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## Behavior

# Behavioral Responses of *Drosophila suzukii* (Diptera: Drosophilidae) to Visual Stimuli Under Laboratory, Semifield, and Field Conditions

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## Abstract

*Drosophila suzukii* Matsumura (Diptera: Drosophilidae) is an invasive pest in North America and Europe that attacks soft-skinned ripening fruit such as raspberries, blackberries, and blueberries. Little is known regarding the specific cues *D. suzukii* utilizes to locate and select host fruit, and inconsistencies in trap performance indicate the need for the development of improved monitoring and management techniques for this insect. Our studies focused on identifying attractive visual cues for adult *D. suzukii* and incorporating these cues into a potential attract-and-kill tactic for *D. suzukii* management. We evaluated *D. suzukii* response to color, shape, and size-specific stimuli. For color, we evaluated 10.2-cm-diameter spheres painted black, red, purple, orange, green, yellow, blue, or white. Shape stimuli (254 cm<sup>3</sup> surface area) included sphere, cube, pyramid, inverted pyramid, vertical or horizontal cylinder and were painted red. Size stimuli included red 2.5-, 10.2-, 15.2-, and 25.4-cm-diameter spheres. Trials were conducted under laboratory, semifield, and field conditions. For color, adults preferred black and red spheres to all other colors evaluated. Among shapes, there was no significant preference. For size, larger spheres captured significantly more *D. suzukii* compared with a small 2.5-cm-diameter sphere. Determining *D. suzukii* visual preference will aid in trapping and behaviorally based management programs.

**Key words:** visual stimuli, invasive, raspberry, spotted-wing drosophila

Spotted-wing drosophila, *Drosophila suzukii* Matsumura, is an invasive insect accidentally introduced to the United States from Asia. In North America, *D. suzukii* was first discovered in California in 2008. It is currently established in at least 45 states and has also spread to South America and Europe (Calabria et al. 2012, Cini et al. 2012, Asplen et al. 2015). *Drosophila suzukii* are polyphagous and attack a wide variety of small and stone fruit, including canberries, blueberries, strawberries, cherries, peaches, apricots, and plums (Lee et al. 2011, Walsh et al. 2011, Asplen et al. 2015, Lee et al. 2015). Unlike most drosophilids, *D. suzukii* females have serrated ovipositors, enabling them to lay eggs inside ripening fruit when crops are most vulnerable, resulting in severe economic damage (Atallah et al. 2014). Emerging larvae feed in the fruit, causing rapid quality decline and consumer rejection. In the western United States alone, total losses from *D. suzukii* are estimated to potentially reach US\$511 million annually (Walsh et al. 2011).

To assist in the triggering of insecticide-based management programs, numerous laboratory and field studies have endeavored to develop more effective monitoring tools for *D. suzukii* based on combinations of attractive olfactory and visual stimuli (Beers et al. 2011; Bruck et al. 2011; Walsh et al. 2011; Cha et al. 2012; Haviland and Beers 2012; Landolt et al. 2012a,b; Lee et al. 2012;

Basoalto et al. 2013; Abraham et al. 2015). However, no information is available on the relationship between trap capture and fruit infestation, and no available monitoring tools have proven sensitive enough to allow economic thresholds for this pest to be established (Landolt et al. 2012a, Lee et al. 2013, Kleiber et al. 2014). Thus, growers may apply materials unnecessarily or perhaps after infestation has already occurred. Furthermore, current trapping designs are difficult to monitor because of nontarget captures and baits have not been competitive with preferred hosts (Asplen et al. 2015, Burrack et al. 2015). Therefore, growers currently rely on weekly or twice-weekly preventative insecticidal applications to manage *D. suzukii* during susceptible periods (Haviland and Beers 2012, Van Timmeren and Isaacs 2013). Obviously, improvement in monitoring tools and IPM-based management is needed.

One approach, behavioral manipulation, requires that stimuli that induce or inhibit a particular behavior can be used to manipulate behavioral expression by the pest species (Foster and Harris 1997). Attract-and-kill, in particular, is a behaviorally based management tool that utilizes highly attractive olfactory, visual, or other appropriate stimuli to attract and aggregate pests to a particular location where they can be annihilated with a killing agent. Attract-and-kill systems have been developed with some level of success for

other pests, including dipteran olive fruit flies, *Bactrocera oleae* (Rossi) (Mazomenos et al. 2002), and apple maggot fly, *Rhagoletis pomonella* (Walsh) (Wright et al. 2012). Apple maggot fly is a key pest of apple and is considered to be a visual specialist in that it is visually attracted to stimuli that mimic the shape, size, and color of ripe fruit (Prokopy and Owens 1978). When these visual stimuli were combined with a feeding stimulus (sucrose) and toxicant (spinosad) to create what is known as attracticidal spheres, they provided statistically identical levels of management of invading fly populations with standard insecticide applications in commercial apple orchards (Morrison et al. 2016).

A similar behaviorally based management system may be possible against *D. suzukii* in small fruit plantings; however, few studies have examined *D. suzukii* foraging behavior and little is known about their visual ecology. Drosophilids, in general, are highly responsive to visual cues and many species are attracted to red colors (Barrows 1907, Reed 1938, West 1961, Wave 1964, Stökl et al. 2010, Cha et al. 2012, Hottel et al. 2015). Recent studies suggest *D. suzukii* are attracted to red and black colors, because traps with red and black caps captured more *D. suzukii* compared with white (Basoalto et al. 2013), and laboratory bioassays suggest *D. suzukii* are visually attracted to 5-cm red, black, and purple disks when presented with white backgrounds (Kirkpatrick et al. 2015). Surprisingly few studies have examined *D. suzukii* visual response to trap shape and size. The objective of our studies is to fully define attractive visual stimuli for *D. suzukii*. We evaluate color, shape, and size for behavioral preferences under laboratory, semifield, and field conditions for this invasive species.

## Materials and Methods

### *D. suzukii* Colony

*Drosophila suzukii* used in laboratory and semifield trials were obtained from a colony at Rutgers University (C. Rodriguez-Saona) in 2013 and maintained at the USDA-ARS Appalachian Fruit Research Station in Kearneysville, WV. Flies were held in 50-ml plastic drosophila vials (Flystuff.com, San Diego, CA) in groups of 20–30 adults, and fed 2.5 g of artificial drosophila diet (Formula 4-24 instant drosophila medium, Carolina Biological Supply, Burlington, NC) with 3–5 grains of yeast. Vials were held in environmental chambers at  $25 \pm 2^\circ\text{C}$ ,  $50 \pm 10\%$  RH, and a photoperiod of 16:8 (L:D) h. All flies used in experiments were 7–14 d old and sexually mature (Asplen et al. 2015). Flies were transferred to empty vials without diet, containing a cotton wick with 20% sugar water, and stored at  $20^\circ\text{C}$  for 15–18 h prior to use in assays.

