seasonal patterns of the upward and downward walking dispersal of *H. halys* nymphs on cultivated and wild tree hosts at the orchard–woodland interface.

The relative suitability of available hosts may affect the extent to which *H. halys* nymphs disperse among hosts at the orchard–woodland interface. Our data suggest that nymphs from eggs laid on apple, catalpa, or Tree of Heaven early in the season would be more likely to disperse to other hosts than those on peaches. Host phenology and the presence and maturity of fruiting structures appear to strongly influence seasonal patterns of host use by adults and nymphs (Martinson et al. 2015). Moreover, Bakken et al. (2015) reported that among the 78 plant species surveyed, *H. halys* egg masses, nymphs, and adults were found on 34 species, including Tree of Heaven and catalpa, while only nymphs and adults were found on 41 species and none were detected on three species. These findings further support the likelihood that *H. halys* nymphs and adults disperse among available plants, that some species serve as its feeding and reproductive hosts, and that others are only feeding hosts or are unsuitable.

At the orchard–woodland interface, many known wild and tree fruit hosts of *H. halys* are commonly found growing close to one another (Acebes-Doria, unpublished data) and well within the dispersal distance of which nymphs are capable (Lee et al. 2014).

Consequently, additional and very relevant questions that follow from the data reported here include: 1) how long do nymphs remain on a particular host, 2) do nymphs that disperse from one host species move to the same or different species, 3) do nymphs disperse from wild hosts into orchards, and if so, 4) how far into the orchard do nymphs move? Moreover, the potential geographic distribution of *H. halys* based on niche modeling indicates that much of the Eastern United States and portions of its Pacific coastal regions could be successfully colonized by this invasive species (Zhu et al. 2012). Our results indicate that within a particular ecosystem, available host plants also could have a major impact on the survivorship and population growth of *H. halys*, particularly if available hosts are suboptimal. The apparent need for diet mixing due to suboptimal hosts could limit *H. halys* establishment and build-up in areas that lack suitable host diversity. Indeed, some suboptimal hosts may be considered a “dead end” for nymphal survivorship and development if alternate hosts that provide additional nutritional benefits are not available nearby.

In summary, *H. halys* nymphs are commonly found on wild hosts adjacent to fruit orchards and have the capacity to disperse between the two habitats (Lee et al. 2014). Indeed, transects of pheromone-baited traps that extended from woodlots into apple orchards revealed highest captures of adults and nymphs in traps at the orchard and woodland edges (Bergh, unpublished data). In addition, field studies using trunk traps deployed on apple and peach trees and known tree hosts of *H. halys* at the orchard–woodland interface revealed movement of *H. halys* nymphs both up and down the trees during much of the growing season (Acebes-Doria, unpublished data). As well, more *H. halys* injury has been recorded from apples in trees at orchard edges adjacent to woodlands than from orchard interior trees (Leskey et al. 2012b, Joseph et al. 2014). These findings and our demonstration of the effects of host plant species and diet mixing on nymphal performance suggest the likelihood that *H. halys* nymphs move between these two habitats during much of the growing season and that effective management programs targeting *H. halys* in orchards next to woodlands might be perimeter-driven. Restricting applications of the most efficacious insecticides against *H. halys* to the orchard perimeter, whether via border sprays (Blaauw et al. 2014) or sprays to pheromone-baited trees at intervals along the borders (“attract-and-kill”; Morrison III et al. 2015), should translate to fewer secondary pest problems throughout the orchard and facilitate a return to the more ecologically and economically sustainable programs that were widely practiced before *H. halys* became an issue.

## Acknowledgments

We are greatly thankful for Dr. Shimat Joseph, Sean Gresham, Jean Engelman, Eliezer Doria, and the student assistants for their excellent technical assistance. This material is based on work that is supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award number #2011-51181-30937.

## References

- Acebes-Doria, A. L., T. C. Leskey, and C. J. Bergh. 2016. Development and comparison of trunk traps to monitor movement of *Halyomorpha halys* nymphs on host trees. *Entomol. Exp. Appl.* 158: 44–53.
- Bakken, A. J., S. C. Schoof, M. Bickerton, K. L. Kamminga, J. C. Jenrette, S. Malone, M. A. Abney, D. A. Herbert Jr, D. Reisig, T. P. Kuhar, et al. 2015. Occurrence of brown marmorated stink bug (Hemiptera: Pentatomidae) on wild hosts in nonmanaged woodlands and soybean fields in North Carolina and Virginia. *Environ. Entomol.* 44: 1011–1021.

