Dispersal, Patch Leaving, and Distribution of *Homalodisca vitripennis* (Hemiptera: Cicadellidae)

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ABSTRACT *Homalodisca vitripennis* (Germar) and related species have caused millions of dollars in damage to southern California vineyards in recent years through the vectoring of Pierce's disease. However, the effects of surrounding vegetation on the dispersal and distribution of *H. vitripennis* are poorly understood. Therefore, the relationship between dispersal rates and patch quality was tested, as well as the basic predictions of the marginal value theorem. Additional experiments were conducted to compare the *H. vitripennis* distribution in an isolated crape myrtle (*Lagerstroemia indica*) patch and a *L. indica* patch bordering two alternative host patches. In mark-release-recapture tests, *H. vitripennis* dispersed farther from the release point in a patch of low-quality host plants (*Prunus persica*) than in patches of high-quality host plants (*L. indica*). In addition, *H. vitripennis* remained in *L. indica* patches longer than in *P. persica* patches and adjusted patch residence times in *P. persica* in correlation with known changes in plant physiology. These data suggest that *H. vitripennis* follows the basic predictions of marginal value theorem. In distribution tests, *H. vitripennis* were more abundant in the patch center than patch edges in the isolated *L. indica* patch, but in a patch bordering cottonwood (*Populus* sp.) and peach (*P. persica*), *H. vitripennis* numbers were generally higher along the edges of the patch. These data suggest that alternate hosts bordering cropping systems may be important to the spatial dynamics of *H. vitripennis*. Implications of these spatial observations on the biology of *H. vitripennis* and potential control methods are discussed.

KEY WORDS   foraging behavior, marginal value theorem, spatial analysis of distance indices

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), is a vector of *Xylella fastidiosa* Wells et al. The bacterium disrupts the flow of xylem fluid and induces different symptoms in a wide variety of plants causing diseases such as phony peach (Turner and Pollard 1959), Pierce's disease in grapes (Alderz and Hopkins 1979, Wells et al. 1987), and leaf scorch in almond, plum, elm, and oak (Purcell and Hopkins 1996). *H. vitripennis* is native to the southeastern United States, but when it invaded California from Texas in the late 1980s or early 1990s, it became the most damaging vector of Pierce's disease in southern California vineyards (Blua and Morgan 2003, Tubajika et al. 2004), and caused more than $30 million in damage from 1994 to 2000 (CDFA 2005).

Because of the importance of *H. vitripennis* as a vector of *X. fastidiosa*, understanding its dispersal and trivial movement will help predict the spread of *X. fastidiosa* in cropping systems and aid in the development of optimal control measures. Two of the main components of insect movement are the trivial movement or dispersal within a patch of host plants and the relationship between the dispersal rate and the effect of patch quality (Hassell et al. 1991, Wiens et al. 1995). Previous studies have shown the dispersal ability of *H. vitripennis* nymphs (Tipping et al. 2004) and adults (Blackmer et al. 2004) between host patches. In addition, Blackmer et al. (2006) compared *H. vitripennis* dispersal rate in host patches to dispersal outside of host patches. However, *H. vitripennis* dispersal has never been assessed in patches of hosts of varying nutritional quality. Evaluating the relationship between dispersal rate and host patch quality allows the prediction of dispersal rate by plant patch type and aids in the general understanding of *H. vitripennis* behavior.

Evaluating the temporal rate of dispersal from host patches allows the testing of basic behavioral theory, such as the marginal value theorem. According to the marginal value theorem, foragers should spend more time in patches of higher nutritional quality and less time in patches of lower quality (Charnov 1976). The principles of marginal value theorem have been tested in herbivorous insects (see Stephens and Krebs 1986 for review), but never in xylophagous insects such as *H. vitripennis*. *H. vitripennis* host selection and feeding rates are greatly affected by host nutrition (see Redak

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et al. 2004 for review), and variation in nutrition may affect patch leaving characteristics as well (Stephens and Krebs 1986). However, part of the marginal value theorem relates to the depletion of resources caused by feeding, and this depletion of patch quality with patch residence time may not occur in xylophagous systems, because xylem fluid feeders cause little or no host deterioration through feeding alone (Andersen et al. 2003). Therefore, the patch leaving behavior may be different in xylophagous foragers than for most herbivorous insects.

Understanding the spatial distribution of *H. vitripennis* in host patches is also important in predicting disease occurrence. The distribution of Pierce's disease in southern California vineyards is highly correlated to that of vector species (Tubajika et al. 2004), and some Cicadellidae species aggregate in host plant patches (Orenstein et al. 2003). If *H. vitripennis* also shows aggregation behavior along plant patch edges, it may be reflected in the spatial distribution of the vectored disease. The presence of alternative hosts has been shown to impact the spatial distribution of Pierce's disease in vineyards (Perring et al. 2001). However, incidence of Pierce's disease is sometimes unrelated to alternative *H. vitripennis* and *X. fastidiosa* hosts (Tubajika et al. 2004). Understanding the distribution of *H. vitripennis* as it relates to bordering vegetation may help explain these discrepancies. Therefore, one of our objectives was to evaluate the effects of bordering host patches on the distribution of *H. vitripennis.* We hypothesized that the presence of alternative hosts near the edge of a host patch would lead to increased movement along the edges of the host patch.