### *D. suzukii* Response to Visual Stimuli

#### Laboratory Experiments

The response of *D. suzukii* to color was evaluated among red, orange, yellow, green, blue, purple, white, and black. Red plastic spheres (9 cm diameter, Great Lakes IPM, Vestaburg, MI) were primed white to block any background color and then spray-painted one of eight colors: Apple Red (269457), Real Orange (249095), Sun Yellow (249092), Meadow Green (249100), Deep Blue (269419), Purple (249047), White (249090), or Black (249061) (Rust-Oleum Gloss) and allowed to dry. A thin coating of Tangle-Trap (Bioquip, Rancho Dominguez, CA) was applied to the surface of each sphere. Reflectance of each colored sphere was quantified before (Fig. 1A) and after Tangle-Trap (Fig. 1B) application using a StellarNet EPP2000 spectrometer (StellarNet INC. Tampa, FL).

To evaluate *D. suzukii* response to shape, spheres, cubes, horizontal cylinders, vertical cylinders, pyramids, and inverted pyramids were compared. Shapes were constructed from pressure-treated lumber, except cylinders which were cut from birch wood dowels. Shapes were primed white, spray painted “Apple Red” (based on results from the above experiment) and then coated with a thin layer of Tangle-Trap. Each shape had an equal surface area ( $254\text{ cm}^2$ ) as that of the spheres used in the previous experiment.

Color and shape stimuli no-choice experiments were conducted in an environmental condition-controlled room at  $27 \pm 1^\circ\text{C}$ ,  $50 \pm 10\%$  RH, and a photoperiod of 16:8 (L:D) h. Spheres (and shapes) were evaluated individually (no-choice conditions) by hanging them from a 7.5-cm hook from the top of a clear acrylic box (45.7 by 45.7 by 45.7 cm, 0.32 cm thick). A single box side was removed, then covered and sealed with plastic wrap to allow access. A translucent plastic sheet covered the boxes to diffuse light more evenly. Overhead fluorescent lights (CH Lighting F54T5 6500K/HO, 54 Watt) were positioned 1 m above observation boxes. Twenty  $\text{CO}_2$ -anesthetized *D. suzukii* adults (1:1 sex ratio, 7–14 d old) were placed in 30-ml cups without lids (Bio-Serv, Frenchtown, NJ) and placed on the floor of each box. After 6 h, the number of male and female *D. suzukii* captured on each colored sphere or shape stimuli was recorded.

Each color treatment was replicated a minimum of 20 times and the mean proportion of total flies captured was compared among each color treatment using ANOVA with Tukey’s HSD mean separation test. Each shape treatment was replicated a minimum of 20 times and the mean proportion of total flies captured was compared among each shape treatment using Wilcoxon–Mann–Whitney with a Dwass–Steel–Critchlow–Fligner mean separation test because of violation of normality. A paired t-test was used to compare captures of male and female flies.

Next, choice trials were conducted using the stimuli capturing the most (red, black, and orange) and the fewest (white) adults in the no-choice color trials. Two spheres were suspended 20 cm apart in the acrylic boxes. Forty repetitions of all color combinations were compared, including spheres of the same color, to account for fly directional and positional preference within the testing arena. No positional preference was recorded and those data are not presented. The mean proportion of flies captured on each sphere was compared among color treatments using ANOVA with Tukey’s HSD mean separation test.

#### Semifield Experiments

Visual treatments evaluated in semifield trials were colored spheres and shapes identical to those used in laboratory trials. In addition, responses to red spheres of increasing diameters (2.5, 10.2, 15.2, and 25.4 cm) were evaluated. Semifield experiments were conducted in August of 2013 and 2014. Raspberry (cv. Joan J) root cuttings (Nourse Farms, Deerfield, MA) were potted and maintained in greenhouses until ripe fruit were present, at which time plants were transferred to an open field. Three potted plants (spaced 23 cm apart) were grouped and positioned in a triangular configuration. Each group was spaced at least 1.2 m apart. A single visual stimulus was suspended in the center of each plant grouping from a string attached to bamboo supports. Each visual stimulus was coated with a thin layer of Tangle-Trap to capture flies. Thirty (1:1 sex ratio, 7–14 d old)  $\text{CO}_2$ -anesthetized *D. suzukii* were released from cups placed on the ground in the middle of each plant grouping. After 48 h, the number of *D. suzukii* captured on each trap was counted. During

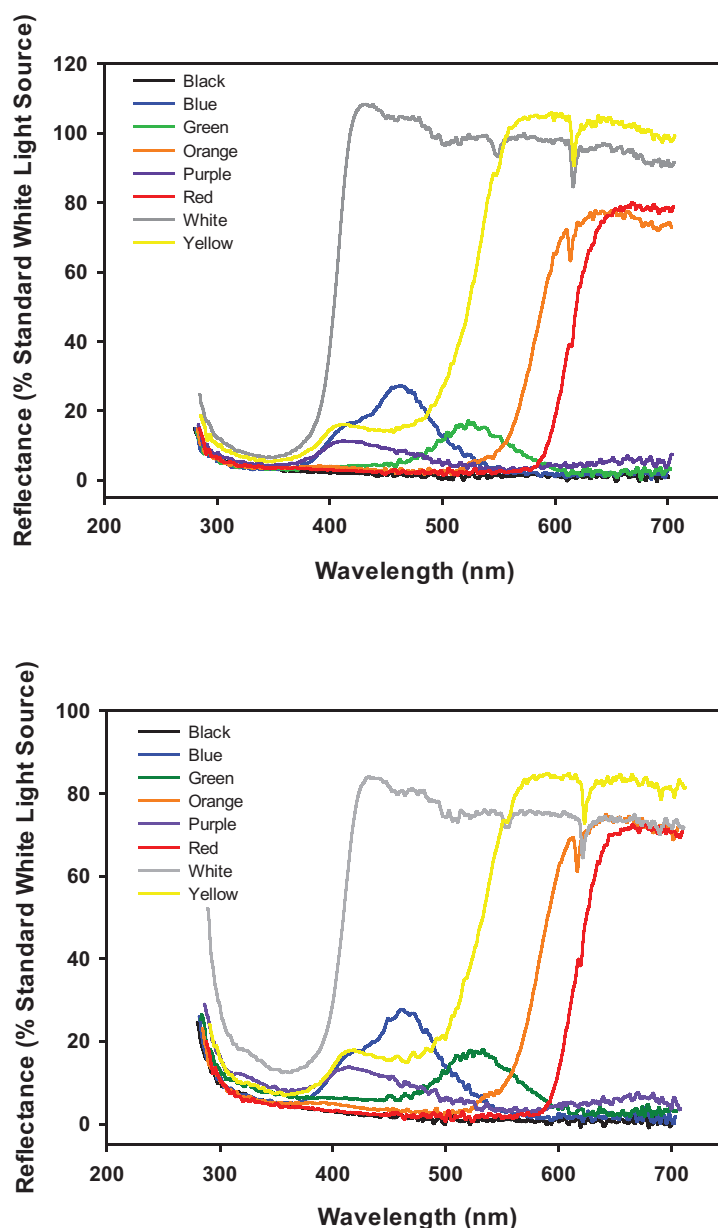


Fig. 1. Reflectance of colored spheres before (A) and after (B) TangleTrap applications using a StellarNet EPP2000 spectrometer.

