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Spotted Wing Drosophila Prefer Low Hanging Fruit: Insights into Foraging Behavior and Management Strategies

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Abstract Spotted wing drosophila, *Drosophila suzukii*, is an invasive insect that attacks ripe, small fruit such as raspberries, blackberries and blueberries. Little is known about its foraging ecology and current trapping methods and monitoring systems are ineffective at commercial scales. In semi-field studies, we evaluated adult alightment and ovipositional preference within and among raspberry plants using sentinel Tangletrap-coated and clean raspberry fruit, respectively, positioned within the exterior and interior plant canopy at four different heights (60, 85, 110 and 135 cm from the base) and conducted in field cages using sexually mature adults. Alightment of adults on Tangle-trap-coated fruit indicated a preference for fruit positioned at lower heights and/or interior locations based on significantly greater numbers being captured on sentinel sticky-coated berries at the two lowest heights. Oviposition in clean raspberry fruit also yielded a similar pattern. In mark-release-recapture studies conducted in the field, spotted wing drosophila prefer sentinel sticky fruit positioned on exterior rows as they alighted on these berries in significantly greater numbers than fruit at in the central portion of the plot. Likewise, in field trials with wild fly populations, infestations were significantly greater in edge rows compared with interior rows. Collectively, our results suggest that monitoring and behaviorally based management strategies may be more effective if they target adults foraging in the lower canopy of small fruit plants located on the crop perimeter.

Keywords *Drosophila suzukii* · invasive species · mark-release-recapture

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Introduction

Top-down and bottom-up forces influence insect herbivore populations (Hunter and Price 1992). In invaded regions, herbivore species often escape these pressures (Lawton et al. 1986; Crawley 1987; Blossey and Notzold 1995; Wolfe 2002) and thus, experience increased population densities (Noble 1989; Blossey 1993), resulting in greater economic and ecological damage (Pimentel et al. 2000, 2005; Walsh et al. 2016). Invasive species experiencing novel resources and enemy-free space may alter their foraging behaviors (Holway et al. 1998; Rossong et al. 2012). Therefore, management strategies developed in native ranges may not be as effective in invaded regions because of greater population densities and behavioral modifications.

Spotted wing drosophila, *Drosophila suzukii* (Diptera: Drosophilidae), is an invasive insect originating from Asia that has established populations throughout North America, South America and Europe (Grassi et al. 2009; Goodhue et al. 2011; Calabria et al. 2012; Cini et al. 2012; Price et al. 2012; Deprá et al. 2014; Asplen et al. 2015). Females lay eggs in soft skinned fruit such as caneberries, blueberries, strawberries, cherries, peaches, apricots and plums (Lee et al. 2011, 2015 Walsh et al. 2011; Bellamy et al. 2013; Asplen et al. 2015), and developing larvae feed in the fruit, resulting in severe damage to fruit (Walsh et al. 2011). In invaded regions, spotted wing drosophila likely experience enemy-free space, resulting in greater population densities and severe economic damage. Consequently, small fruit growers have switched to calendar based weekly insecticide applications (Haviland and Beers 2012, Van Timmeren and Isaacs 2013), leading to greater production costs (Walsh et al. 2011) and the potential for secondary pest outbreaks.

Behaviorally based management, such as attract-and-kill, can provide protection from economic damage, while reducing chemical inputs. For example, the apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae), can be managed with devices referred to as attracticidal spheres. These spheres mimic apple fruit, and contain a feeding stimulant and toxicant, which are deployed in association with the odors of ripening fruit. Adult flies are visually attracted to spheres, feed on them, and die after ingesting toxins (Wright et al. 2012). When deployed in commercial apple orchards, attracticidal spheres provided protection equivalent to standard insecticide programs (Morrison et al. 2016). Recent studies suggest red spherical devices may also be useful in managing spotted wing drosophila (Rice et al. 2016a, 2017). Attracticidal spheres similar to those used for apple maggot fly, deployed at a rate of one per plant and positioned at the top of raspberry plants provided equivalent protection against spotted wing drosophila when compared with weekly insecticide applications (Rice et al. 2017). However, it is not known if this deployment strategy is optimal or if other locations within the plant or throughout the crop could improve overall performance and potentially reduce the number of spheres required. Larval infestations within fruit and abiotic factors associated with specific canopy location of blackberry plants have been characterized recently (Diepenbrock and Burrack 2016) but the foraging behavior of the adults themselves remain unknown. Insights into within-plant and -field foraging patterns of spotted wing drosophila could refine attracticidal sphere canopy deployment location as well as sphere densities and deployment strategies to enhance overall efficacy of this behaviorally based management tactic. The goal of this study was to quantify the foraging behavior of spotted wing drosophila within single raspberry plants and field plots to determine preferred alightment and oviposition behavior.

Materials and Methods

Semi-field Foraging Trials

Sentinel Berries

To determine spotted wing drosophila alightment patterns, we produced sentinel sticky berries by applying a thin coating of Tangle-Trap (The Tangle-Foot Company, Grand Rapids, MI) to fresh raspberry fruits. Those sentinel fruits used for oviposition bioassays were not coated with Tangle-trap. Open paper clips (#1 Skilcraft, Ira, MI) were inserted into the hull depression of each sticky-coated or clean raspberry fruit (Driscolls, Watsonville, CA) and affixed with hot glue (Fig. 1a). Sentinel berries were hung on wire rungs to avoid contact with objects prior to deployment.

