



## Pest Management

# Effects of Color Attributes on Trap Capture Rates of *Chrysobothris femorata* (Coleoptera: Buprestidae) and Related Species

Cynthia L. Perkovich,<sup>1,✉</sup> Karla M. Adesso,<sup>1,✉</sup> Joshua P. Basham,<sup>1</sup> Donna C. Fare,<sup>2</sup> Nadeer N. Youssef,<sup>1</sup> and Jason B. Oliver,<sup>1,3,✉</sup>

<sup>1</sup>Department of Agricultural and Environmental Sciences, College of Agriculture, Tennessee State University, Otis L. Floyd Nursery Research Center (TSU-NRC), 472 Cadillac Lane, McMinnville, TN 37110, USA, <sup>2</sup>USDA-ARS National Arboretum, Otis L. Floyd Nursery Research Center, 472 Cadillac Lane, McMinnville, TN, USA, and <sup>3</sup>Corresponding author, e-mail: [joliver@tnstate.edu](mailto:joliver@tnstate.edu)

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### Abstract

*Chrysobothris* spp. (Coleoptera: Buprestidae) and other closely related buprestids are common pests of fruit, shade, and nut trees in the United States. Many *Chrysobothris* spp., including *Chrysobothris femorata*, are polyphagous herbivores. Their wide host range leads to the destruction of numerous tree species in nurseries and orchards. Although problems caused by *Chrysobothris* are well known, there are no reliable monitoring methods to estimate local populations before substantial damage occurs. Other buprestid populations have been effectively estimated using colored sticky traps to capture beetles. However, the attraction of *Chrysobothris* to specific color attributes has not been directly assessed. A multi-color trapping system was utilized to determine color attraction of *Chrysobothris* spp. Specific color attributes (lightness [ $L^*$ ], red to green [ $a^*$ ], blue to yellow [ $b^*$ ], chroma [ $C^*$ ], hue [ $h^*$ ], and peak reflectance [ $PR$ ]) were then evaluated to determine beetle responses. In initial experiments with mostly primary colors, *Chrysobothris* were most attracted to traps with red coloration. Thus, additional experiments were performed using a range of trap colors with red reflectance values. Among these red reflectance colors, it was determined that the violet range of the electromagnetic spectrum had greater attractance to *Chrysobothris*. Additionally, *Chrysobothris* attraction correlated with hue and  $b^*$ , suggesting a preference for traps with hues between red to blue. However, males and females of some *Chrysobothris* species showed differentiated responses. These findings provide information on visual stimulants that can be used in *Chrysobothris* trapping and management. Furthermore, this information can be used in conjunction with ecological theory to understand host-location methods of *Chrysobothris*.

**Key words:** beetle, flatheaded borer, reflectance, sequential cues hypothesis, trapping method

Metallic wood-boring beetles (Coleoptera: Buprestidae) are a large family with ~15,000 species worldwide (750 in North America) (Bellamy and Volkovitsh 2016, Tong et al. 2021), some of which are significant pests of woody plants (Lebude and Adkins 2014, Haack and Petrice 2019). The larvae of buprestids cause the most damage, typically tunneling and feeding just beneath the bark of roots, trunks, and branches (Bellamy and Volkovitsh 2016). Most species attack dead or dying plant material, but some can girdle and kill apparently healthy trees (Moraal and Hilszczanski 2000, Redilla and McCullough 2017).

Most recent studies conducted on buprestid beetles have focused on a few economically important species like emerald ash borer (*Agrilus plannipennis* Fairmaire) (Coleoptera: Buprestidae) (Imrei et al. 2020a). However, several less documented buprestid species (Coleoptera: Buprestidae) such as the flatheaded appletree borer (*Chrysobothris femorata* Olivier) (Potter et al. 1988, Dawadi et al. 2019), the Pacific flatheaded borer (*Chrysobothris mali* Horn) (Acheampong et al. 2016), and the bronze birch borer (*Agrilus anxius* Gory) (Haack and Petrice 2019) routinely cause serious damage to production nursery or landscape plantings, often during

the first season following transplant when trees are under establishment stress.