2013, three trials with three replicates were conducted for each experiment ( $n=9$ ). For color trial, white was not evaluated in 2013. During 2014, five trials with two replicates were completed ( $n=10$ ). During 2013, the number of flies captured on each sphere color and each shape (square root transformed) was compared using ANOVA with Tukey's HSD mean separation test. During 2014, both shape, color and size data were analyzed using Wilcoxon-Mann-Whitney with a Dwass-Steel-Critchlow-Fligner mean separation test because of violation of normality.

#### Field Experiments

To establish visual responses of wild *D. suzukii* populations to color, shape, and size stimuli, field experiments were conducted using the same visual stimuli as in the laboratory trials. Trials were conducted during August of 2013 and 2014 in a 0.25-ha plot of 'Loring' peaches planted in 1997 (spacing 3.1 by 3.4 m) and maintained at the USDA-ARS Appalachian Fruit Research Station in

Kearneysville, WV. This plot received standard fungicide and herbicide treatments (Brannen and Smith 2014), but no insecticide treatments to allow for build-up of *D. suzukii* populations. In this case, colored sphere, shape and size traps were evaluated in separate trials. During 2013, three trials with four replicates were conducted for color and shape and one trial with four replicates for size experiments. During 2014, three trials with four replicates were conducted for each experiment. Each trap was coated with a thin layer of Tangle-Trap, then deployed within the outer portion of the upper third of the canopy (~1.5 m). Nearby branches and foliage were removed to improve visual apparency. Traps were spaced a minimum of 10 m apart and remained in place for 48 h, after which they were retrieved and all *D. suzukii* captured were removed and counted. In 2013, the total number of *D. suzukii* captured on different color spheres and different shapes were compared using Wilcoxon-Mann-Whitney with a Dwass-Steel-Critchlow-Fligner mean separation test because of violation of normality. In 2014, different color

and size spheres were compared using Wilcoxon–Mann–Whitney with a Dwass–Steel–Critchlow–Fligner mean separation test because of violation of normality, and shape was compared using ANOVA with Tukey’s HSD mean separation test (square root transformed).

## Results

### Laboratory Experiments

Under no-choice laboratory trials, red and black spheres captured significantly more *D. suzukii* than spheres of other colors, except

orange and green; white spheres yielded the lowest captures ( $F = 11.75$ ;  $df = 7, 159$ ;  $P < 0.0001$ ; Fig. 2A). Under choice conditions, red, black, and orange spheres captured significantly more *D. suzukii* when paired with white spheres (Table 1). Among shape stimuli, although statistical analysis indicated there was a significant difference in terms of adult captures ( $\chi^2 = 12.5$ ,  $df = 5$ ,  $202$ ;  $P = 0.028$ ), pairwise comparisons were not significant (Fig. 3A). Numerically, more adults were captured on sphere and cube stimuli compared with other shapes. More males were captured on all shape

