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Short Communication

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Influence of Landscape Factors and Abiotic Conditions on Dispersal Behavior and Overwintering Site Selection by *Halyomorpha halys* (Hemiptera: Pentatomidae)

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Abstract

Since the initial detection of the invasive *Halyomorpha halys* (Stål) in the United States in the late 1990s, this insect has emerged as a severe agricultural and nuisance pest. Nuisance problems are due to adult dispersal to overwintering sites in the fall at which time they alight onto and eventually settle within human-made structures in addition to natural harborage. This study examined how three factors, elevation, light, and moisture affected overwintering site selection by *H. halys* in the mid-Atlantic. Observational counts performed along elevational transects revealed elevation was significant predictor of *H. halys* abundance during both years of the study in 2014 and 2015 with more adults observed at higher elevations. Choice tests examining effects of moisture and light on settling behavior demonstrated *H. halys* settled within overwintering shelter boxes in significantly greater numbers when shelters were dry compared with those having moist conditions, and in darkened shelters compared with those augmented with LED lights. Our findings indicate that *H. halys* use cues at both landscape and very localized levels when seeking and selecting overwintering sites.

Key words: brown marmorated stink bug, overwintering, behavior

Halyomorpha halys (Stål), the brown marmorated stink bug, is an invasive species native to Asia that was initially detected in the United States in Pennsylvania in the late 1990s (Hoebeke and Carter 2003). This species has emerged as a severe agricultural pest resulting in significant economic losses in crop quality, insecticide management costs, and overall yield in the United States and Europe (Leskey and Nielsen 2018). Research has focused primarily on managing these significant agricultural issues generated by *H. halys*, although issues associated with *H. halys* as a nuisance pest remain problematic (Ludwick et al. 2020). Problems posed by *H. halys* to homeowners and businesses can be extreme; Inkley (2012) reported that during a 6-mo period (January–June), over 26,000 *H. halys* were removed from a single dwelling. Based on a survey of homeowners, although <2% of respondents reported numbers at a similar scale to Inkley (2012), over 34% reported problems as being 'bad' or 'horrible' despite most having fewer than 100 individuals in their homes (Ludwick et al. 2020). Therefore, having even limited numbers of invading adult *H. halys* is considered problematic by homeowners.

In the mid-Atlantic, *H. halys* disperse to overwintering sites throughout September and into mid-October, with peak dispersal occurring close to the fall equinox (Bergh and Quinn 2018). Observations in Japan indicate ridge tops have higher numbers of dispersing adults in the fall (Watanabe 1994, Lee et al. 2013), and though similar anecdotal observations have been made in the United States, they have never been quantified. These findings and observations suggest landscape factors may play a role in initial overwintering location selection by dispersing *H. halys*. Moreover, what happens after reaching potential overwintering locations is not well understood. In natural landscapes, *H. halys* have been found overwintering in dry, protected areas, such as under bark of dead standing trees (Lee et al. 2014). However, in human-made dwellings, it is not clear what cues they may be using to select specific settling locations, though aggregations are typically found in dark, dry locations (Inkley 2012).

To provide further information regarding *H. halys* overwintering behavior, we conducted experiments to determine: 1) the relationship between landscape elevation and abundance of dispersing adult *H. halys* during the fall dispersal period; and 2) the influence of moisture and light on *H. halys* settling behavior into potential overwintering sites.

Methods and Materials

Elevation

To determine the relationship between elevation and dispersal of *H. halys* to potential overwintering sites, observational counts of adult *H. halys* moving to sites along elevational transects were performed in WV and MD. Each transect followed a straight line down the topographical profile and contained three designated locations representative of high, middle, and low elevation sites. Sites were sampled during peak dispersal periods (Bergh and Quinn 2018) in 2014 and 2015. Five elevational transects were sampled between September 27 and 21 October 2014 and 10 transects were sampled between September 30 and 21 October 2015 (see Table 1 for site details). Transects were selected based on previous *H. halys* presence in rural residential areas on wooded mountains. All sample sites within a transect were ≤15m^2 and included natural and/or human-made harborages for *H. halys* such as rocky outcroppings and trees as well as buildings and stone walls. Within each sample site, 15-min visual counts of *H. halys* were performed once per week between the aforementioned dates. Elevation (meters above sea level) was determined using a Garmin (Model GPS 62s) handheld GPS device. All visual counts at each sample site within a transect were completed within a 2-h window during each sample date.