Materials and Methods

The relationship between host patch type and dispersal rate was evaluated by comparing dispersal in a high-quality host (crape myrtle, *Lagerstroemia indica* L.) (Brodbeck et al. 1990, Andersen et al. 1992) and a lower quality host [peach, *Prunus persica* (Batsch)] (Mizell and French 1987, Andersen et al. 1989, 1995, Brodbeck et al. 1990). The relationship between host patch-leaving behavior and host patch quality was also tested by comparing the time spent by *H. vitripennis* in patches of *L. indica* and *P. persica.* In this study, we evaluated dispersal rate as the rate of diffusion within a host patch over time and patch-leaving as the rate at which the insects left the entire host patch. In addition, the nutritional changes in *P. persica* within a season have been established in previous works (Brodbeck et al. 1990, Gould et al. 1991), so we evaluated the changes in dispersal and host patch residence time in *P. persica* on various dates within the season to detect changes in host patch residence time and dispersal rate. To test the effects of adjacent host patches on *H. vitripennis* spatial dynamics, spatial clustering of adults was evaluated in host plants and clustering was compared in an isolated plant patch and a plant patch bordering alternative host plants.

Mark-Recapture Study. To evaluate *H. vitripennis* dispersal in patches of host plants, all *H. vitripennis* adults were collected from *L. indica* trees at local nurseries. No *H. vitripennis* were collected from *P. persica* plots, because of the low numbers found in *P. persica* throughout the year. *H. vitripennis* were marked externally with aerosol hair dye (High Beams; Continental Fragrances, Birmingham, MI) and released in the center of plots of *L. indica* or *P. persica.* The hair dye was used because of availability and low cost at the time of the first release date. The *L. indica* plot used in dispersal tests in 1994 was located at Simpson's nursery in Monticello, FL, and the plot used in 2007 was at the North Florida Research and Education Center in Quincy, FL. The *P. persica* plot used for releases in 1994 and 1995 was at the North Florida Research and Education Center in Monticello, FL. For each release, a different color was used to distinguish between individuals from different releases. The release sites were surrounded by fallow fields and undeveloped wooded areas.

To determine the effect of the marking method on *H. vitripennis* mortality at each release, three replicates of each 20 marked and unmarked *H. vitripennis* were placed in sleeve cages on the host plants within the release plots. Over the course of the study, the number of live marked and unmarked adults in sleeve cages was determined to test for lethal effects of the marking technique. There are no known sublethal effects on marked insects (Hagler and Jackson 2001), and none were observed. Live, marked *H. vitripennis* were counted once per day for the duration of each study. Brown sticky traps were used to capture *H. vitripennis* in 1994–1995 releases (in *L. indica* and *P. persica*), and yellow sticky traps were used in 2007 (in *L. indica*) to update the study for current trap use (Blackmer et al. 2004, 2006). Traps consisted of 10 by 50-cm pieces of masonite boards covered in Tanglefoot (Tanglefoot, Grand Rapids, MI). Traps were placed at heights of 1 and 2 m in 1994–1995 in *L. indica* and *P. persica* on a wooden stake in the plant patch at distances from the center of the release site of 5, 10, 20, 30, 40, 50, and 60 m at each direction: north, northeast, southeast, south, southwest, and northwest (Fig. 1A).