Caged Foraging Arena-Alightment and Oviposition Preference

To examine within-plant movement and foraging patterns of spotted wing drosophila, we constructed five caged foraging arenas. Each cage (1.8 × 1.8 × 1.8 m) consisted of metal frames surrounded with screen mesh (1 × 1 mm) (Bioquip, Rancho Dominquez, CA). Cages were fastened to plywood platforms in an open field. Single potted raspberry plants with similar height and leaf density (Joan J, Nourse Nursery, Deerfield, MA) were placed in each cage. A 1.4-m tall tomato cage (Home Depot, Atlanta, GA) with circular rails at 60, 87, 110, and 135 cm above ground were placed around the plant. Prior to experimentation, all ripe fruit were removed from plants. Then, to represent exterior positioned fruit, four evenly spaced sentinel sticky berries were hung on each trellis rail. To replicate fruit placement on the interior of the plant, nylon strings were tied across each trellis rail and a single sentinel sticky berry was hung next to the central plant stalk (Fig. 1b). One-hundred twenty spotted wing drosophila (7–10 days old, 1:1 sex ratio) were removed from colony and transferred to empty 50-ml vials (15 flies per vial)(Flystuff.com, San Diego, CA) containing a cotton wick with 20% sugar water, and stored at 20 °C for 15–18 h prior to use in assays. Vials were held horizontally with a PVC pipe (8.9 cm diam.) mounted to stakes at each corner of the cage. Two release heights (50 cm and 135 cm above ground) were tested separately. Two vials containing 15 flies each were released at each corner (total 120 flies) by gently removing vial caps. After 24 h, sentinel sticky berries were visually inspected and the number of flies captured at each location was recorded. Overall capture rates between high and low release heights were compared with ANOVA. Because more exterior berries were present than interior berries at each height level, we compared the number of spotted wing drosophila captured on

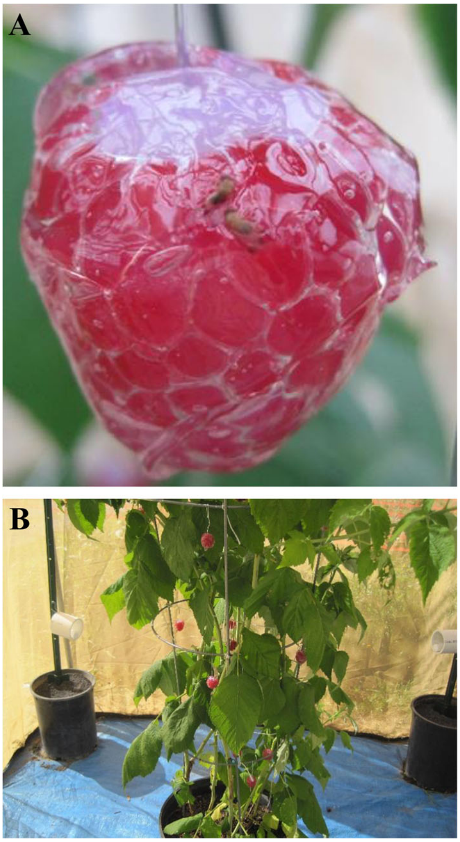

Fig. 1 Raspberry fruit coated with Tangle-Trap to produce sticky berries to monitor and capture spotted wing drosophila alightment preference (**a**). Caged foraging arena with exterior and interior sticky berries located at four heights (**b**)

sentinel sticky berries on a per berry basis by calculating the mean number of flies on interior berries and exterior berries across all heights and compared these averages with ANOVA.

For oviposition preference trials, clean sentinel fruit were hung on each trellis rail (see above). After 24 h, fruit were removed and placed into a 30-ml plastic vial with a cap and stored in an environmentally controlled room at 25 ± 2 °C, 50 ± 10% RH and 16:8 L:D photoperiod for 14 d to allow flies to pupate and emerge as adults. The total number of adult flies emerging from each fruit was recorded. Data were square root transformed because of violations of normality, and we compared the number of emerging flies at each height using ANOVA with Tukey's HSD mean separation test. Because more exterior berries were present than interior berries at each height level, we compared the number of spotted wing drosophila emerging from berries on a per berry basis by calculating the mean number of flies on interior berries and exterior berries across all heights and compared these averages with ANOVA. All foraging trials were conducted in July and August of 2015 with each experiment replicated four times (n = 10).

Field-Based Foraging Experiments

Field Sites

To examine within-plot movement, field plots were established at the Appalachian Fruit Research Station in Kearneysville, WV. Raspberry plants (cv. Joan J) were grown in greenhouses from bare dormant roots (Nourse Nursery Deerfield, MA) in pots (35.5 cm diameter, 30.5 cm height). In August 2015, 1.5-m tall potted plants were transferred to the field to establish four field plots. Plots were spaced 7.6 m apart and each plot consisted of five rows with 10 potted plants per row. Plants were supported with trellis wire and spaced 0.5 m apart with 3 m between rows. Field experiments were conducted from August through September 2015.