For each low, middle, and high elevation sample site, we performed an analysis of variance, using elevation as the response variable and categorical elevation (low, middle, and high) as the explanatory variable to ensure that sampled elevations were significantly different from each other. Upon a significant result from

Table 1. Transect sampling sites for *H. halys* adults during autumnal dispersal period in 2014 and 2015

Year	Location (County, State)	Geocoordinates (Low, Middle, High)	Elevation (m)		
			Low	Middle	High
2014	Washington County, MD	N 39° 19' 28.6" W 77° 43' 34.7" N 39° 19' 36.7" W 77° 43' 30.5" N 39° 20' 29.6" W 77° 42' 58.6"	89	254	435
	Frederick County, MD	N 39° 35' 11.7" W 77° 26" 6.8" N 39° 34' 41.3" W 77° 26' 25.6" N 39° 34' 8.9" W 77° 27'10.7"	183	261	424
	Frederick County, MD	N 39° 28' 2.1" W 77° 30' 34.7" N 39° 27' 25.9" W 77° 29' 40.1" N 39° 28' 2.1" W 77° 30' 34.7"	175	343	466
	Washington County, MD	N 39° 19' 58.1" W 77° 40' 56.6" N 39° 19' 59.7" W 77° 40' 49.2" N 39° 19' 55.3" W 77° 40' 35.3"	120	181	235
	Frederick County, MD	N 39° 15' 6.4" W 77° 23' 37.1" N 39° 15' 38.8" W 77° 23' 38.8" N 39° 15' 44.4" W 77° 23' 37.1"	160	316	375
2015	Washington County, MD	N 39° 19' 58.1" W 77° 40' 56.6" N 39° 19' 59.7" W 77° 40' 49.2" N 39° 19' 55.3 W 77° 40' 35.3"	120	181	235
	Frederick County, MD	N 39° 15' 6.4" W 77° 23' 37.1" N 39° 15' 38.8" W 77° 23' 38.8" N 39° 15' 44.4" W 77° 23' 37.1"	160	316	375
	Jefferson County, WV	N 39° 13' 53.4" W 77° 48' 25.3" N 39° 13' 27.1" W 77° 47' 35.6" N 39° 12' 28.7" W 77° 47' 44.9"	121	301	441
	Jefferson County, WV	N 39° 13' 5.1" W 77° 48' 29.1" N 39° 12' 44.9" W 77° 48' 14.8" N 39° 12' 26.2" W 77° 47' 46.0"	134	230	428
	Jefferson County, WV	N 39° 23' 3.2" W 77° 50' 29.0" N 39° 12' 41.1" W 77° 48' 3.4" N 39° 11' 52.7" W 77° 48' 0.1"	162	218	428
	Jefferson County, WV	N 39° 11' 44.6" W 77° 50' 37.8" N 39° 12' 56.9" W 77° 48' 9.1" N 39° 11' 43.1" W 77° 48' 2.2"	131	277	439
	Washington County, MD	N 39° 43' 16.2" W 77° 32' 28.4" N 39° 43' 1.7" W 77° 30' 28.7" N 39° 41' 42.0 W 77° 31' 24.9"	206	387	548
	Washington County, MD	N 39° 24' 11.9" W 77° 43' 19.7" N 39° 24' 5.6" W 77° 42' 17.2" N 39° 42' 4.8" W 77° 42' 31.8"	135	246	285

the model, Tukey HSD was used for pairwise comparisons. For this, and all other tests, R Software was used (R Core Team 2016), and α = 0.05. To predict the effect of changing elevation on *H. halys* dispersal, total number of dispersing adult *H. halys* at a given elevation was analyzed separately for each year of sampling (2014 and 2015) using a linear regression model with data pooled across sample dates. Data were log (x + 0.1) transformed prior to analysis to conform to parametric assumptions.