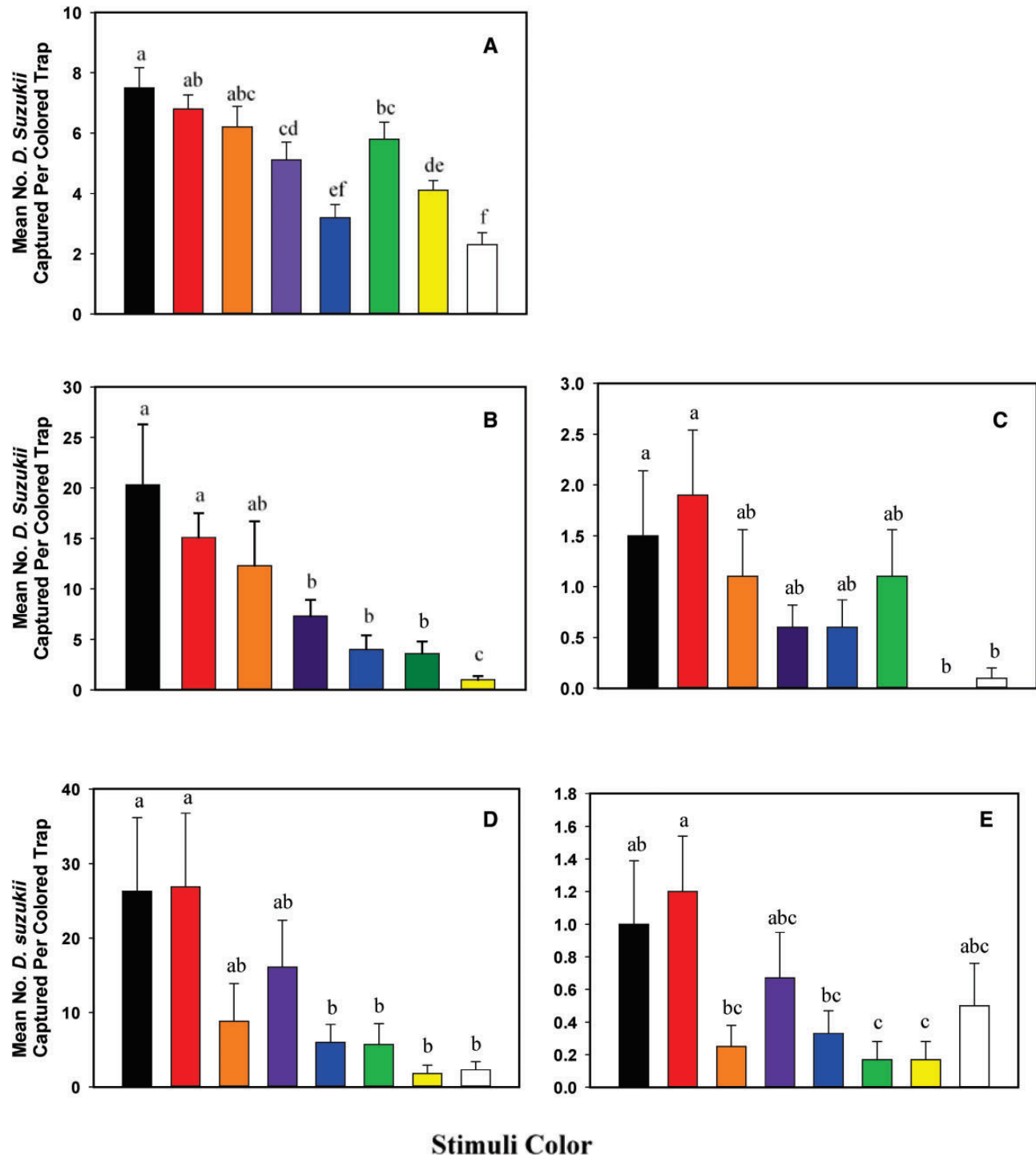


Fig. 2. Mean  $\pm$  SE *D. suzukii* captured on different colored sticky spheres in no-choice laboratory tests (A), semifield raspberry plots during 2013 [white spheres were not tested] (B) and 2014 [yellow spheres captured zero *D. suzukii*] (C), and in peach orchards during 2013 (D) and 2014 (E).

**Table 1.** *Drosophila suzukii* captures on different colored spheres in laboratory choice test

	Mean capture	SE	P value	n
Red	5.9	0.36	0.74	12
Black	5.4	0.29		
Orange	5.8	0.39	0.51	12
Black	5.3	0.31		
Black	7.9	0.4	<0.0001	14
White	2.0	0.29		
Red	6	0.4	0.16	15
Orange	5.4	0.31		
Orange	8.7	0.5	<0.0001	14
White	2.0	0.32		
Red	8.0	0.39	<0.0001	16
White	1.7	0.28		

Each replicate consisted of 20 released adult flies (1:1 sex ratio).

(Table 2) and color stimuli (Table 3) compared with females. Because the pattern of male and female captures remained consistent for all stimuli tested, male and female captures in semifield and field experiments were pooled.

### Semifield Experiments

The number of *D. suzukii* captured on visual stimuli differed between 2013 and 2014 for both color ( $F=43.6$ ;  $df=1, 141$ ;  $P<0.0001$ ) and shape ( $F=59.2$ ;  $df=1, 111$ ;  $P<0.0001$ ) trials, thus, each year was analyzed independently. When colony-reared *D. suzukii* were released outdoors in the center of raspberry plant groups, we observed significant differences in response to sphere color stimuli. In 2013, significantly greater captures of *D. suzukii* were recorded on red, black, and orange spheres compared with spheres of other colors ( $F=8.26$ ;  $df=6, 56$ ;  $P<0.0001$ ; Fig. 2B). Black spheres captured fivefold more *D. suzukii* compared with blue, green, or yellow spheres. In 2014, captures were lower, but red and black spheres captured significantly more *D. suzukii* compared with white and yellow spheres ( $\chi^2=18.7$ ;  $df=7, 73$ ;  $P=0.0091$ ; Fig. 2C).

Among shape treatments, spheres captured numerically more *D. suzukii* compared with all other shapes in both years (Fig. 3B, C). During 2013, spheres captured significantly more *D. suzukii* compared with pyramid shaped stimuli ( $F=3.58$ ;  $df=5, 48$ ;  $P=0.0052$ ). During 2014, no significant difference ( $\chi^2=4.1$ ;  $df=5, 54$ ;  $P=0.54$ ) occurred among shapes, but *D. suzukii* preferred larger sized spheres to smaller spheres ( $\chi^2=23.3$ ;  $df=3, 45$ ;  $P<0.0001$ ; Fig. 4A).

### Field Experiments

Trap color, shape, and size were also evaluated in peach orchards bearing ripe fruit to document responses of wild populations of *D. suzukii*. The number of *D. suzukii* captured on traps differed between 2013 and 2014 for both color ( $F=25.13$ ;  $df=1, 190$ ;  $P<0.0001$ ) and shape ( $F=31.78$ ;  $df=1, 142$ ;  $P<0.0001$ ) trials, thus, each year was analyzed independently. During 2013, a significant effect of color was observed ( $\chi^2=16.2$ ;  $df=7, 89$ ;  $P=0.0232$ ), yet no pairwise test was significant; no color preference was observed during 2014 ( $\chi^2=13.5$ ;  $df=7, 89$ ;  $P=0.06$ ). During both years, however, red and black spheres captured more *D. suzukii* than all other colors (Fig. 2D, E). *Drosophila suzukii* did not show a preference for stimuli shape during 2013 ( $\chi^2=2.2$ ;  $df=5, 67$ ;  $P=0.82$ ) or 2014 ( $F=1.8$ ;  $df=5, 66$ ;  $P=0.12$ ; Fig. 3D, E), or size during 2014 ( $\chi^2=3.8$ ;  $df=3, 45$ ;  $P=0.28$ ; Fig. 4B).

## Discussion

Our results indicate *D. suzukii* have a strong visual preference for red and black colors in the laboratory and under field conditions. Insect herbivores use visual cues to locate food resources and oviposition sites. Visual cues can be used to determine host plant quality (Raubenheimer and Tucker 1997). For instance, leaf color can indicate nitrogen content and the presence of toxic compounds (Haribal and Feeny 2003, Raese et al. 2007), factors that affect insect survival, development, and fitness (Mattson 1980, Clancy and Price 1987). Shape and size can indicate the quality of fruit for oviposition. Insects use shape and color to detect individual fruit at close range (Prokopy 1968, Roitberg 1985, Owens and Prokopy 1986). Traps that utilize attractive cues can increase capture rates. For example, 31 Australian fly morphotaxa were attracted to white and yellow colors, coinciding with the most abundant flower color in the region and white and yellow traps catch more flies than other colors (Pickering and Stock 2003). Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), prefer spherical objects over other shapes, possibly due to their resemblance to host fruit characteristics (Nakagawa et al. 1978). *Drosophila* spp. use visual cues to determine acceptable oviposition sites (Carfagna and Lancieri 1971). Our results indicate that *D. suzukii* adults use visual cues as a component of their foraging behavior.