Mark-Release-Recapture Experiment

To estimate the number of flies released during mark-release-recapture experiments, we first created a best-fit regression line using fly mass and number of flies. Colony-reared flies were separated into vials in groups of 10 through 50 and the mass of each was recorded. Each of the 40 weight classes was replicated four times (200 vials total). The number of flies per vial and the mass of flies were plotted using linear regression and the best-fit line calculated (SAS 9.4). Using parameters from the best-fit line, the total number of flies released in subsequent experiments were calculated.

Groups of ~25 colony-reared flies were placed into empty 50-ml vials and their mass was recorded. Flies were then transferred to a 1-L plastic graduated cylinder and two puffs (~ 6.4 mg) of fluorescent powder (Rocket Red, Dayglo Color Corp, Cleveland, OH) were administered to mark the flies using powder blowers (DeVilbiss Heathcare, Model 175). Flies were transferred back into vials and several drops of 20% sucrose solution were added to a cotton stopper. Flies were stored in environmental chambers at 20 °C for up to 12 h prior to release.

Adult alightment in the field was quantified by hanging sentinel sticky berries on the wire trellis randomly at a height of either 50, 100, or 150 cm next to each plant. Each row contained two sentinel berries at each height (six sentinel sticky berries total). Releases were made from a 2 m high post placed 2 m away from each raspberry plot. Release sites were alternately positioned on the opposite side of adjacent plots. Drosophila vial trays (Genesee Scientific, San Diego, CA) were attached to the release posts at 1.5 m. At 0500 h, vials containing marked flies were placed at release sites and vial caps were removed before sunrise. At 2100 h, plots were surveyed with handheld UV flashlights, with the locations and heights of fluorescently marked flies recorded (mean daily temperature ± SEM = 25.6 ± 0.3 °C, mean RH ± SEM = 69.1 ± 1.2). Adjacent wood lines, grass and orchards (total area searched = 13,000 m^2) were also scouted for marked flies. Release vials were capped, transferred to the laboratory and the mass of flies remaining in vial was subtracted from the mass of released flies. The number of recaptured marked flies were compared using a general linear model with a Poisson distribution with number of adults used as the response variable and height and row number as predictor variables. For the purposes of the analysis, row one was the row nearest the release site, while row five was the furthest away as adults were released on only one side of each plot.

Field-Based Alightment and Oviposition of Wild Populations

We assessed the foraging behavior of wild spotted wing drosophila in the field under low and high population densities. Based on spotted wing drosophila developmental rates (Tochen et al. 2014), all ripe fruit on plants were removed and fruit on ground were collected twice a week for two weeks to reduce the potential for in-plot populations and overall population densities and enable assessments at low population densities. Sentinel sticky berries were placed at each plant at 50, 100, and 150 cm as described above. After 24 h, the number of adults captured on each berry were recorded (mean daily temperature ± SEM = 17.8 °C ± 0.48, mean RH ± SEM = 63.9 ± 1.7). To assess foraging behavior under high population density, we discontinued harvesting fruit for 14 days, allowing ripe fruit to mature, and wild populations to complete an entire lifecycle (Tochen et al. 2014). Sentinel sticky berries were deployed as described above for 24 h (mean daily temperature ± SEM = 16.4 °C ± 0.4, mean RH ± SEM = 72.0 ± 1.7). When fly populations were low, there was an excess of zero counts of spotted wing drosophila on sentinel berries (82% of the samples were zeros). As a consequence, a zero-inflated generalized linear model based on a Poisson distribution implemented with the package *pscl* in R Software (R Core Development Team (2015) Vienna, Austria) was used to analyze the data. The zero counts were modeled using a logit function with invariant regressors, while the main model used the total number of *D. suzukii* captured on berries as the response, and distance from the edge of the field (exterior, interior, center), the height of the fruit (upper, middle, and lower), and their interaction as fixed, explanatory variables. The model was checked for overdispersion, which was not a problem. Likelihood ratio based on a χ^2-distribution was used to test the overall model and variables for significance. Upon a significant result for a variable, pairwise comparisons were performed using a χ^2-test.

The abundance of adults captured on sentinel sticky berries were compared at high population densities using a general linear model with a Poisson distribution using number of spotted wing drosophila as the response variable and height and row location as predictor variables. Rows designation was assigned differently from mark-release-recapture experiments, because wild adults enter plots from each side (whereas in the mark-release-recapture experiment, releases were made from a single side). Here the two perimeter rows (rows one and five) were classified as exterior, the second two rows (rows two and four) were classified as interior and the middle row (row three) was classified as center for the purposes of analysis.

To establish within-plot oviposition patterns under high population densities, all ripe fruit were harvested based on canopy location in groups of 10 or less and placed into individual 473-ml paper cups with mesh lids. Harvested fruit was designated as growing in the lower (0–50 cm), middle (51–100 cm) or upper canopy (101 cm to the top) of each plant. Cups were stored in environmental conditioned chambers (25 ± 2 °C, 50 ± 10% RH and 16:8 L:D) for 9–10 days and the total number of spotted wing drosophila emerging across all sample dates were compared using a general linear model with a quasi-Poisson distributions to account for over dispersion (Aho 2014). Height and row were used as predictor variables and the number of berries collected as a covariate. Fruit density was compared among heights using a Dwass-Steel-Critchlow-Fligner mean separation test because of violation of normality.