- Bernays, E. A., and R. F. Chapman. 1994. Host-plant selection by phytophagous insects, Springer Science & Business Media, New York, NY.
- Bernays, E., K. Bright, N. Gonzalez, and J. Angel. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75: 1997–2006.
- Blaauw, B. R., D. Polk, and A. L. Nielsen. 2014. IPM - CPR for peaches: Incorporating behaviorally - based methods to manage *Halyomorpha halys* and key pests in peach. *Pest Manag. Sci.* 71: 1513–1522.
- Castillo, L., and C. Rossini. 2010. Bignoniaceae metabolites as semiochemicals. *Molecules* 15: 7090–7105.
- De Feo, V., E. Mancini, E. Voto, M. Curini, and M. C. Digilio. 2009. Bioassay-oriented isolation of an insecticide from *Ailanthus altissima*. *J. Plant Interact.* 4: 119–123.
- Funayama, K. 2002. Comparison of the susceptibility to injury of apple cultivars by stink bugs. *Jpn. J. Appl. Entomol. Zool.* 46: 37–40.
- Funayama, K. 2006. A new rearing method using carrots as food for the brown-marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae). *Appl. Entomol. Zool.* 41: 415–418.
- Hägele, B. F., and M. Rowell-Rahier. 1999. Dietary mixing in three generalist herbivores: nutrient complementation or toxin dilution? *Oecologia* 119: 521–533.
- Hoebcke, E. R., and M. E. Carter. 2003. *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): A polyphagous plant pest from Asia newly detected in North America. *Proc. Entomol Soc. Wash.* 105: 225–237.
- Kowarik, I., and I. Säumel. 2007. Biological flora of central Europe: *Ailanthus altissima* (Mill.) swingle. *Perspect. Plant Ecol. Evol. Syst.* 8: 207–237.
- Joseph, S. V., J. W. Stallings, T. C. Leskey, G. Krawczyk, D. Polk, B. Butler, and J. C. Bergh. 2014. Spatial distribution of brown marmorated stink bug (Hemiptera: Pentatomidae) injury at harvest in mid-Atlantic apple orchards. *J. Econ. Entomol.* 107: 1839–1848.
- Joseph, S. V., M. Nita, T. C. Leskey, and J. C. Bergh. 2015. Temporal effects on the incidence and severity of brown marmorated stink bug (Hemiptera: Pentatomidae) feeding injury to peaches and apples during the fruiting period in Virginia. *J. Econ. Entomol.* 108: 592–599.
- Kester, K., and C. M. Smith. 1984. Effects of diet on growth, fecundity and duration of tethered flight of *Nezara viridula*. *Entomol. Exp. Appl.* 35: 75–81.
- Lee, D. H., and T. C. Leskey. 2015. Flight behavior of foraging and overwintering brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae). *Bull. Entomol. Res.* 105: 566–573.
- Lee, D. H., B. D. Short, S. V. Joseph, J. C. Bergh, and T. C. Leskey. 2013. Review of the biology, ecology, and management of *Halyomorpha halys* (Hemiptera: Pentatomidae) in China, Japan, and the Republic of Korea. *Environ. Entomol.* 42: 627–641.
- Lee, D. H., A. L. Nielsen, and T. C. Leskey. 2014. Dispersal capacity and behavior of nymphal stages of *Halyomorpha halys* (Hemiptera: Pentatomidae) evaluated under laboratory and field conditions. *J. Insect Behav.* 27: 639–651.
- Leskey, T. C., and G. Hamilton. 2014. Brown Marmorated Stink Bug IPM Working Group Meeting. (<http://www.northeastipm.org/neipm/assets/File/BMSB-Working-Group-Meeting-Report-Dec-2014.pdf> accessed 3 February 2016)
- Leskey, T. C., G. C. Hamilton, A. L. Nielsen, D. F. Polk, C. Rodriguez-Saona, J. C. Bergh, D. A. Herbert, T. P. Kuhar, D. Pfeiffer, G. P. Dively, et al. 2012a. Pest status of the brown marmorated stink bug, *Halyomorpha halys* in the USA. *Outlooks Pest Manag.* 23: 218–226.
- Leskey, T. C., B. D. Short, B. R. Butler, and S. E. Wright. 2012b. Impact of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål), in mid-Atlantic tree fruit orchards in the United States: case studies of commercial management. *Psyche: J. Entomol.* 2012: 1–14.