Fig. 1. Experimental overwintering shelter collection deployment for adult *H. halys* collection. Shelters installed at ~1.5 m height inside a wooden crate placed atop two additional crates.

Settling Behavior

All experiments were conducted using wild populations of diapausing *H. halys*. To collect the adult *H. halys* for these studies, experimental overwintering shelters described by Bergh et al. (2017) were deployed within unheated storage sheds adjacent to sawmills at several locations in WV and MD from early September until mid-November (after *H. halys* dispersal had ceased) in 2015 and 2016. Overwintering shelters were deployed by either affixing shelters directly to interior walls or placing inside wooden apple crates with the entire structure located within a protected location (see Fig. 1). Shelter exteriors consisted of a 19 × 22 × 24 cm box constructed from 0.6-cm-thick plywood, with an open bottom and a 1 cm opening at the top to allow for *H. halys* movement inside. Each shelter was filled with 16 cardboard inserts (0.3 × 17.8 × 21.6 cm) with cardboard spacers creating a 0.3 cm gap between them. Inserts were oriented vertically and held in place by the construction of rims on the interior of the shelter. Collected shelters were stored in an unheated shed under ambient conditions (6.3 ± 0.03°C) until *H. halys* were removed for experiments.

For each experiment, 50 adults (1:1 male:female) were placed into a plastic food storage container (30 × 12 × 10 cm) with a mesh panel on the lid. Containers were placed in a climate-controlled colony room at ~25°C, 16:8 (L:D) h, ~60% RH for 24 h prior to the start of experiment to encourage *H. halys* movement. Adults were provided with water during this period. All settling experiments were conducted in a greenhouse under ambient light conditions at 12–23°C between early January and mid-March each year. Experiments were conducted inside four-person recreational camping tents (Alps Engineering 2 door, New Haven, MO) with four wooden overwintering shelters (see Fig. 2a and b). Two treatment of the same variable and two unaltered control shelters were placed at random in each corner of each arena. One plastic container with 50 adults was placed at the center of each arena. Adults were given 24 h to settle within potential treatment or control shelters. Only those that entered a shelter were counted; all others were considered nonresponders and excluded from analysis. Treatments included shelters in which moisture and light conditions were manipulated. For those shelters manipulated for moisture (n = 27), all cardboard inserts were dipped in water with excess shaken off before inserting into the wood shelter. Temperature and relative humidity sensors were randomly placed in three treatment and three control shelters during each trial. For light manipulation (n = 35), 4 LED light units