Results

Semi-field Foraging Trials

Caged Foraging Arena Alightment and Oviposition Preference Trials

In caged foraging arenas examining alightment, high and low release points did not affect spotted wing drosophila alightment preference on berries (F = 1.74, df = 1, 199, P = 0.19), and therefore the data for the subsequent statistical analysis were combined. Spotted wing drosophila alighted in significantly greater numbers on low positioned fruit compared with higher locations (χ^2 = 39.9, df = 3, 200, P < 0.0001) (Fig. 2a) and on interior positioned fruit within the canopy compared with exterior fruit (F = 12.92, df = 1, 20, P = 0.0021) (Fig. 2b).

In oviposition trials, infestation rates did not differ when flies were deployed at high or low release heights (F = 1.12, df = 1, 200, P = 0.29), therefore those data were also combined for statistical analysis. Females deposited significantly more eggs in lower positioned fruit compared with those at higher positions (F = 8.68, df = 3, 199, P < 0.001) as greater numbers of adults emerged from fruit positioned at 60 and 85 cm compared with those at 110 and 135 cm (Fig. 3a). Females also deposited significantly more eggs in fruit located at interior locations within the canopy compared with those on the exterior (F = 4.83, df = 1, 20, P = 0.041) (Fig. 3b).

Field-Based Foraging Trials

Mark Release Recapture Experiment

Approximately 2822 spotted wing drosophila were fluorescently marked and released. After 15 h, only 2.5% flies remained in vials. Sentinel sticky berries recaptured 3.3% of marked adults, but no marked flies were observed on plant foliage or in the surrounding habitat. Significantly more flies were recaptured on sentinel sticky berries located in low positions (mean = 1.03 ± 0.27) within the canopy compared with fruit in the highest positions (mean ± SEM = 0.6 ± 0.17) (χ^2 = 4.03, df = 1, 119, P = 0.044), but no difference was observed between low and middle positioned fruit (mean ± SEM = 0.68 ± 0.14) (χ^2 = 2.58, df = 1119, P = 0.11) . We observed a strong edge effect with significantly greater numbers of flies recaptured on the most exterior row (row one – the row closest to the release site), (χ^2 = 17.17, df = 4, 119, P < 0.0001) and on row two (χ^2 = 12.34, df = 4, 119, P = 0.0004) compared with rows 3–5 (Fig. 4).

Alightment and Oviposition Preference of Wild Populations

When spotted wing drosophila population densities were low, greater numbers of wild adults were captured on sentinel berries at lower positions within the canopy compared with berries at middle and high positions (Fig. 5a), and berries on exterior rows and interior rows captured more flies than central rows (χ^2 = 35.7 df = 7, 360, P = < 0.0005) (Fig. 5).

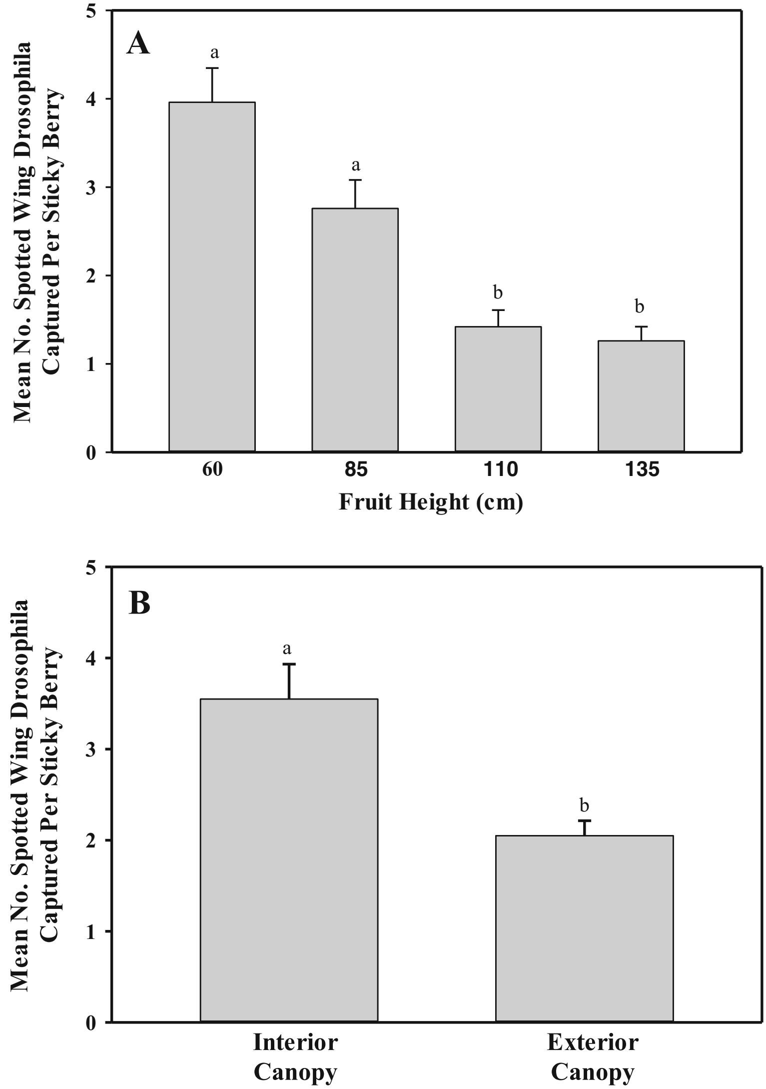

Fig. 2 Comparison of spotted wing drosophila captures on sentinel sticky berries at four heights (**a**) and interior and exterior positions (**b**) in caged foraging arenas