In natural habitats, *D. suzukii* lays eggs on autumn olive (*Elaeagnus umbellata* Thund.), honeysuckle (*Lonicera* spp.), buckthorn (*Frangula* spp.), and pokeweed (*Phytolacca americana* L.), species that produce small red or black berries (Lee et al. 2011, Walsh et al. 2011, Lee et al. 2015). Thus, one might anticipate that *D. suzukii* may be attracted to red and black colors. Indeed in our studies, we found that *D. suzukii* were consistently attracted to red and black spheres in greater numbers compared with other colors under laboratory, semifield, and field bioassays. These results are strengthened by the results of laboratory trials that found that red and black disks attracted significantly more *D. suzukii* than disks of other colors (Kirkpatrick et al. 2015). We also observed that spherical shape stimuli yielded numerically greater captures of flies compared with other shapes. Interestingly, however, the small size of fruit typically utilized by *D. suzukii* in its native range did not necessarily correspond with size preferences observed in our behavioral bioassays. Indeed, *D. suzukii* preferred larger red spheres compared with smaller spheres in our tests, possibly exhibiting a super normal stimulus response. Previous studies have shown similar responses with tephritids. For example, Mediterranean fruit fly prefer larger spherical shapes compared with smaller spheres that resemble real fruit (Nakagawa et al. 1978) and larger traps captured more Mexican fruit flies compared with smaller traps (Robacker 1992).

In our no-choice laboratory experiments, significantly more male *D. suzukii* were captured on all stimuli shapes compared with females. Significantly more males were captured on all sphere colors except black, where high numbers of both males and females were captured. Previous studies have observed increased male response to visual cues compared with females (Lelito et al. 2007, 2008), possibly because males move more in order to find female mates and are thus more likely to encounter traps (Lawrence 1982). Alternatively, because *D. suzukii* females use host fruit as an oviposition site, olfactory cues may also be necessary to maximize attractiveness of spherical stimuli.

It has been documented that combined visual and chemical cues can increase trap effectiveness. For example, visually attractive red spheres baited with attractive odors capture more apple maggot flies



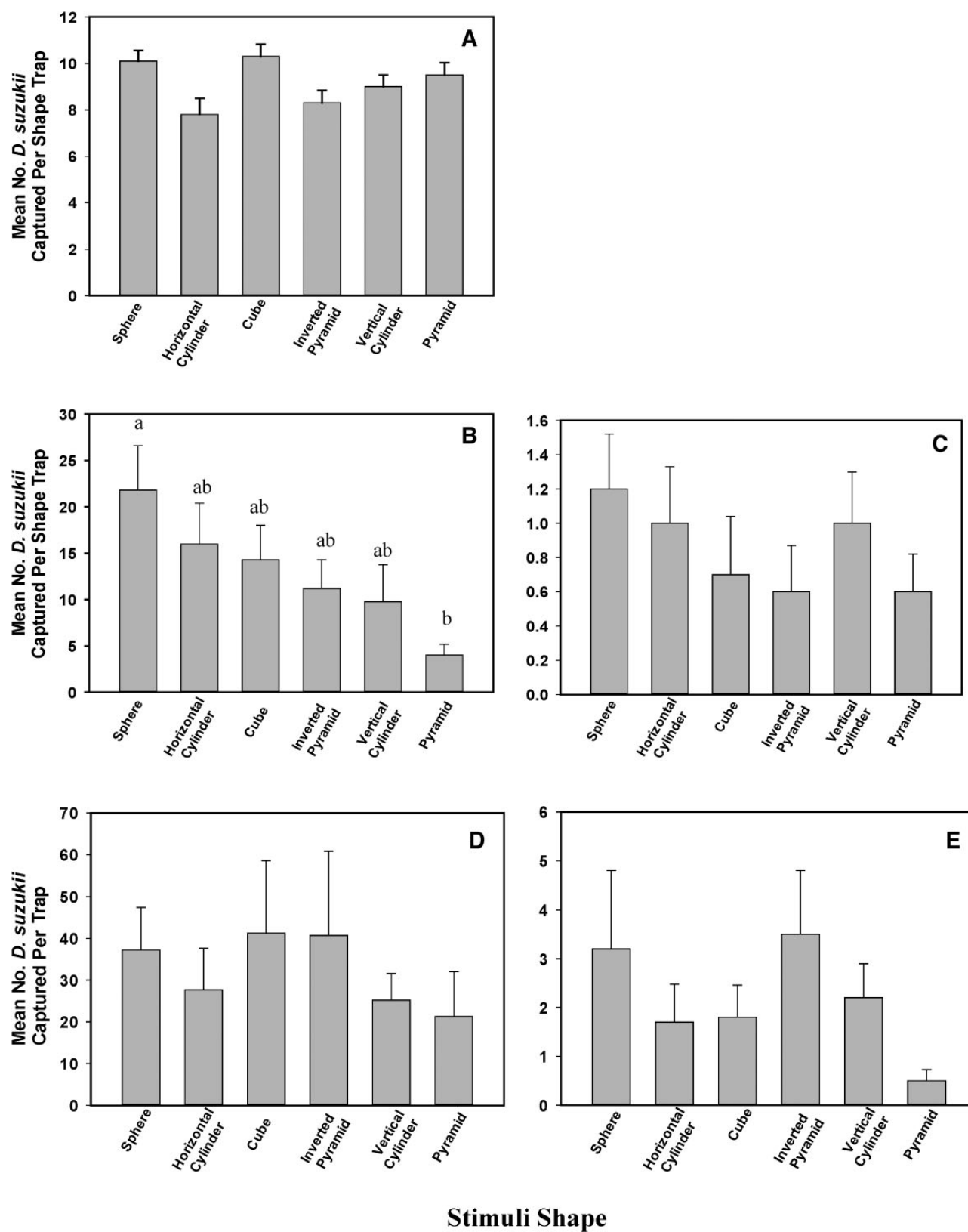


Fig. 3. Mean  $\pm$  SE *D. suzukii* captured on shape stimuli painted red in no-choice laboratory test (A), semield raspberry plots during 2013 (B) and 2014 (C), and peach orchards during 2013 (D) and 2014 (E).