In the 2007 release in *L. indica*, traps were only set at the 2 m height because of low trap catch at the 1 m height on previous release dates. However, the trap spatial arrangement was the same as the previous releases. Before each release, *H. vitripennis* adults were held overnight in sleeve cages on potted *P. persica* or *L. indica* plants, respectively, to ensure host familiarity before release. Adults were released from the sleeve cages at 0800 hours by removing the cage from the plant and any adults that fell to the ground and did not fly within the first 4 h after release were collected and excluded from the analyses. Traps were checked at increasing time intervals as the number decreased (Table 1). Data were recorded until no marked *H. vitripennis* were collected beyond 5 d. A single mark-recapture experiment was conducted in *L. indica* in each year, 1994 and 2007 (Table 1). Three releases in
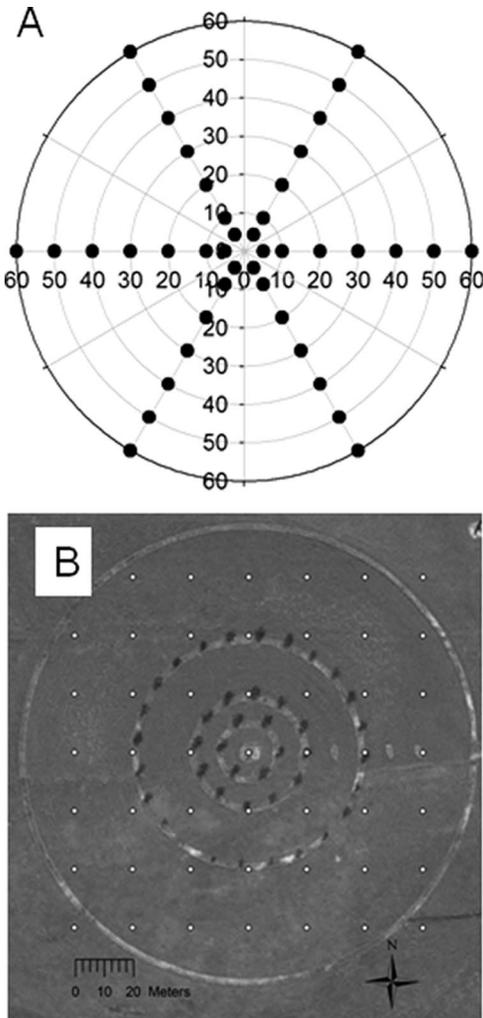
Fig. 1. Trap arrangements for the mark-recapture experiment (A) and the distribution experiment (B). (A) Each black circle indicates the presence of one 1-m-high trap (in 1994 and 1995 only) and one 2-m-high trap (all years) on a single wooden stake. Mark-recapture was conducted two times in *L. indica* and five times in *P. persica*. Distances are in meters. The aerial photograph in B depicts the arrangement of traps (light colored circles) and trees (dark objects in concentric circles) for the distribution analysis in the isolated *L. indica* patch. The second *L. indica* patch was identical except that it was bordered to the northeast by a patch of *Populus* sp. trees and to the east by a patch of *P. persica* trees. Each *L. indica* patch consisted of a total of 42 trees 10 m apart, organized in three concentric circles with radii of 10 (6 trees), 20 (12 trees), and 40 m (24 trees). Yellow, cylindrical sticky traps were placed in a 7 by 7 grid overlapping each *L. indica* plot, with each trap placed 20 m apart.

P. persica plots were conducted in 1994 and two were conducted in *P. persica* in 1995 (Table 1). Releases in *L. indica* generally occurred later in the season than *P. persica* (Table 1), because the *P. persica* is used as a host by *H. vitripennis* earlier than *L. indica* (Mizell and French 1987, Brodbeck et al. 1990), and we wanted to conduct releases when each plant species was used as

a host. The male to female ratio in every release was not adjusted from the ratio collected to preserve the naturally occurring sex ratio at the time of release. Previously, Gould et al. (1991) and Brodbeck et al. (1990) found that peak population occurrence of *H. vitripennis* on *P. persica* and highest nutritional value of *P. persica* is in the middle of June at the experimental site and the releases in *P. persica* were made to bracket these dates. Trap catch data were used to measure dispersal distance, patch leaving behavior, and directional movement from the release point. The proportion of marked *H. vitripennis* collected at each trap height (1 and 2 m) was arcsine transformed, and a *t*-test was conducted to test for a difference in trap catch between trap heights.

Dispersal Data Analysis. We used a common exponential model (Turchin and Thoeny 1993) to estimate the number of *H. vitripennis* collected at each distance from the central release point after 5 d. For releases in *P. persica* conducted on 2 June 1994 and 12 June 1994, no more *H. vitripennis* were collected after 3 d, so the total number of *H. vitripennis* collected at each distance was used. The number caught (N) at distance r from the release point was estimated using the equation:

$$N(r) = a \exp[-br]$$

where a is a scaling parameter that estimates the number of *H. vitripennis* collected at $r = 0$ (the y intercept), and b is a spatial scale parameter that influences the rate of decrease of *H. vitripennis* collected at increasing radius r. We fit the model to our data by using maximum likelihood estimation in R version 2.6 (R Core Development Team 2005), assuming a Poisson error distribution. The underlying χ^2 distribution of maximum likelihood estimates for b was used to obtain 95% confidence intervals, and parameter b was used to estimate the median dispersal distance $r_{0.5}$ by using the negative exponential half-life equation:

$$r_{0.5} = \log(2)/b$$

The 95% CL for b were inserted into the equation for $r_{0.5}$ to obtain the 95% confidence intervals for the median dispersal distance. A one-way analysis of variance (ANOVA) was conducted in SYSTAT Version 11.0 (Systat Software 2004) to compare the median dispersal distances for the two plant species. Another ANOVA was conducted in SYSTAT to test for differences in median dispersal distance by year for the releases conducted in *P. persica* in 1994 and 1995. The median dispersal distance was used to compare dispersal on different release dates in each plant species, and differences were considered significant if the confidence intervals did not overlap. Differential dispersal between males and females was tested by fitting male and female data separately for each repetition and conducting a paired *t*-test on the median dispersal distances.