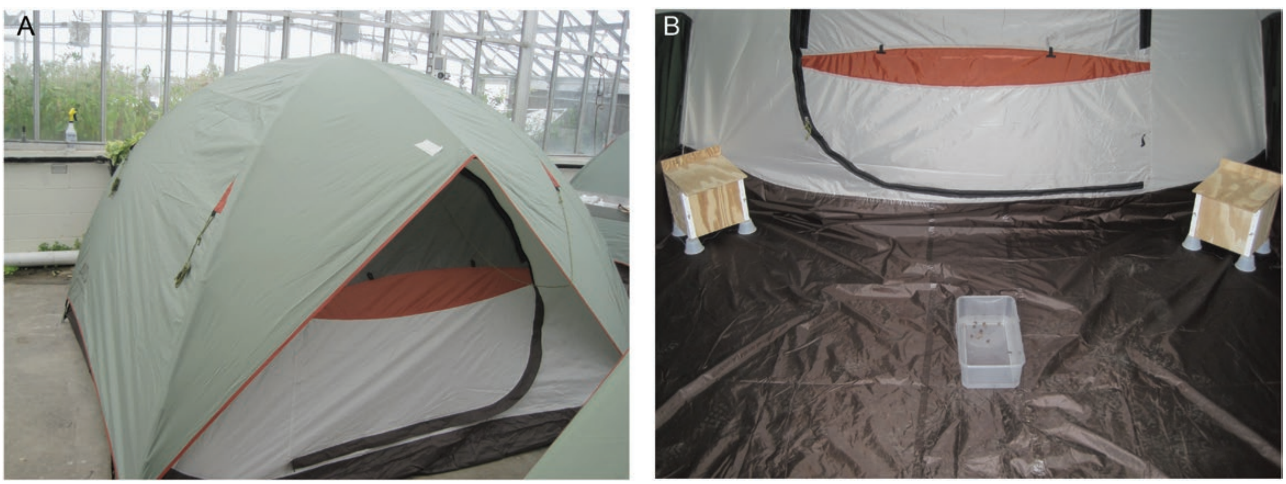

Fig. 2. Exterior (a) and interior (b) of enclosures used for *H. halys* settling behavior experiments.

(3 LEDS per unit) (Maxximia Style Touch Light, Hauppauge, NY) were affixed to the underside of the roof to illuminate the interior of the shelter. To assess the effect of each abiotic factor (light and humidity), *H. halys* response proportions were analyzed using separate chi-squared tests. For each test, H_0 assumed that there was an equal distribution of *H. halys* adults in control and treatment shelters.

Results and Discussion

In 2014, mean elevations for low, middle, and high elevation sampling sites were 145 ± 18, 271 ± 28, 387 ± 41 m above sea level, respectively, and were significantly different from each other (F = 15.9; df = 2, 12; P < 0.001; Fig. 3a). In 2015, mean elevations for low, middle, and high elevation sampling sites were 163 ± 14, 290 ± 24, 413 ± 29 m above sea level, respectively, and were significantly different from one another (F = 28.6; df = 2, 40; P < 0.001; Fig. 4a). Elevation was a significant predictor of *H. halys* abundance in 2014 (F = 5.27; df = 1, 13; P = 0.039; Fig. 3b) and 2015 (F = 11.9; df = 1, 32; P = 0.0016; Fig. 4b), explaining 28.9 and 12.9% of variation in the data, respectively. In 2014 and 2015, a 10 m increase in elevation resulted in approximately 1 and 2.3 more dispersing *H. halys* individuals in the landscape, respectively. This finding is consistent with observations made in Asia (Watanabe 1994, Lee et al. 2013) and indicates that adult *H. halys* may disperse to higher elevations to seek overwintering sites. However, this study was conducted only in the mid-Atlantic United States and it would be interesting to determine whether this pattern holds in higher elevation terrains in areas where *H. halys* has spread in recent years such as OR and WA, or parts of Italy (Leskey and Nielsen 2018). Interestingly, we also tried to measure this phenomenon using overwintering shelters (Bergh et al. 2017) deployed at different elevations, but found that most shelters yielded no adults (or minimal numbers) indicating a variety of factors play an important role for *H. halys* when choosing a specific overwintering site within a particular location following arrival. Adults disperse to human-made structures such as homes (Malek et al. 2018), alighting in greater numbers on those that are darker in color, and with exteriors comprised of natural materials such as stone and wood (Hancock et al. 2019). Factors such as elevation are likely to influence these relative numbers, but how they choose to settle within a particular location after entry into a structure has not been well-studied.

Halyomorpha halys can enter potential overwintering structures through slits ≥3 mm and holes ≥ 7mm (Chambers et al. 2019a), making physical exclusion challenging particularly for older homes (Inkley 2012). We were able to demonstrate that adult *H. halys* settle in significantly greater numbers in dry locations (χ^2 = 239; df = 1; P < 0.001) compared with those with increased moisture by a 2.7-fold difference (Fig. 5). On average 20.8 ± 1.7 SE adults settled in control shelters (dry) compared with 6.2 ± 0.6 SE adults in shelters with wetted inserts. Relative humidity in control shelters was no greater than 44% while those with wetted inserts reached as high 75%. Additionally, adult *H. halys* settled in significantly greater