When population densities were high, greater numbers of adults were captured on sentinel sticky berries at middle positions within the canopy compared with lower positions (χ^2 = 5.59, df = 1, 360, P = 0.018) but captures did not differ between low and high positioned berries (χ^2 = 0.3, df = 1, 360, P = 0.58) (Fig. 6). Sentinel sticky berries in exterior rows (mean ± SEM = 2.2 ± 0.4) captured more flies compared with central rows (mean ± SEM = 1.5 ± 0.28) (χ^2 = 13.71 df = 1, 360, P = 0.0002), while captures on berries deployed in interior (mean ± SEM = 1.6 ± 0.22) and exterior rows did not differ (χ^2 = 0.54, df = 1, 360, P = 0.46) under high fly densities.

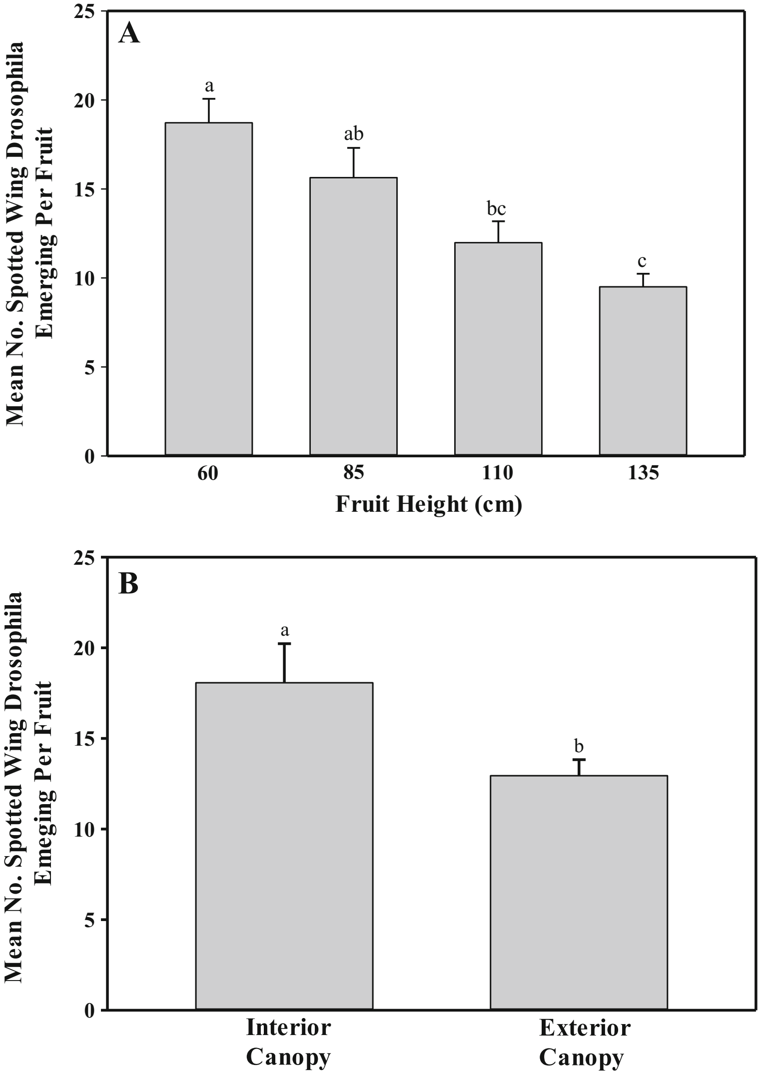

Fig. 3 Comparison of spotted wing drosophila oviposition preference on raspberry fruit at different heights (**a**) and interior and exterior locations (**b**) in caged foraging arenas

Under high population densities, oviposition by females on fruit was greater in fruit located at the top of the canopy based on infestation rates (χ^2 = 13.3 df = 1, P = 0.0013) (Fig. 7a) when compared with fruit located in the lower and middle portions of the canopy, with no statistical difference between low and middle. However, fruit densities were significantly greater in the upper canopy compared with middle (χ^2 = 9.81, df = 2480 P < 0.0001) and lower canopy positions (χ^2 = 17.87, df = 2480 P < 0.0001) (Fig. 7b). Spotted wing drosophila infestations among exterior, interior and central rows were not statistically different (χ^2 = 2.71, df = 1, P = 0.26).