Closely related species in the *C. femorata* complex are serious pests of landscape and nursery trees (Potter et al. 1988, Oliver et al. 2010). These species frequently attack newly transplanted trees in nursery and orchard production and will also damage branches of established orchard trees (Baspinar et al. 2018). The damage from flatheaded borers is unapparent until the larva becomes large enough to produce visible injury on the trunk surface (Oliver et al. 2010, LeBude and Adkins 2014). Death of the subsurface vascular tissues by larval feeding often causes visible bark surface splits, darkened and discolored bark, or plant dieback. Infestations may not be apparent until after adult beetles emerge, which leave behind a characteristic D-shaped exit hole. Damage by the larvae can kill the tree or make nursery trees unmarketable. Other members of this family can reduce the value of harvested logs and lumber (Haack et al. 2002, 2014) or reduce yields of fruits and nuts when branches are damaged (Andrews et al. 2017, Beers 2017). In middle Tennessee, Woodiel (1979) reported infestation rates of maple liners by *C. femorata* to be from 0 to 100%, and Fare (2015) found nursery damage on flowering dogwood (*Cornus florida* L.) (Cornales: Cornaceae) and maple (*Acer* spp.) (Sapindales: Sapindaceae) trees ranging up to 26%. Furthermore, in the western United States, another *Chrysobothris* species (*C. mali*) has caused orchard losses ranging from 35% in hazelnut (*Corylus avellana* L. [Fagales: Betulaceae]) to 100% in *Prunus* spp. (Burke and Boving 1929, Wiman et al. 2019).

It is widely acknowledged that many wood-boring beetles use color as a visual cue to locate hosts and potential mates (e.g., Francese et al. 2005, Petrice et al. 2013, Imrei et al. 2020a,b). However, recent research suggests that understanding borer perception mechanisms and interpretation of color may be more important than color attraction alone (Crook et al. 2009, Domingue et al. 2016, Cavaletto et al. 2020). Color attributes, as defined by the CIE (Commission Internationale de l'Éclairage, or International Commission on Illumination)  $L^*a^*b^*$  color space models (i.e., lightness [ $L^*$ ], red to green [ $a^*$ ], blue to yellow [ $b^*$ ], chroma [ $C^*$ ], hue [ $h^*$ ], and peak reflectance [ $PR$ ]; see Table 1), are useful in parsing color preferences of buprestids and other wood-boring beetles. Beetle physiology allows for the recognition of color attributes, which may affect visual recognition (Meglic et al. 2020, Zhi-zhi et al. 2021). For example, in the case of *Dendroctonus frontalis* Zimmerman (Coleoptera: Curculionidae: Scolytinae), reflectance was a better predictor for capture rates than absolute color (Strom and Goyer 2001). Furthermore, perception of colors may catalyze behavioral responses (Francese et al. 2010, Domingue et al. 2016). Domingue et al. (2016) found that male *Agrilus angustulus* Illiger (Coleoptera: Buprestidae) have a spectral preference for female color morphs with higher chroma values. In this scenario, color attributes can act as a mechanism to alter male sexual behaviors.

Much of our current understanding of color attraction and trapping methods for buprestids arose from studies performed on the genus *Agrilus* in forest systems (Imrei et al. 2020a). Many *Agrilus* spp. are attracted to green traps (Francese et al. 2010, Petrice et al. 2013, Petrice and Haack 2015, Rassati et al. 2019, Rutledge 2020). Trapping methods also have been researched on other buprestid genera such as *Coreaebus* in oak forests (e.g., Fürstenau et al. 2015) and *Ovalisia* (Nitzu et al. 2016). As with *Agrilus*, other buprestid genera show an attraction to specific colors (Petrice et al. 2013, Cavaletto et al. 2020). Much of this buprestid trapping research has been performed in forested systems (e.g., Fürstenau et al. 2015, Imrei et al. 2020b), where light penetration through thicker forest canopies can alter color reflectance and affect perception. It is important to determine if *Chrysobothris* attraction patterns also extend to more open landscape settings such as nurseries. There are several reports of *Chrysobothris* spp. being trapped in studies targeting other forest pests (e.g., Varandi et al. 2018, Westcott et al. 2018, Cavaletto et al. 2020). However, the *Chrysobothris* spp. caught were not the focus of the trapping study. Furthermore, studies have reported *Chrysobothris* spp. captures on very different trap types. For example, Varandi et al. (2018) reported catching *Chrysobothris affinis* Fabricius (Coleoptera: Buprestidae) most effectively on red sticky traps, and Westcott et al. (2018) found *Chrysobothris rugosiceps* Melsheimer (Coleoptera: Buprestidae) in black Lindgren funnel traps, baited with  $\alpha$ -pinene and ethanol.