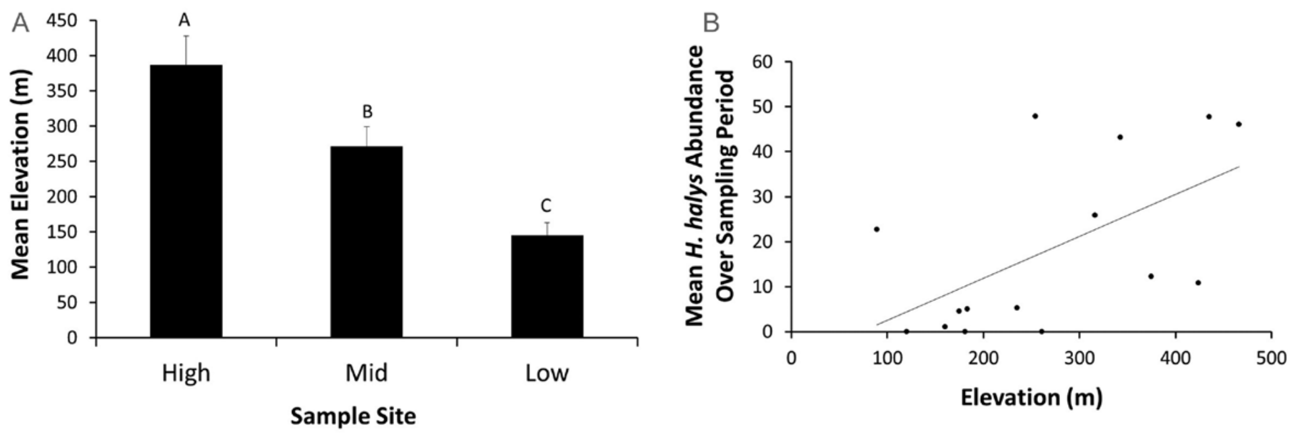

Fig. 3. Average elevation and low, middle, and high elevations sites (a) and linear regression of the relationship (y = 0.0932x – 6.7915, R^2 = 0.289) between *H. halys* abundance and site elevation (b) in 2014.

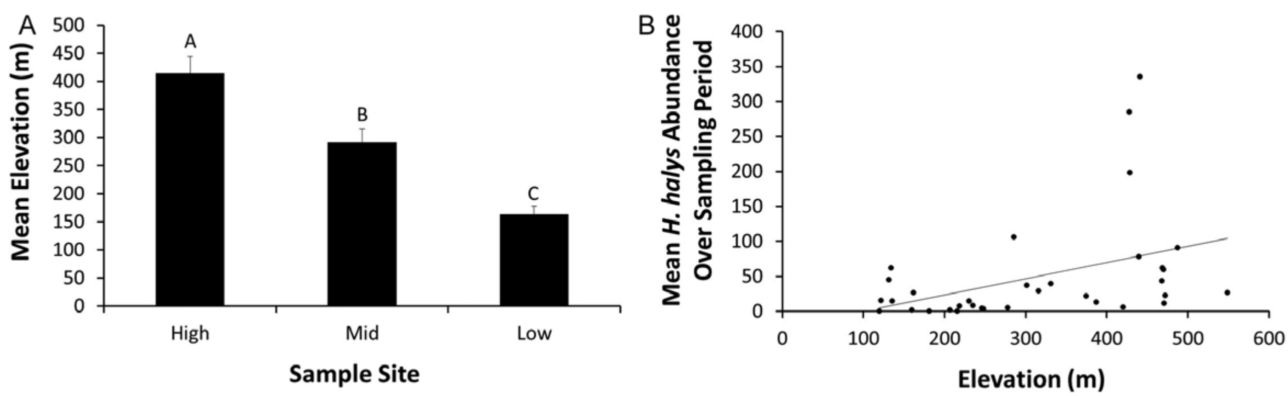

Fig. 4. Average elevation at low, middle, and high elevations sites (a) and linear regression of the relationship (y = 0.2313x – 22.885, R^2 = 0.129) between *H. halys* abundance and site elevation (b) in 2015.