Patch-Leaving Data Analysis. Host patch leaving behavior was evaluated by measuring the rate of decrease of the number of *H. vitripennis* collected by sticky traps per hour with increasing time. A modifi-

Table 1. Release dates and check times and proportion *H. vitripennis* recaptured during mark-recapture experiments (in chronological order) in *P. persica* on various dates in 1994 and 1995 and in *L. indica* on various dates in 1994 and 2007

Plant	Year	Date	Female		Male		Trap check times (h)
			No. released	Percent recaptured	No. released	Percent recaptured	
P. persica	1994	2 June	752	6.5	671	13	1, 3, 5, 7, 12, 24, 29, 31.5, 52, 61, 85, 128
P. persica	1994	12 June	660	5.9	416	5.9	1, 3, 5, 8, 11, 27, 34, 52, 59
P. persica	1994	17 June	426	6.6	463	8	1, 9, 13, 25.5, 29, 32, 37, 53, 56.5, 60.5, 79, 85, 102.5, 121, 127, 133, 153, 245
L. indica	1994	29 June	760	4.2	330	34.8	1, 3, 8, 24, 32, 48, 56, 72, 97, 120, 144, 168, 192, 216, 240, 264, 288, 312, 336, 360, 384, 408, 504
P. persica	1995	12 July	524	9.2	230	20.4	2, 4, 6, 8, 10, 13, 26, 28, 30, 32, 34, 37, 50, 52, 54, 56, 58, 61, 85, 109, 133, 157, 181, 205, 253, 277, 301, 325, 349, 373, 397
L. indica	2007	9 July	724	7.9	247	8.9	2, 17, 19, 21, 42, 45, 64, 69, 88.5, 93, 112, 117, 136, 141, 150, 155, 198, 203, 227, 251, 276, 299, 323, 347, 371, 419, 443, 467

Releases in *P. persica* were conducted to bracket the time of highest nutritional quality (mid-June) and later in the season for *L. indica* to include the time of highest nutritional quality for *L. indica*. Trap check intervals increased as numbers of *H. vitripennis* captured decreased and ended when no more *H. vitripennis* were collected.

cation of equation 1 was used to measure the number of *H. vitripennis* adults caught per hour (N) at time t by substituting t for r. In this model, parameter a is a scaling parameter, and b is a temporal parameter used to measure the change in trap catch over time. Maximum likelihood estimation in R version 2.6 (R Core Development Team 2005) was used to determine the best fit parameters, assuming a Poisson distribution, and the underlying χ^2 distribution of maximum likelihood estimates was used to obtain 95% confidence intervals. The best fit value for b and the 95% CL were inserted into the equation for $r_{0.5}$ to obtain the estimated time and 95% confidence intervals for the population half-life. We use the term population half-life here to estimate the point in time when 50% of the individuals could no longer be found in the patch. The equation is often used to describe the point where one half of a "population" of microorganisms or compounds has decayed (Wilson and Buffa 2000). Therefore, in this case, we use it to model the exponential "decay" or decline of marked individuals in a plant patch and estimate the point in time when 50% of the individuals could no longer be found in the patch. We used the population half-life value to compare the temporal decrease in *H. vitripennis* trap capture for different treatments. The population half-life values of releases in different plant species were compared using a one-way ANOVA in SYSTAT version 11.0 (Systat Software 2004). Another ANOVA was conducted in SYSTAT to test for differences in population half-lives by year for the releases conducted in *P. persica* (in 1994 and 1995). The population half-life values and confidence intervals were used to compare the amount of time *H. vitripennis* spent in the plant patch for different dates in each plant species. Differential patch leaving between males and females was tested by fitting male and female data separately for each repetition and conducting a paired *t*-test on the estimated population half-lives.