To expand knowledge on *Chrysobothris* spp. trap preference, experiments were designed to determine if *Chrysobothris* spp. and related buprestid nursery pests are attracted to specific color attributes as is the case with many related buprestids. The objective of this study was to evaluate *Chrysobothris* response to traps simulating nursery tree trunks with various primary colors (i.e., multi-color test). Following the initial multi-color test objective, a secondary objective was to evaluate *Chrysobothris* response to traps with a wider range of red reflectance attributes (i.e., red-reflectance color test). For both the multi-color and the red-reflectance tests, we predicted that color attributes (lightness [ $L^*$ ], red to green [ $a^*$ ], blue to yellow [ $b^*$ ], chroma [ $C^*$ ], hue [ $h^*$ ], and peak reflectance [ $PR$ ]; see Table 1 for definitions) would be correlated with trap success for various *Chrysobothris* species. Understanding how color attributes affect buprestid trapping success may provide better monitoring tools for nursery, orchard, and landscape settings.

## Methods

### Multi-Colored Sticky Traps

To identify potential attractive trap colors for *Chrysobothris* and related buprestids under nursery field conditions in the initial study, primary color space colors of red, green, yellow, and blue, as well

**Table 1.** Definitions and abbreviations of color attribute terms analyzed and discussed in this study

Term	Abbreviation	Definition <sup>a</sup>
Lightness	$L^*$	Visual perception of luminance of an object (lightness or darkness) on the z-axis of the CIE color space
$a^*$	$a^*$	Range from red (+) to green (-) on y-axis of the CIE color space
$b^*$	$b^*$	Range from yellow (+) to blue (-) on the x-axis of the CIE color space
Chroma	$C^*$	Range in brightness (+) to dullness (-) of a visual cue
Hue	$h^*$	Origin of the color or the underlying base color
Peak reflectance	$PR$	Wavelength ( $\lambda$ ) where most reflectance is observed for a specific color

<sup>a</sup> Definitions are provided by the CIE color space model on the Konica Minolta Sensing Americas, INC., website: [www.sensing.konicaminolta.com](http://www.sensing.konicaminolta.com)

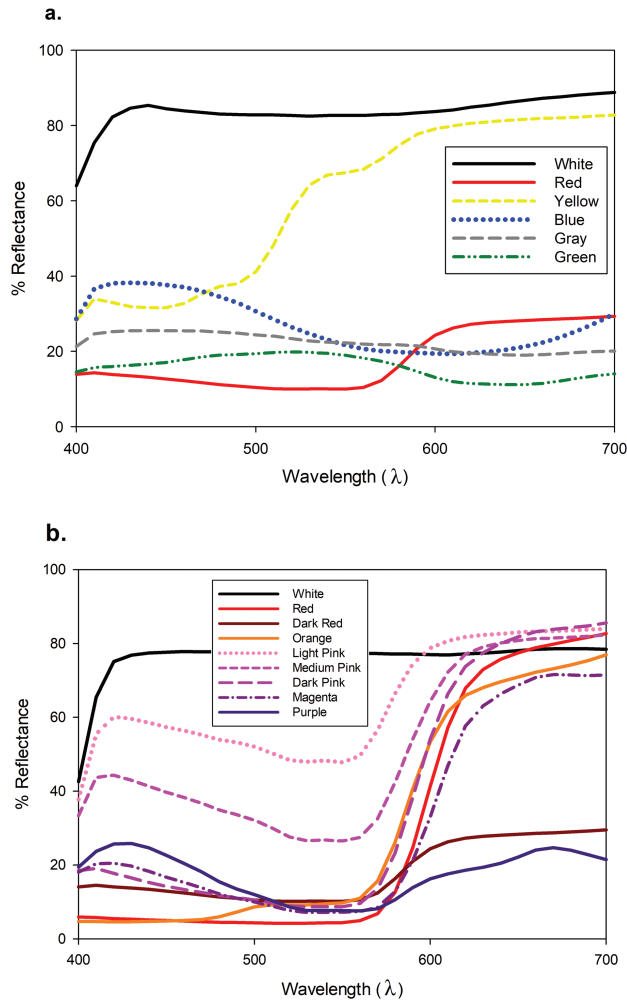
as white (reflects in all visible color wavelengths) and gray (to simulate a common bark color) were selected. Because this was an initial study to look at color cues, stock-vinyl wall liner (pattern# 85013, Graham & Brown Inc., Monroe Township, NJ) with a matt finish was used. The mean trap color attributes and peak reflectance spectrum for each color (mean reflectance values shown in Fig. 1a; mean  $L^*$ ,  $a^*$ ,  $b^*$ ,  $C^*$ , and  $h^*$  for these colors are given in Table 2) were recorded using a portable spectrophotometer (CM2600d, Konica Minolta Sensing Americas, Inc. Ramsey, NJ). Five scans of

each color were averaged for the spectrophotometer measurements. The settings for the spectrophotometer were observer illuminant Daylight 65, observer angle at 10° (CIE1964), specular component included (SCI) and UV at 100% (see Werle et al. 2014 for further details). Spectrophotometer measurements were taken in stable laboratory conditions.