numbers in control shelters (darkened) compared with those augmented with LED lights (χ^2 = 3.93; df = 1; P = 0.0476; Fig. 6). On average, 18.4 ± 1.1 SE adults settled in control shelters compared with 15.9 ± 1.0 SE adults in those augmented with lights. The propensity of overwintering *H. halys* to settle in dark and dry shelter locations agrees with field studies as diapausing individuals were recovered beneath dry bark or within dry wood of dead, standing trees (Lee et al. 2014), and in laboratory studies by Toyama et al. (2011) who reported that *H. halys* settled in darkened locations. This contrasts with the behavior of foraging individuals in the field, which are attracted to light (Leskey et al. 2015). Interestingly dead *H. halys* adults present in overwintering sites from the previous year do not repel live *H. halys* adults seeking overwintering sites, as adults will settle at suitable sites with corpses present (Chambers et al. 2019b). However, after settling, some overwintering adults do become active and leave their concealed locations to forage within human-made dwellings, presumably due to a lack of nutritive resources to sustain them during winter months (Funayama 2012). In this state, they will orient to light traps to some degree (Aigner and Kuhar 2014)

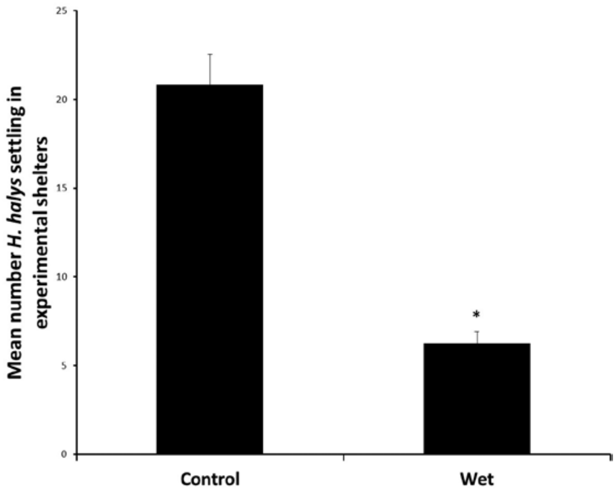

Fig. 5. Average number of settled *H. halys* in choice trials comparing dry and damp shelters. Asterisk denotes significant difference in counts (α = 0.05).

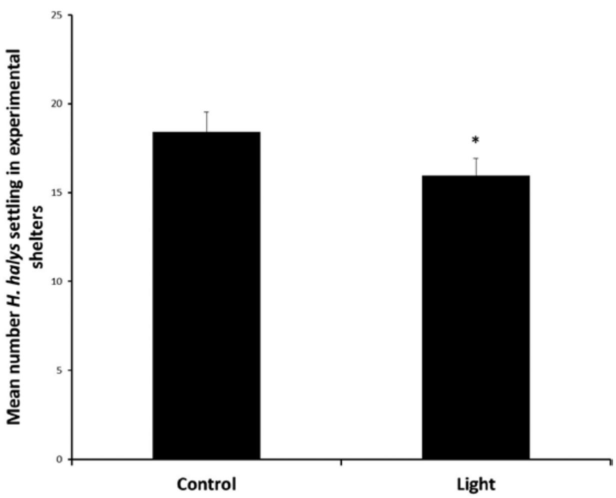

Fig. 6. Average number of settled *H. halys* in choice trials comparing darkened and lit shelters. Asterisk denotes significant difference in counts (α = 0.05).

but will not respond to pheromone-baited traps (Morrison et al. 2017). This exacerbates their problem as a nuisance pest, as they cannot be removed reliably or completely using trapping systems. Ultimately, physical exclusion prior to adult entry and settling within an overwintering structure is likely the best way to reduce further nuisance problems, and our data provide insight into *H. halys* behavior during these overwintering events.

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