**Table 2.** Comparison of male and female *D. suzukii* captured on different shapes in no-choice experiments

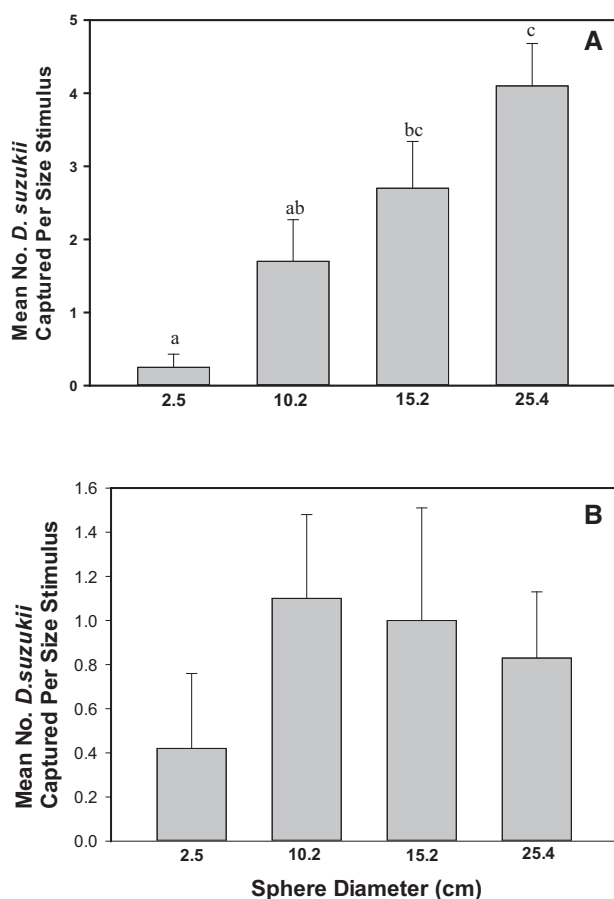
Shape	Males	Females	t-value	P-value
Cube	5.8 ± 0.33	4.5 ± 0.39	2.7	0.011
Horizontal cylinder	5.3 ± 0.53	4.5 ± 0.39	4.7	0.0001
Vertical cylinder	5.4 ± 0.3	3.6 ± 0.3	5.4	<0.0001
Pyramid	5.6 ± 0.33	3.9 ± 0.34	4.0	0.0002
Inverted pyramid	5.4 ± 0.37	2.9 ± 0.42	4.4	0.0003
Sphere	5.9 ± 0.28	4.2 ± 0.30	4.7	<0.0001

Each replicate consisted of 20 released adult flies (1:1 sex ratio).

**Table 3.** Comparison of male and female *D. suzukii* captured on different colored spheres in no-choice experiments

Color	Males	Females	t-value	P-value
Black	3.9 ± 0.47	3.6 ± 0.44	0.41	0.69
Blue	2.3 ± 0.34	0.9 ± 0.24	3.4	0.0031
Green	4.2 ± 0.4	1.6 ± 0.32	5.6	<0.0001
Orange	4.0 ± 0.51	2.2 ± 0.35	3.3	0.004
Purple	3.6 ± 0.5	1.6 ± 0.3	3.6	0.0021
Red	4.3 ± 0.38	2.5 ± 0.24	4.3	0.0003
White	1.6 ± 0.29	0.75 ± 0.22	2.6	0.02
Yellow	3.1 ± 0.25	0.96 ± 0.17	7.43	<0.0001

Each replicate consisted of 20 released adult flies (1:1 sex ratio).

**Fig. 4.** Mean ± SE *D. suzukii* captured on different sized red spheres in semi-field raspberry plots (A) and peach orchards (B).

than do unbaited spheres (Prokopy and Mason 1996, Rull and Prokopy 2000). A similar approach may work with *D. suzukii*. The visual response to red spheres might be increased with added olfactory stimulants, particularly for females. Several studies have baited traps with apple cider vinegar and fermentation volatiles to capture or monitor *D. suzukii* (Cha et al. 2012, 2013; Landolt et al. 2012a,b; Lee et al. 2012, 2013; Iglesias et al. 2014). These baits use general drosophila attractants that capture numerous nontarget drosophilids requiring a significant amount of expertise and time for identification (Burrack et al. 2015). Unlike most *Drosophila* spp., *D. suzukii* are attracted to ripe fruit, therefore, specific fruit volatiles may reduce nontarget species attraction and increase overall *D. suzukii* attraction to monitoring traps, particularly when deployed in combination with attractive visual cues such as red spherical objects. In addition, the inclusion of these stimuli could also lead to effective attract-and-kill designs for *D. suzukii*. In semifeild trials, we found that the presence of Tangletrap-coated red spheres used as a potential attract and kill device in association with raspberry plants reduced *D. suzukii* infestation in ripe raspberry fruit by 42.5% compared with raspberry plants without spheres present (Leskey et al. unpublished data), suggesting behavioral-based management options might be appropriate to manage *D. suzukii*.

Similar approaches have worked to manage key pests in commercial orchards. The apple maggot fly is a destructive pest of North American apple. Tangle-Trap-covered red spheres combined with odor attractants have been shown to successfully capture apple maggot fly (Reissig et al. 1982) and have been used to monitor flies in orchards (Agnello et al. 1990, Prokopy et al. 1990, Prokopy 1991). Moreover, apple orchards protected using red attracticidal spheres against apple maggot (Wright et al. 2012), red spheres provisioned with an insecticide killing agent and feeding stimulant to remove the need for Tangle-Trap, protected orchards against apple maggot injury (Morrison et al. 2016). This behaviorally based management tactic not only reduces pesticide applications, but also increases natural enemy abundance (Prokopy et al. 1990). Based on our preliminary studies, *D. suzukii* attraction to red spheres could lead to use of attracticidal spheres against this invasive species as well.

Our findings show *D. suzukii* have a strong visual preference to red and black spherical objects under a variety of conditions. In addition, multiple studies have reported that *D. suzukii* strongly prefer red and black colors (Basoalto et al. 2013, Lee et al. 2013, Renkema et al. 2014, Kirkpatrick et al. 2015) suggesting that future research should target their inclusion in monitoring traps and attract-and-kill systems that combine other attractants such as attractive olfactory stimuli could further improve overall performance. Recent improvements in attracticidal spheres for apple maggot fly incorporate an insecticide killing agent in combination with a feeding stimulant that replaces the need for Tangle-Trap coating on spheres, making deployment and maintenance less time consuming (Wright et al. 2012, Morrison et al. 2016). Thus, black or red spherical objects could be used to monitor *D. suzukii* populations, similar to apple maggot fly, and red attracticidal spheres could annihilate foraging *D. suzukii*, possibly reducing pesticide applications and nontarget impacts.