Traps were established at the Tennessee State University Otis L. Floyd Nursery Research Center (NRC), McMinnville, TN from 2001 to 2002 using a sticky trap that simulated a sapling tree (Supp Fig. 1 [online only]). Before installation, plots were initially cleared using Roundup (1.5% solution) (Bayer CropScience, St. Louis, MO). Once plots were sufficiently cleared, Surflan (applied at 4.48 kg active ingredient/hectare) (United Phosphorous, King of Prussia, PA), Pendulum 60 WDG (3.70 kg/hectare) (BASF, Research Triangle Park, NC), and Gallery (0.84 kg/hectare) (Corteva Agriscience, Indianapolis, IN) preemergent herbicides were applied. Individual sticky traps were made from 0.9 m long steel rods (i.e., 3 ft rebar). Wallpaper strips ~7 cm wide were folded longitudinally with a 0.6 cm diameter (approximately the diameter of some nursery trees at that height) and stapled along the cut sides to form an elongated ‘tear-drop’ shaped tube. To simulate young tree silhouettes, wallpaper tubes were sheathed over metal stakes that had been driven into the ground two weeks after initial weed clearing. A 36 cm diameter geotextile disk was placed at the base of each metal stake and held in place by landscaping staples to prevent vegetation from growing around and obscuring the trap visibility (Supp Fig. 1 [online only]). Rows were spaced 91 cm apart, and traps were spaced 58 cm apart within rows to simulate nursery crop systems that generally have greater distance between tree row spacing than within tree row spacing. Break through weed growth was spot treated with Roundup. Traps were covered with Pestick insect glue (Hummert International Horticultural Supplies, Earth City, MO). Sticky traps (wallpaper tubes with glue) were replaced weekly. To minimize positional effects, trap treatments were arranged in a completely randomized design using 25 and 15 replicates per treatment color in 2001 and 2002, respectively. In 2001, trapping was initiated on 1 May and continued until 5 September (2 wk after the last buprestid capture). In 2002, trapping began on 15 April and continued until 7 October (2 wk after last buprestid capture). Trapping was initiated earlier in the season during 2002, since buprestids were captured on the first trapping period of 2001 indicating the beginning of the flight period may have been missed.

**Red-Reflecting Sticky Traps**

During 2002 and 2003, the Royal Horticultural Colour Chart (Voss 1992, 2002) was referenced to select a wide range of trap treatment colors with greater red reflectance based on higher buprestid collections on the red trap color used in the multi-colored test. The



**Fig. 1.** Average reflectance spectra of each trap color used (a) in the multi-color test and (b) the red color tests ( $n = 5$ ). Spectral measurements were taken using a portable CM2600d spectrophotometer, Konica Minolta Sensing Americas, Inc. Ramsey, NJ, USA.

**Table 2.** Mean color attributes ( $\pm$ SE); red to green ( $a^*$ ), blue to yellow ( $b^*$ ), chroma ( $C^*$ ), hue ( $h^*$ ), and lightness ( $L^*$ ) of each color used in the multi-color trapping tests

Color	$a^*$	$b^*$	$C^*$	$h^*$	$L^*$
Red	22.51 $\pm$ 0.21	4.52 $\pm$ 0.08	22.96 $\pm$ 0.19	11.37 $\pm$ 0.28	44.63 $\pm$ 0.64
Yellow	6.05 $\pm$ 0.17	33.67 $\pm$ 0.24	34.21 $\pm$ 0.27	79.83 $\pm$ 0.21	84.22 $\pm$ 0.38
Blue	-0.70 $\pm$ 0.11	-19.25 $\pm$ 0.11	19.26 $\pm$ 0.11	267.91 $\pm$ 0.33	55.91 $\pm$ 0.14
Green	-11.30 $\pm$ 0.07	-0.18 $\pm$ 0.11	11.30 $\pm$ 0.07	180.92 $\pm$ 0.56	48.64 $\pm$ 0.25
Gray	4.16 $\pm$ 0.19	17.13 $\pm$ 0.11	17.63 $\pm$ 0.15	76.39 $\pm$ 0.54	66.74 $\pm$ 0.56
White	1.10 $\pm$ 0.01	-0.27 $\pm$ 0.10	1.16 $\pm$ 0.02	342.78 $\pm$ 3.36	93.06 $\pm$ 0.08