Distribution Analysis. *Homalodisca vitripennis* distribution was evaluated in two *L. indica* plots at the

North Florida Research and Education Center in Quincy, FL, in 2003 and 2007 to test how clustering is affected by host patch isolation. Each *L. indica* patch consisted of a total of 42 trees 10 m apart, organized in three concentric circles with radii of 10 (6 trees), 20 (12 trees), and 40 m (24 trees). One *L. indica* plot was surrounded on all sides by fallow fields for at least 100 m, and the other was bordered at ≈50 m on two adjacent sides by cottonwood (*Populus* sp.) and *P. persica*. Yellow, cylindrical sticky traps were placed in a 7 by 7 grid overlapping each *L. indica* plot, with each trap placed 20 m apart (Fig. 1B). Sticky traps consisted of 30-cm-tall mailing tubes ≈8 cm in diameter painted safety yellow, with Tanglefoot (Tanglefoot, Grand Rapids, MI) applied generously. This trap design provides an increase in trap catch in comparison to the two-dimensional sticky traps commonly used because of the attractiveness in 360° (R.F.M., unpublished data). Traps were checked and cleaned daily, and the number of *H. vitripennis* was recorded from 16 to 27 June 2003. Any insects were removed from the traps and Tanglefoot was added. In 2007, the same study was repeated from 20 June through 5 July. However, before the 2007 field season, the two rows of *P. persica* adjacent to the *L. indica* plot were removed for reasons unrelated to this study. Cluster indices, v_i and v_j, as well as the mean (v) of the v_i and absolute value of v_j, were calculated in SADIE (spatial analysis of distance indices, version 1.2; Rothamsted Experimental Station, Harpenden Herts, United Kingdom) for each date and plot. Random permutations were conducted to test for the probability, p, that a randomly distributed population would be more clustered (had a higher value of v) than the data for each date and plot (Perry et al. 1999). To test for a difference in trap catch inside and outside the *L. indica* patch, data were log-transformed, and a two-way repeated-measures ANOVA in SYSTAT version 11.0 (Systat Software 2004) was used to compare mean trap catch on traps within the circles to traps outside the circles over time (in-out effect), as well as test for a difference in the
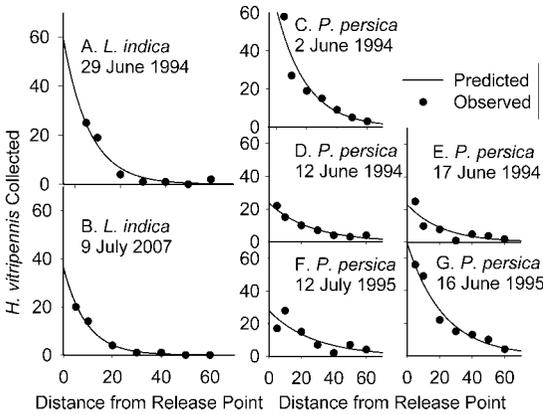
Fig. 2. Cumulative number of *H. vitripennis* recaptured at each distance from the release point and the best fit model 5 d after being released into *L. indica* (A and B) or *P. persica* (C–G) on various release dates in 1994, 1995, and 2007.
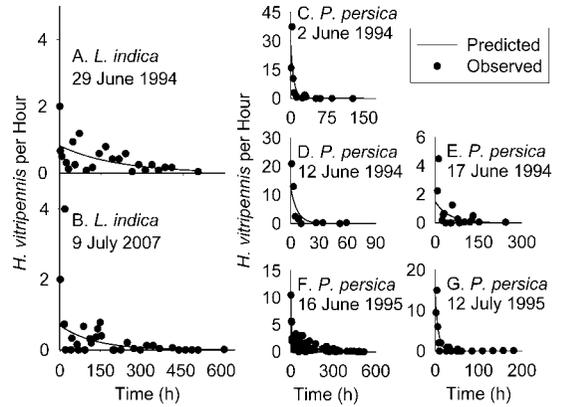

Fig. 3. Number of *H. vitripennis* recaptured per hour over time and the best fit model in *L. indica* (A and B) and *P. persica* (C–G) plots on various release dates in 1994, 1995, and 2007. The scales for *x* and *y* axes in *P. persica* plots vary by release date to better show how the model fits the data for each release date.

patterns for the two plots (plot × in-out interaction). Two error terms are used in the analysis. The error term used to evaluate the temporal effect and temporal interactions included temporal variation in the calculation, whereas temporal variation was not included in the calculation of the error term for all nontemporal effects and interactions (Ott and Longnecker 2001). This analysis was conducted separately for each year. Significance in the plot × in-out interaction indicates that the ratio of trap catch inside the *L. indica* plot to outside the plot was different for the isolated plot and the plot bordering *Populus* sp. and *P. persica* patches. In the adjacent plot, two traps were partially in a cottonwood (*Populus* sp.) patch, so they were removed from the analysis both years.

Results

Mark-Recapture Study. Less than 1% mortality on any date was observed in the sleeve cages to determine the effects of the High Beam marker dye on *H. vitripennis*. Because of the limited mortality and because the dye lasted at least 2 wk on the marked *H. vitripennis*, it was concluded that the number of released insects was a suitable estimate for the analyses.