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## References Cited

- Abraham, J., A. Zhang, S. Angeli, S. Abubeker, C. Michel, Y. Feng, and C. Rodriguez-Saona. 2015. Behavioral and antennal responses of *Drosophila suzukii* (Diptera: Drosophilidae) to volatiles from fruit extracts. *Environ. Entomol.* 44: 356–367.
- Agnello, A. M., S. M. Spangler, and W. H. Reissig. 1990. Development and evaluation of a more efficient monitoring system for apple maggot (Diptera: Tephritidae). *J. Econ. Entomol.* 83: 539–546.
- Asplen, M. K., G. Anfora, A. Biondi, D. Choi, D. Chu, K. M. Daane, P. Gilbert, A. P. Gutierrez, K. A. Hoelmer, W. D. Hutchinson, et al. 2015. Invasion biology of spotted wing drosophila (*Drosophila suzukii*): a global perspective and future priorities. *J. Pest Sci.* 88: 469–494.
- Allallah, J., L. Teixeira, R. Salazar, G. Zaragoza, and A. Kopp. 2014. The making of a pest: The evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. *Proc. R. Soc. B.* 281: 1781.
- Barrows, W. M. 1907. The reactions of the pomace fly, *Drosophila ampelophila* Loew, to odorous substances. *J. Exp. Zool.* 4: 515–537.
- Basoalto, E., R. Hilton, and A. Knight. 2013. Factors affecting the efficacy of a vinegar trap for *Drosophila suzukii*. *J. Appl. Entomol.* 137: 561–570.
- Brannen, P., and P. Smith. 2014. 2014 Southeast regional caneberries integrated management guide. The University of Georgia Bulletin 47.
- Beers, E. H., R. A. Van Steenwyk, P. W. Shearer, W. W. Coates, and J. A. Grant. 2011. Developing *Drosophila suzukii* management programs for sweet cherry in the western United States. *Pest Manag. Sci.* 67: 1386–1395.
- Bruck, D. J., M. Bolda, L. Tanigoshi, J. Klick, J. Kleiber, J. DeFrancesco, B. Gerdeman, and H. Spitler. 2011. Laboratory and field comparisons of insecticides to reduce infestation of *Drosophila suzukii* in berry crops. *Pest Manag. Sci.* 67: 1375–1385.
- Burrack, H. J., M. Asplen, L. Bahder, J. Collins, F. A. Drummond, C. Guédot, R. Isaacs, D. Johnson, A. Blanton, J. C. Lee, et al. 2015. Multistate comparison of attractants for monitoring *Drosophila suzukii* (Diptera: Drosophilidae) in blueberries and caneberries. *Environ. Entomol.* 44:704–712.
- Calabria, G., J. Máca, G. Bächli, L. Serra, and M. Pascual. 2012. First records of the potential pest species *Drosophila suzukii* (Diptera: Drosophilidae) in Europe. *J. Appl. Entomol.* 136: 139–147.
- Carfagna, M., and M. Lancieri. 1971. Colour vision and the choice of substrate during oviposition in *Drosophila melanogaster* Meig. *Monit. Zool. Ital.* 5: 215–222.
- Cha, D. H., T. Adams, H. Rogg, and P. J. Landolt. 2012. Identification and field evaluation of fermentation volatiles from wine and vinegar that mediate attraction of spotted wing drosophila, *Drosophila suzukii*. *J. Chem. Ecol.* 38: 1419–1431.
- Cha, D. H., S. P. Hesler, R. S. Cowles, H. Vogt, G. M. Loeb, and P. J. Landolt. 2013. Comparison of a synthetic chemical lure and standard fermented baits for trapping *Drosophila suzukii* (Diptera: Drosophilidae). *Environ. Entomol.* 42: 1052–1060.
- Cini, A., C. Ioriatti, and G. Anfora. 2012. A review of the invasion of *Drosophila suzukii* in Europe and a draft research agenda for integrated pest management. *B. Insectol.* 65: 149–160.
- Clancy, K. M., and P. W. Price. 1987. Rapid herbivore growth enhances enemy attack: Sublethal plant defenses remain a paradox. *Ecology* 68: 733–737.
- Foster, S. P., and M. O. Harris. 1997. Behavioral manipulation methods for insect pest-management. *Annu Rev Entomol.* 42: 123–146.
- Haribal, M., and P. Feeny. 2003. Combined roles of contact stimulant and deterrents in assessment of host-plant quality by ovipositing zebra swallowtail butterflies. *J. Chem. Ecol.* 29: 653–670.
- Haviland, D. R., and E. H. Beers. 2012. Chemical control programs for *Drosophila suzukii* that comply with international limitations on pesticide residues for exported sweet cherries. *J. Integr. Pest Manag.* 3: F1–F6.
- Hottel, B. A., J. L. Spencer, and S. T. Ratcliffe. 2015. Trapping *Drosophila repleta* (Diptera: Drosophilidae) using color and volatiles. *Fla. Entomol.* 98: 272–275.
- Iglesias, L. E., T. W. Nyoike, and O. E. Liburd. 2014. Effect of trap design, bait type, and age on captures of *Drosophila suzukii* (Diptera: Drosophilidae) in berry crops. *J. Econ. Entomol.* 107: 1508–1518.
- Kirkpatrick, D. M., P. S. McGhee, S. L. Hermann, L. J. Gut, and J. R. Miller. 2015. Alightment of spotted wing drosophila (diptera: Drosophilidae) on odorless disks varying in color. *Environ. Entomol.* 1: 7.
- Kleiber, J. R., C. R. Unelius, J. C. Lee, D. M. Suckling, M. C. Qian, and D. J. Bruck. 2014. Attractiveness of fermentation and related products to spotted wing drosophila (Diptera: Drosophilidae). *Environ. Entomol.* 43: 439–447.
- Landolt, P. J., T. Adams, and H. Rogg. 2012a. Trapping spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), with combinations of vinegar and wine, and acetic acid and ethanol. *J. Appl. Entomol.* 136: 148–154.
- Landolt, P. J., T. Adams, T. S. Davis, and H. Rogg. 2012b. Spotted wing drosophila, *Drosophila suzukii* (Diptera: Drosophilidae), trapped with combinations of wines and vinegars. *Fla. Entomol.* 95: 326–332.
- Lawrence, W. S. 1982. Sexual dimorphism in between and within patch movements of a monophagous insect: Tetraopes (Coleoptera: Cerambycidae). *Oecologia* 53: 245–250.
- Lee, J. C., D. J. Bruck, H. Curry, D. Edwards, D. R. Haviland, R. A. Van Steenwyk, and B. M. Yorgey. 2011. The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. *Pest Manag. Sci.* 67: 1358–1367.
- Lee, J. C., H. J. Burrack, L. D. Barrantes, E. H. Beers, A. J. Dreves, K. A. Hamby, D. R. Haviland, R. Isaacs, T. A. Richardson, P. W. Shearer, et al. 2012. Evaluation of monitoring traps for *Drosophila suzukii* (Diptera: Drosophilidae) in North America. *J. Econ. Entomol.* 105: 1350–1357.
- Lee, J. C., P. W. Shearer, L. D. Barrantes, E. H. Beers, H. J. Burrack, D. T. Dalton, A. J. Dreves, L. J. Gut, K. A. Hamby, D. R. Haviland, et al. 2013. Trap designs for monitoring *Drosophila suzukii* (Diptera: Drosophilidae). *Environ. Entomol.* 42: 1348–1355.
- Lee, J. C., A. J. Dreves, A. M. Cave, S. Kawai, R. Isaacs, J. C. Miller, S. Van Timmeren, and D. J. Bruck. 2015. Infestation of wild and ornamental non-crop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). *Ann. Entomol. Soc. Am.* 108: 117–129.
- Lelito, J. P., I. Fraser, V. C. Mastro, J. H. Tumlinson, K. Böröczky, and T. C. Baker. 2007. Visually mediated ‘paratrooper copulations’ in the mating behavior of *Agrilus planipennis* (Coleoptera: Buprestidae), a highly destructive invasive pest of North American ash trees. *J. Insect Behav.* 20: 537–552.
- Lelito, J. P., I. Fraser, V. C. Mastro, J. H. Tumlinson, and T. C. Baker. 2008. Novel visual-cue-based sticky traps for monitoring of emerald ash borers, *Agrilus planipennis* (Col., Buprestidae). *J. Appl. Entomol.* 132: 668–674.
- Mattson, W. J. Jr. 1980. Herbivory in relation to plant nitrogen content. *Annu Rev. Ecol. Evol. Syst.* 11: 119–161.
- Mazomenos, B. E., A. Pantazi-Mazomenou, and D. Stefanou. 2002. Attract and kill of the olive fruit fly *Bactrocera oleae* in Greece as a part of an integrated control system. *IOBC WPRS Bull.* 25: 137–146.
- Morrison, W. R., D. H. Lee III, W. H. Reissig, D. Combs, K. Leahy, A. Tuttle, D. Cooley, and T. C. Leskey. 2016. Inclusion of specialist and generalist stimuli in attract-and-kill programs: Their relative efficacy in apple maggot fly (Diptera: Tephritidae) pest management. *Environ. Entomol.* 45: 974–982.
- Nakagawa, S., R. J. Prokopy, T. T. Wong, J. R. Ziegler, S. M. Mitchell, T. Urugo, and E. J. Harris. 1978. Visual orientation of *Ceratitis capitata* flies to fruit models. *Entomol. Exp. Appl.* 24: 193–198.
- Owens, E. D., and R. J. Prokopy. 1986. Relationship between reflectance spectra of host plant surfaces and visual detection of host fruit by *Rhagoletis pomonella* flies. *Physiol. Entomol.* 11: 297–307.
- Pickering, C. M., and M. Stock. 2003. Insect colour preference compared to flower colours in the Australian Alps. *Nordic J. Bot.* 23: 217–223.
- Prokopy, R. J. 1968. Sticky spheres for estimating apple maggot adult abundance. *J. Econ. Entomol.* 61: 1082–1085.
- Prokopy, R. J. 1991. A small low-input commercial apple orchard in eastern North America: management and economics. *Agric. Ecosyst. Environ.* 33: 353–362.