- Leskey, T. C., S. E. Wright, B. D. Short, and A. Khrimian. 2012c. Development of behaviorally based monitoring tools for the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae) in commercial tree fruit orchards. *J. Entomol. Sci.* 47: 76–85.
- Martinson, H. M., M. J. Raupp, and P. M. Shrewsbury. 2013. Invasive stink bug wounds trees, liberates sugars, and facilitates native Hymenoptera. *Ann. Entomol. Soc. Am.* 106: 47–52.
- Martinson, H. M., P. D. Venugopal, E. J. Bergmann, P. M. Shrewsbury, and M. J. Raupp. 2015. Fruit availability influences the seasonal abundance of invasive stink bugs in ornamental tree nurseries. *J. Pest Sci.* 88: 461–468.
- McLain, D. K., D. L. Lanier, and N. B. Marsh. 1990. Effects of female size, mate size, and number of copulations on fecundity, fertility, and longevity of *Nezara viridula* (Hemiptera: Pentatomidae). *Ann. Entomol. Soc. Am.* 83: 1130–1136.
- Medal, J., T. Smith, A. Fox, A. S. Cruz, A. Poplin, and A. Hodges. 2012. Rearing the brown marmorated stink bug *Halyomorpha halys* (Heteroptera: Pentatomidae). *Fla. Entomol.* 95: 800–802.
- Miura, K., and N. Ohsaki. 2004. Diet mixing and its effect on polyphagous grasshopper nymphs. *Ecol. Res.* 19: 269–274.
- Morrison, W. R. III, D.-H. Lee, B. D. Short, A. Khrimian, and T. C. Leskey. 2015. Establishing the behavioral basis for an attract-and-kill strategy to manage the invasive *Halyomorpha halys* in apple orchards. *J. Pest Sci.* 89: 81–96. (DOI: 10.1007/s10340-015-0679-6).
- Nielsen, A. L., and G. C. Hamilton. 2009. Seasonal occurrence and impact of *Halyomorpha halys* (Hemiptera: Pentatomidae) in tree fruit. *J. Econ. Entomol.* 102: 1133–1140.
- Nielsen, A. L., G. C. Hamilton, and D. Matadha. 2008. Developmental rate estimation and life table analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae). *Environ. Entomol.* 37: 348–355.
- Panizzi, A. R. 1997. Wild hosts of pentatomids: ecological significance and role in their pest status on crops. *Annu. Rev. Entomol.* 42: 99–122.
- Panizzi, A. R. 2000. Suboptimal nutrition and feeding behavior of hemipterans on less preferred plant food sources. *An. Soc. Entomol. Brasil* 29: 1–12.
- Panizzi, A. R., and J. R. Parra. 2012. Insect bioecology and nutrition for integrated pest management, CRC Press, Boca Raton, FL.
- Rice, K. B., C. J. Bergh, E. J. Bergmann, D. J. Biddinger, C. Dieckhoff, G. Dively, H. Fraser, T. Garipey, G. Hamilton, T. Haye, et al. 2014. Biology, ecology, and management of brown marmorated stink bug (Hemiptera: Pentatomidae). *J. Integr. Pest Manag.* 5: A1–A13.
- Scriber, J. M. 1984. Host-plant suitability, pp. 159–202. In W. J. Bell and R. T. Cardé (eds.), *Chemical Ecology of Insects*. Springer.
- Taylor, C. M., P. L. Coffey, B. D. DeLay, and G. P. Dively. 2014. The importance of gut symbionts in the development of the brown marmorated stink bug, *Halyomorpha halys* (Stål). *PLoS ONE* 9: e90312.
- Tsao, R., F. E. Romanchuk, C. J. Peterson, and J. R. Coats. 2002. Plant growth regulatory effect and insecticidal activity of the extracts of the Tree of Heaven (*Ailanthus altissima* L.). *BMC Ecol.* 2: 1. (DOI: 10.1186/1472-6785-2-1)
- Todd, J. 1989. Ecology and behavior of *Nezara viridula*. *Annu. Rev. Entomol.* 34: 273–292.
- Wiman, N. G., V. M. Walton, P. W. Shearer, S. I. Rondon, and J. C. Lee. 2014. Factors affecting flight capacity of brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae). *J. Pest Sci.* 88: 37–47.
- Zhang, K., N. Di, J. Ridsdill - Smith, B. W. Zhang, X. L. Tan, H. H. Cao, Y. H. Liu, and T. X. Liu. 2014. Does a multi - plant diet benefit a polyphagous herbivore? A case study with *Bemisia tabaci*. *Entomol. Exp. Appl.* 152: 148–156.
- Zhu, G., W. Bu, Y. Gao, and G. Liu. 2012. Potential geographic distribution of brown marmorated stink bug invasion (*Halyomorpha halys*). *PLoS ONE* 7: e31246.