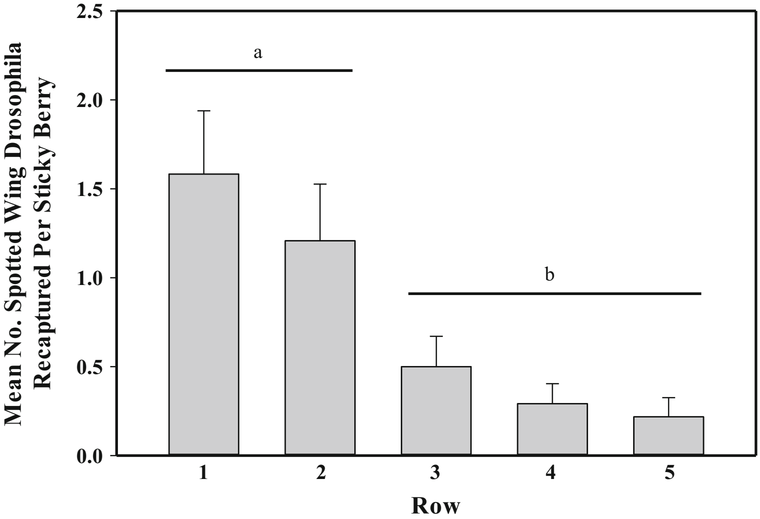

Fig. 4 Comparison of row location of fluorescent marked spotted wing drosophila recaptured in mark-release-recapture field studies. Contrast performed using general linear model with Poisson distribution

Discussion

In mark-release recapture and field studies conducted under low fly populations, spotted wing drosophila demonstrated a strong preference for fruit located in the interior of and at lower heights within the plant canopy. We found similar patterns in caged foraging arenas, although lower positioned berries were closer to the center of the plant compared with higher positioned berries, which might have also affected alightment and oviposition preference. Microclimates can influence the vertical distribution of insects within plant canopies (Coley and Barone 1996; Ulyshen 2011; Chaij et al. 2016) thus, lower positioned fruit in the interior canopy might provide favorable conditions for spotted wing drosophila development and survival. Temperatures in shaded interior regions of small fruit plants can be 8 °C cooler (Kliewer and Lider 1968) and have higher relative humidity compared to the ambient air (Kaspi and Yuval 1999). At temperatures above 28 °C, spotted wing drosophila experience reduced fecundity, developmental rates, and survival (Tochen et al. 2014). Likewise, higher relative humidity increases survival, and reproduction (Tochen et al. 2016). Therefore, adults may seek favorable temperatures and relative humidity in lower fruit located in the plant interior to optimize development and survival (Diepenbrock and Burrack 2016), although different patterns may occur in cooler climates. Insect herbivores often respond to adverse environmental conditions by seeking favorable microclimates. The melon fruit fly, *Bactrocera cucurbitae,* finds refuge under plants when temperatures rise and humidity decreases (Dhillon et al. 2005). Likewise, the Costa Rican weevil, *Exophthalmus jekelianus,* prefers microclimates with lower temperatures and higher humidity (Henderson and Roitberg 2006).

Additionally, predator avoidance may also select for an oviposition preference in lower positioned fruit. Unlike most drosophilid females that oviposit only in over-ripe fruit, spotted wing drosophila have serrated ovipositors, allowing eggs to be inserted

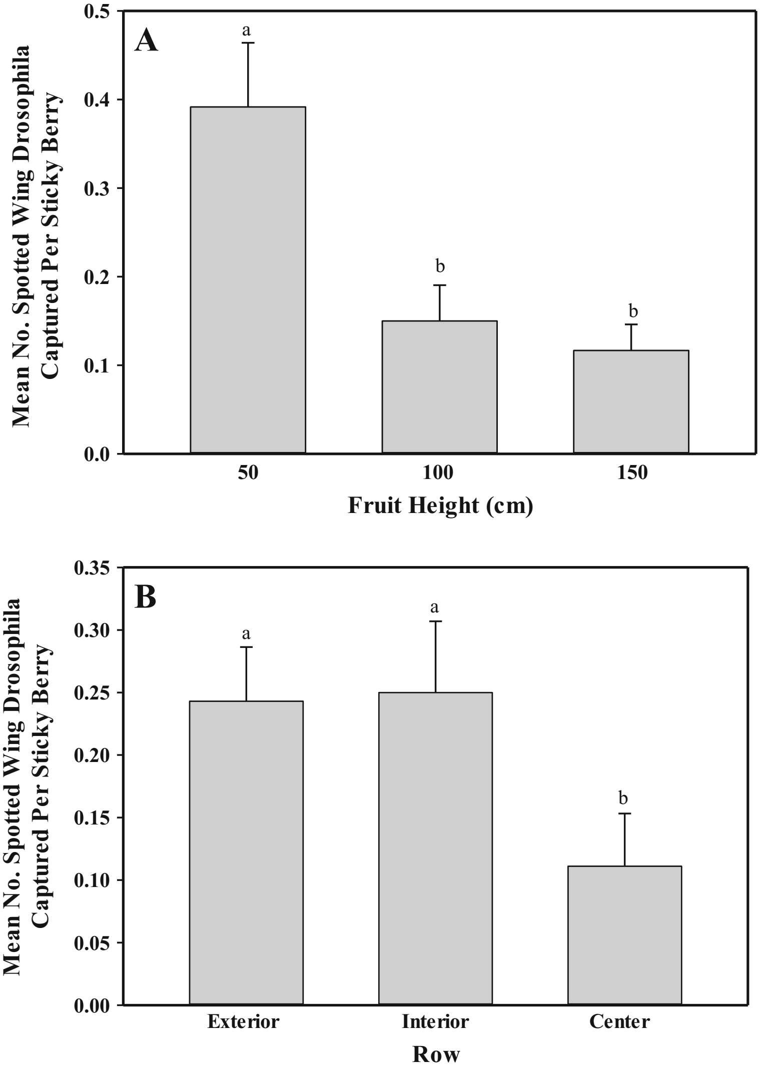

Fig. 5 Comparison of spotted wing drosophila captures on sentinel sticky berries at varying heights (**a**) and rows (**b**) in raspberry plots when fly population densities are low. Contrast performed using general linear model with Poisson distribution