Dispersal Distance. The exponential decay models provided a good fit to the dispersal distance data in both *L. indica* (Fig. 2A, B) and *P. persica* (Fig. 2C–G). The mean estimated median dispersal distances for males and females were 13.49 ± 2.01 and 20.10 ± 3.19 (SE) m, respectively, and the means were almost significantly different ($t = 2.42$; df = 6; $P = 0.0516$). The number of the median dispersal distance for *H. vitripennis* released on *L. indica* was significantly less than the *H. vitripennis* released on *P. persica* ($F = 25.65$; df = 1,5; $P = 0.004$). However, there were no significant differences in the median dispersal distances of *H. vitripennis* on different release dates within *P. persica* or *L. indica* (Table 2). In addition, there was no effect of year on median dispersal distance in *P. persica* ($F = 0.643$; df = 1,3; $P = 0.481$). Therefore, there were no temporal trends by release date in the median dispersal distances in *P. persica* or *L. indica*.

Patch-Leaving. In addition to providing a good fit to the dispersal distance data, the exponential decay models provided a good fit to the data for population half-lives in *L. indica* (Fig. 3A, B) and *P. persica* (Fig. 3C–G). The mean population half-lives for males and

Table 2.   Maximum likelihood estimates for the model parameters and confidence limits predicting the median dispersal distance for *H. vitripennis* in *L. indica* and *P. persica* plots in 1994, 1995, and 2007

| Plant | Year | Date | Parameter | | Median dispersal | Confidence limits | | Significance[a] |
			a	b		2.5%	97.5%	
L. indica	1994	29 June	38.05	0.087	7.98	6.48	9.90	A
L. indica	2007	9 July	36.24	0.11	6.46	5.13	8.15	A
P. persica	1994	2 June	61.90	0.051	13.52	11.61	15.86	B
P. persica	1994	12 June	23.68	0.039	18.00	14.09	23.82	B
P. persica	1994	17 June	23.09	0.046	14.94	11.71	19.58	B
P. persica	1995	16 June	69.31	0.045	15.38	13.33	17.91	B
P. persica	1995	12 July	27.93	0.036	19.13	15.20	24.76	B

Parameter *a* is a scaling parameter and *b* is a spatial scale parameter that influences the rate of decrease of *H. vitripennis* collected at increasing radius *r*.

[a] Means with the same letter have overlapping confidence intervals and were not considered significantly different at $\alpha = 0.05$.

Table 3. Maximum likelihood estimates and confidence intervals estimating the amount of time (h) when one half of the *H. vitripennis* had been collected (the population half-life) as an estimate of the length of time *H. vitripennis* individuals spent in the patch of *L. indica* and *P. persica*

Plant	Year	Date	Parameter		Half-life (h)	Confidence intervals		Significance[a]
			a	*b*		2.5%	97.5%	
L. indica	1994	29 June	0.82	0.0048	145.88	124.89	172.00	A
L. indica	2007	9 July	0.70	0.0078	89.38	78.23	111.08	B
P. persica	1994	2 June	28.46	0.16	4.40	3.92	4.92	D
P. persica	1994	12 June	12.54	0.14	4.90	4.13	5.78	D
P. persica	1994	17 June	1.50	0.021	33.61	28.06	40.53	C
P. persica	1995	16 June	2.28	0.0085	81.39	74.13	91.81	B
P. persica	1995	12 July	13.92	0.14	4.99	4.31	5.78	D

Parameter *a* is a scaling parameter, and *b* is a temporal parameter used to measure the change in trap catch over time.
[a] Means with the same letter have overlapping confidence intervals and were not considered significantly different at $\alpha = 0.05$.

females was 67.9 ± 24.3 and 51.7 ± 18.9 (SE) h, respectively, and the means for males and females were not significantly different ($t = 1.68$; df = 6; $P = 0.14$). The population half-lives of *H. vitripennis* released on *L. indica* were significantly longer than those released on *P. persica* ($F = 9.90$; df = 1,5; $P = 0.025$), and there were significant differences in the population half-lives among release dates in *P. persica* (Table 3). *H. vitripennis* patch residence times were longest on 16 June 1995 and 17 June 1994. There was no effect of year on population half-life in *P. persica* releases ($F = 0.864$; df = 1,3; $P = 0.421$).

Distribution Test. *Homalodisca vitripennis* were significantly clustered on six of nine sample dates in the *L. indica* plot adjacent to *P. persica* and *Populus* sp. and on one of nine sample dates in the isolated plot between 16 and 27 June 2003 (Table 4). However, *H. vitripennis* was rarely clustered in either plot in 2007 (Table 4).

In the 2003 isolated plot, mean *H. vitripennis* trap capture was highest inside the circle, whereas in the adjacent plot, mean *H. vitripennis* trap capture was highest outside the *L. indica* circles. Similarly, in 2007, from 20 June to 5 July, *H. vitripennis* trap capture was highest within the crape myrtle circles of the isolated plot but was highest outside the circles in the adjacent plot (Fig. 4). In both 2003 and 2007, there was a significant plot × in-out interaction. These interaction terms suggest that the difference between trap catch inside and outside the *L. indica* circles varied by plot for both years (Table 5). Therefore, the presence of bordering patches was correlated with a significantly different ratio of trap catch inside and outside the *L. indica* plot.