- Prokopy, R. J., and E. D. Owens. 1978. Visual generalist with visual specialist phytophagous insects: Host selection behaviour and application to management. *Entomol. Exp. Appl.* 24: 609–620.
- Prokopy, R. J., and J. Mason. 1996. Behavioral control of apple maggot flies. pp. 555–559. *In* B. A. McPherson and G. J. Steck, (eds.), *Fruit fly pests a world assessment of their biology and management*. St. Lucie Press, Delray Beach, FL.
- Prokopy, R. J., M. Christie, S. A. Johnson, and M. T. O'Brien. 1990. Transitional step toward second-stage integrated management of arthropod pests of apple in Massachusetts orchards. *J. Econ. Entomol.* 83: 2405–2410.
- Raubenheimer, D., and D. Tucker. 1997. Associative learning by locusts: Pairing of visual cues with consumption of protein and carbohydrate. *Anim. Behav.* 54: 1449–1459.
- Raese, J. T., S. R. Drake, and E. A. Curry. 2007. Nitrogen fertilizer influences fruit quality, soil nutrients and cover crops, leaf color and nitrogen content, biennial bearing and cold hardness of 'Golden Delicious'. *J. Plant Nutr.* 30: 1585–1604.
- Reed, M. R. 1938. The olfactory reactions of *Drosophila melanogaster* Meigen to the products of fermenting banana. *Physiol. Zool.* 11: 317–325.
- Reissig, W. H., B. L. Fein, and W. L. Roelofs. 1982. Field tests of synthetic apple volatiles as apple maggot (Diptera: Tephritidae) attractants. *Environ. Entomol.* 11: 1294–1298.
- Renkema, J. M., R. Buitenhuis, and R. H. Hallett. 2014. Optimizing trap design and trapping protocols for *Drosophila suzukii* (Diptera: Drosophilidae). *J. Econ. Entomol.* 107: 2107–2118.
- Robacker, D. C. 1992. Effects of shape and size of colored traps on attractiveness to irradiated, laboratory-strain Mexican fruit flies (Diptera: Tephritidae). *Fla. Entomol.* 230–241.
- Roitberg, B. D. 1985. Search dynamics in fruit-parasitic insects. *J. Insect Physiol.* 31: 865–872.
- Rull, J., and R. J. Prokopy. 2000. Attraction of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae) of different physiological states to odour-baited traps in the presence and absence of food. *B. Entomol. Res.* 90: 77–88.
- Stökl, J., A. Strutz, A. Dafni, A. Svatos, J. Doubsky, M. Knaden, S. Sachse, B. S. Hansson, and M. C. Stensmyr. 2010. A deceptive pollination system targeting drosophilids through olfactory mimicry of yeast. *Curr. Biol.* 20: 1846–1852.
- Van Timmeren, S., and R. Isaacs. 2013. Control of spotted wing drosophila, *Drosophila suzukii*, by specific insecticides and by conventional and organic crop protection programs. *Crop Prot.* 54: 126–133.
- Walsh, D. B., M. P. Bolda, R. E. Goodhue, A. J. Dreves, J. Lee, D. J. Bruck, V. M. Walton, S. D. O'Neal, and F. G. Zalom. 2011. *Drosophila suzukii* (Diptera: Drosophilidae): invasive pest of ripening soft fruit expanding its geographic range and damage potential. *J. Integr. Pest Manag.* 2: 1–7.
- Wave, H. E. 1964. Effect of bait-trap color on attractancy to *Drosophila melanogaster*. *J. Econ. Entomol.* 57: 295–296.
- West, A. S. 1961. Chemical attractants for adult *Drosophila* species. *J. Econ. Entomol.* 54: 677–681.
- Wright, S. E., T. C. Leskey, I. Jacome, J. C. Pinero, and R. J. Prokopy. 2012. Integration of insecticidal, phagostimulatory, and visual elements of an attract and kill system for apple maggot fly (Diptera: Tephritidae). *J. Econ. Entomol.* 105: 1548–1556.