into ripe fruit (Lee et al. 2011). Because plants invest in fruit production to increase seed dispersal by vertebrates (Ridley 1930; Van der Pijl 1982; Herrera 1982), phytophagous insects that lay eggs in ripe fruit are at risk of vertebrate predation (Lamprey et al. 1974; Halevy 1974), and predation risk can affect foraging behavior (Sih 1980; Thaler and Griffin 2008). Indirect vertebrate predation is a leading mortality factor for tephritid larvae feeding in fruit (Bigler and Delucchi 1981; Drew 1987). Avian frugivore foraging behavior is positively correlated with fruit availability (Shanahan and Compton 2001; Saracco et al. 2004; Plein et al. 2013) and fruit density is often greater at the top of plants (Schaefer et al. 2002). In our field studies, spotted wing drosophila

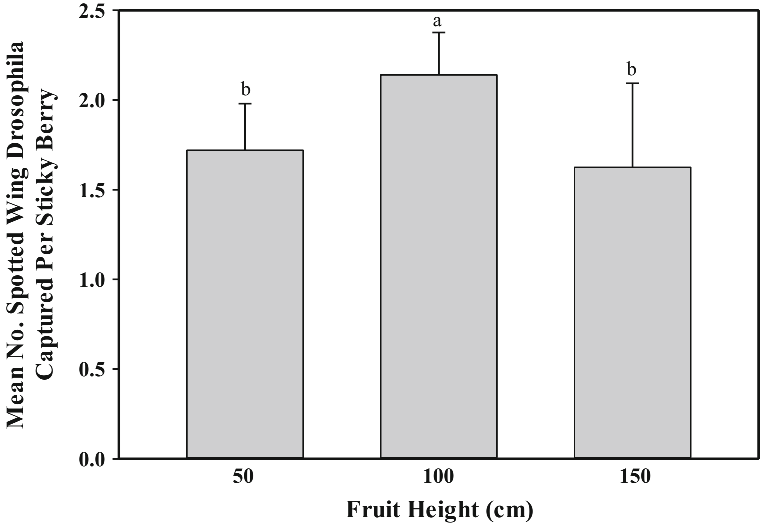

Fig. 6 Comparison of wild spotted wing drosophila captures on sentinel sticky berries at varying heights within the plant canopy) in raspberry plots when fly population densities are high. Contrast performed using general linear model with Poisson distribution

oviposition preference was related to fruit abundance, suggesting "bottom up" effects influence foraging behavior. However, plant characteristics such as canopy height can influence top down effects (Van Bael et al. 2003; Chaij et al. 2016), and trophic interactions (Paniagua et al. 2009). Some avian frugivores remove fruit on the wing (Levey et al. 1984; Marini 1992) and prefer more accessible fruit positioned higher in the canopy compared with fruit located near the ground (Schaefer et al. 2002; Flörchinger et al. 2010). Therefore, spotted wing drosophila's preference for low hanging fruit within the interior plant canopy may be the result of avoiding fruit likely to be consumed by birds.

In field experiments, we found that initial spotted wing drosophila alightment on sentinel sticky berries was higher on exterior rows compared with interior rows indicating spotted wing drosophila is likely an "edge species", at least before in-plot populations become present. Moreover, because our field plots only consisted of five rows, edge effects might be more apparent on larger commercial farms. Attracticidal spheres can effectively reduce spotted wing drosophila infestation in raspberry plots (Rice et al. 2017), but in these small-scale experimental trials, each plant within a plot received a sphere. A perimeter deployment of attracticidal spheres along field edges may be effective against adults and prevent infestation based on their foraging patterns, and simultaneously lower the numbers of attracticidal spheres needed to manage this pest. Similar patterns of deployment have been used for attracticidal spheres against apple maggot fly (Wright et al. 2012; Morrison et al. 2016). Alternatively, repeated insecticide applications along border rows may provide efficient spotted wing drosophila management, while reducing impacts on natural enemies and lowering production costs. Indeed, recent field trials suggest borders sprays reduce spotted wing drosophila infestations (Iglesias and Liburd 2017; Klick et al. 2016).