Discussion

Dispersal Study. *Lagerstroemia indica* is a substantially superior host compared with *P. persica* (Mizell

Table 4. SADIE cluster indices (*v*) and *P* values (proportion of random permutations that were more clustered than the actual data) for *H. vitripennis* caught by sticky traps in an isolated *L. indica* plot and a plot with a border adjacent to a patch of *P. persica* and a border adjacent to a patch of cottonwood

Year	Julian date	Adjacent plot		Isolated plot	
		v	*P*	*v*	*P*
2003	167	1.21	0.097	1.05	0.33
2003	168	1.68	<0.001[a]	1.45	0.011[b]
2003	169	1.61	0.0023[c]	0.87	0.77
2003	170	1.57	0.0023[c]	1.05	0.32
2003	171	1.45	0.0096[b]	0.94	0.62
2003	175	1.26	0.062	0.95	0.55
2003	176	1.45	0.0085[c]	0.93	0.63
2003	177	1.29	0.047[a]	1.02	0.16
2003	178	1.05	0.31	0.91	0.67
2007	171	1.31	0.047	1.05	0.30
2007	173	1.41	0.015[b]	1.12	0.20
2007	176	1.02	0.38	1.087	0.24
2007	177	0.96	0.52	1.10	0.22
2007	179	1.00	0.43	1.08	0.25
2007	181	0.85	0.87	1.08	0.26
2007	183	1.09	0.22	0.91	0.69

Research was conducted in 2003 and 2007.
[a] $P < 0.001$.
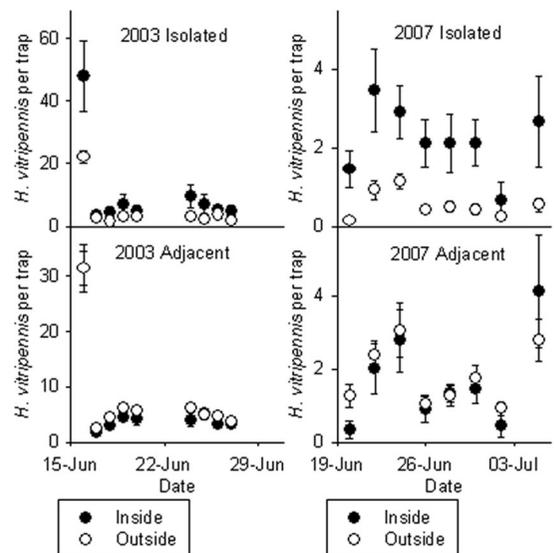[b] $P < 0.05$.
[c] $P < 0.01$.

Fig. 4. Mean number of *H. vitripennis* captured by 49 traps arranged in a 7 by 7 square grid overlaying *L. indica*, arranged in concentric rings in an isolated plot and an identical plot adjacent to a *P. persica* orchard and a *Populus* sp. stand in 2003 and 2007. Traps were divided into traps inside the *L. indica* patch and outside the patch.

Table 5.   Results from two-way repeated-measures analyses conducted on *H. vitripennis* abundance collected over ≈2 wk from two square trapping grids during 2003 and 2007

Source	df	F	P
2003			
Plot	1,92	1.39	0.242
In-out	1,92	2.50	0.117
Time	8,736	95.64	<0.001
Plot × in-out	1,92	4.25	0.042
Time × in-out	8,736	1.38	0.200
Time × plot	8,736	2.48	0.012
Time × plot × in-out	8,736	0.74	0.658
2007			
Plot	1,92	1.87	0.175
In-out	1,92	7.91	0.006
Time	7,644	17.75	<0.001
Plot × in-out	1,92	7.87	0.006
Time × in-out	7,644	2.86	0.006
Time × plot	7,644	2.36	0.022
Time × plot × in-out	7,644	1.28	0.256

The plot effect compares counts in an isolated *L. indica* patch and a patch adjacent to alternative host patches. The in-out effect compares trap capture within the *L. indica* circles to trap capture outside the circles. The plot × in-out interaction tests for differences in the distribution (ratio of inside the plot versus outside the plot) of trap capture between the isolated and adjacent plots.

and French 1987, Andersen et al. 1989, 1995, Brodbeck et al. 1990), and the difference in dispersal in the two hosts suggests that host quality should be considered when determining the spread of *H. vitripennis* in host patches. The effect of patch quality on insect dispersal distance supports the findings of past studies (Turchin and Thoeny 1993, Cronin and Haynes 2004) but has never specifically been evaluated in *H. vitripennis.*