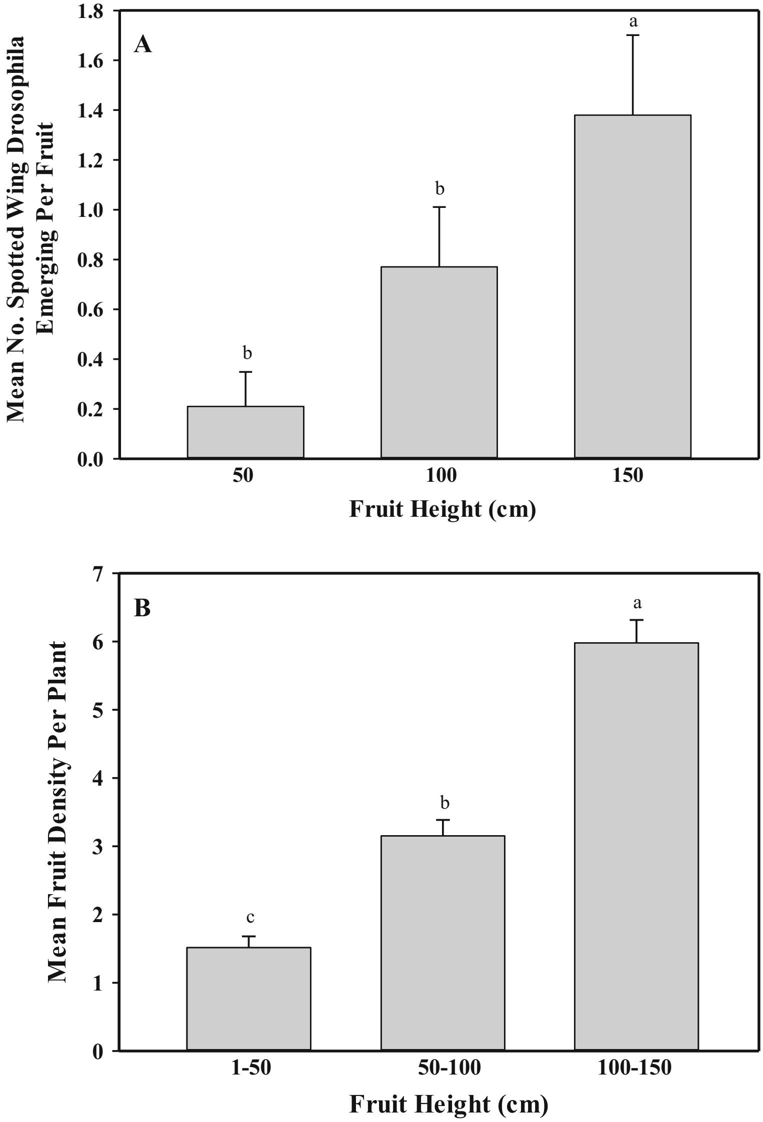

Fig. 7 Comparison of spotted wing drosophila infestation per fruit at varying heights (**a**) and fruit density at each height (**b**) in raspberry plots

Surprisingly, the only flies recovered during mark-release-recapture field trials were captured on sentinel berries and no marked flies were detected on raspberry foliage or adjacent crops, suggesting most flies dispersed away from raspberry plots, leaving a highly preferred host plant species (Burrack et al. 2013). Although we surveyed wood lines directly adjacent to release sites we did not survey wood lines greater than 30 m from release site In our field trial, fluorescent marked spotted wing drosophila may have dispersed further into woodlots than our search area. Insect herbivores often move between agriculture and wooded systems to find alternative host plant species (Holland and Fahrig 2000; Voegtlin et al. 2005; Reay-Jones 2010; Venugopal et al. 2014; Rice et al. 2016b). In its native range, spotted wing drosophila were consistently captured in forest systems and greater numbers were captured in traps located in the upper canopy compared with traps in the understory (Tanabe 2002). Furthermore, this species oviposits in fruit from several tree species (Lee et al. 2015) and wild herbaceous plant species that are present in wooded areas (Kimura et al. 1977; Mitsui et al. 2010; Cini et al. 2012; Poyet et al. 2014; Lee et al. 2015). Previous studies have found higher adult captures in wooded areas compared with adjacent crops (Asplen et al. 2015). Thus, understanding if spotted wing drosophila move between fruit crops and adjacent wooded habitat could be important in developing effective management tactics.

In semi-field foraging arenas, adults preferred to alight on and females preferred to deposit eggs in lower positioned fruit compared with higher positioned fruit within the plant canopy in our bioassay. In field studies in blackberry, similar patterns were found with natural infestation rates being greater in fruit growing in the lower portion of the canopy (Diepenbrock and Burrack 2016). However in our field trials, we found greater natural infestations rates from wild populations in fruit located in the upper portion of the canopy, though we did not control fruit density, quality, or prior infestations, and plants produced significantly more fruit in the upper canopy. Spotted wing drosophila are visually attracted to red coloration (Kirkpatrick et al. 2015; Rice et al. 2016a), thus higher ripe berry density at the tops of plants may increase attraction to the upper canopy because of greater attraction to visual cues.

Based on field experiments when fly populations were low and mark-release-recapture trials, our results provide strong support that spotted wing drosophila prefer to forage on low hanging fruit in the interior of plant canopies. Similar trends were found in commercial blackberry, with increased infestation rates occurring in lower positioned fruit in the plants interior (Diepenbrock and Burrack 2016). Moreover, we also observed strong edge effects. Taken together, these results suggest that spotted wing drosophila is a” edge species” that initially forages in the lower and central portions of the plant canopy and monitoring and management should consider these natural foraging patterns. Thus, for attracticidal spheres, optimal deployment location may be in the lower canopy and plot borders. However, further studies will need to verify that such deployment locations increase attracticidal sphere efficacy, particularly if the visually attractive stimulus offered by these attract-and-kill devices is obscured within the canopy.

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