Patch residence times in *P. persica* were 1.8–33.2 times shorter than in *L. indica*, and there was a significant effect of host plant species on *H. vitripennis* patch leaving behavior. These differences and the status of *L. indica* as a preferred host (Andersen et al. 1992) suggest that *H. vitripennis* followed the general predictions of the marginal value theorem and spent more time in host patches that were nutritionally superior (Charnov 1976). Brodbeck et al. (1990) measured the nutritional quality of *P. persica* in 1987 and found that *P. persica* had much higher amino acid concentrations on 5 June than 20 July. Therefore, nutritional quality is generally higher on dates just before when patch residence times were highest in this study (16 and 17 June) than after patch residence times had decreased (12 July). Furthermore, *P. persica* quality (as measured by *H. vitripennis* relative abundance) presented by Gould et al. (1991) mirrored the temporal pattern of median patch residence times in the current study. Therefore, in this study, patch residence times varied with the known changes in host nutritional quality and host acceptability of *P. persica* trees. In laboratory experiments, *H. vitripennis* adjust feeding time based on nutritional quality, spending less time feeding on lower quality hosts (Andersen et al. 1989, 1992, Brodbeck et al. 1993), and these data suggest that adults also rapidly adjust the amount of time spent in a host patch in reaction to the changes

in plant quality that occur during changes in host phenology.

Although there were significant differences in patch-leaving behavior, there were no significant differences in median dispersal distance between release dates in *P. persica*, based on the overlap in confidence intervals (Table 3). The lack of significance was likely caused by the high variation in patch residence times between releases, making it difficult to select a standard time frame for comparing dispersal distances. Because there were no significant differences between dispersal distance or patch leaving behavior in males and females, grouping them together for analysis seemed most appropriate.

The trap height with the highest trap catch for *H. vitripennis* was higher in this study than has been reported in heterogeneous patches of alfalfa (Blackmer et al. 2004) but was similar to that found in vineyard edges (Blua and Morgan 2003) and in citrus plots (Blackmer et al. 2006). These differences may be because of the variation in vegetation height, because alfalfa plants are lower than fruit trees, and in vineyards, adults must fly higher to clear vine rows. *H. vitripennis* adults generally fly higher than grass-feeding sharpshooter species (Cicadellidae: Proconiini and Cicadellini; Turner and Pollard 1959), and this variation in flight characteristics with plant height may occur within *H. vitripennis* as well.

Distribution Study. In the isolated *L. indica* plot, the majority of *H. vitripennis* were collected in the center of the plot in both years, and there was little clustering in either year. These results suggest that immigration and emigration from the host patch were not major factors during the course of the study. There were higher numbers collected within the isolated plot in both years, suggesting that most movement was within the plot from plant to plant. However, in 2003, trap catch in the *L. indica* plot adjacent to the *Populus* sp. and *P. persica* was often clustered and occurred along the edges more often than the isolated plot. These results indicate that movement between host patches may have been common in the 2003 adjacent patch. In 2007, after many of the adjacent *P. persica* were removed (for reasons unrelated to this study), there was generally little clustering, possibly showing the importance of the *P. persica* trees to the clustering patterns. However, there was higher capture by traps outside the circles in the adjacent plot than in the isolated plots, suggesting that the *P. persica* and *Populus* sp. trees may have still had some effect. The difference in distribution patterns between plots as shown by the plot × in-out interaction in both 2003 and 2007 shows the importance of surrounding vegetation on *H. vitripennis* spatial dynamics within a host patch.

The data from the patch leaving tests suggested that *H. vitripennis* spent less time in *P. persica* than *L. indica* and less time in *P. persica* when plant quality was lowest (pre- and postpeak), as expected from the known changes in nutritional quality (Brodbeck et al. 1990). However, the distribution study indicated that the presence of *P. persica* trees was correlated with an

increase in trap catch outside the *L. indica* patch, indicating the presence of frequent movement between *P. persica* and *L. indica*, especially early in the season. This movement indicates that *H. vitripennis* may be drawn into *P. persica* patches from a distance, but leave the patch quickly once they arrive based on plant feedback such as xylem fluid quality. This may also indicate that *H. vitripennis* host selection behavior occurs on the plant in response to plant chemistry rather than from plant visual or physical cues available before landing. Therefore, *H. vitripennis* follow the general predictions of the marginal value theorem once they are in a host patch, but may initially be attracted into patches that are of low quality. This movement between host patches may be important in spreading *X. fastidiosa* from crop margins into cropping systems. Special attention should therefore be paid to plants in field margins when managing *X. fastidiosa*–related diseases, based on their propensity to host *X. fastidiosa*. These findings also suggest that development and use of trap crops in proximity to *X. fastidiosa*–infected crops may be a viable management strategy for *H. vitripennis* and should be studied along with the associated underlying behavioral mechanisms.

Acknowledgments

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