**Table 3.** Mean color attributes ( $\pm$ SE); red to green ( $a^*$ ), blue to yellow ( $b^*$ ), chroma ( $C^*$ ), hue ( $h^*$ ), and lightness ( $L^*$ ) of each color used in the red color trapping tests

Color <sup>a</sup>	$a^*$	$b^*$	$C^*$	$h^*$	$L^*$
Light pink	18.89 $\pm$ 0.87	1.60 $\pm$ 0.04	18.96 $\pm$ 0.08	4.85 $\pm$ 0.11	80.99 $\pm$ 0.07
Medium pink	32.70 $\pm$ 0.06	0.20 $\pm$ 0.10	32.71 $\pm$ 0.06	144.36 $\pm$ 0.12	69.05 $\pm$ 0.17
Dark pink	52.59 $\pm$ 0.19	17.40 $\pm$ 0.16	55.40 $\pm$ 0.23	18.30 $\pm$ 0.19	54.70 $\pm$ 0.17
Magenta	48.60 $\pm$ 1.21	1.25 $\pm$ 0.26	48.62 $\pm$ 1.21	1.45 $\pm$ 0.29	47.95 $\pm$ 1.10
Red	22.42 $\pm$ 0.06	4.27 $\pm$ 0.09	22.82 $\pm$ 0.07	10.78 $\pm$ 0.22	44.85 $\pm$ 0.27
Dark Red	56.30 $\pm$ 0.21	29.16 $\pm$ 0.16	64.39 $\pm$ 0.19	26.17 $\pm$ 0.15	47.15 $\pm$ 0.58
Orange	45.62 $\pm$ 0.25	45.67 $\pm$ 0.32	64.60 $\pm$ 0.37	44.99 $\pm$ 0.15	53.69 $\pm$ 0.40
Purple	24.16 $\pm$ 0.13	-22.10 $\pm$ 0.13	32.74 $\pm$ 0.18	317.54 $\pm$ 0.03	40.49 $\pm$ 0.18
White	-0.61 $\pm$ 0.04	0.54 $\pm$ 0.08	0.83 $\pm$ 0.03	139.54 $\pm$ 5.70	90.58 $\pm$ 0.11

<sup>a</sup>These color selections were scanned from the Royal Horticultural Color Chart to creating matching paint values, and paints were applied to the white wallpaper strips from the multi-color test. White and red in the multi-colored test also were scanned and painted onto the white wallpaper strips.

selected color treatments (white, light pink, medium pink, dark pink, magenta, orange, purple, red, and dark red; [Supp Table 1 \[online only\]](#)) were then scanned to create custom matching paints (Sherwin-Williams, Cleveland, OH), which were painted onto white wallpaper strips (made from white wall liner used in multi-colored study) and used to form tubes as previously described ([Supp Fig 2 \[online only\]](#)). The red color used in the red-reflecting test was made from red paint that was created by scanning the red wallpaper used in the multicolor test; therefore, reflectance values for the red colors were not identical between the multicolor and red tests. The same mean trap color attributes previously described were determined for each trap color treatment (mean reflectance values shown in [Fig. 1b](#), mean  $L^*$ ,  $a^*$ ,  $b^*$ ,  $C^*$ , and  $h^*$  for these colors are given in [Table 3](#)). For each season, trapping continued until no more buprestids were caught. In 2002, trapping ran in unison with the multi-colored test and began on 15 April and continued until 7 October (2 wk after last buprestid capture). Traps were established in a separate plot from the multi-colored test using 15 replicates per color treatment arranged in a completely randomized design using the same trap spacing, glue, and plot maintenance procedures previously described. All specimens were collected and processed, as previously described. In 2003, traps were established from early March through late September.

### Trap Capture and Statistical Analyses

For both tests, all buprestid borers captured on traps were removed with forceps, positioned between a folded sheet of cut wax paper, and placed in a plastic sandwich bag labeled with the individual trap number and date. Specimens were stored frozen until they could be cleaned in Histo-Clear II (National Diagnostics, Atlanta, GA) for 24 h to remove glue, followed by 24 h in 90% ethyl alcohol to remove the Histo-Clear II. Buprestid specimens were pinned, labeled, and identified to species using [Downie and Arnette \(1995\)](#) with updates to the *C. femorata* species complex using [Wellso and Manley \(2007\)](#) in the fall of 2021. Specimens are currently housed in the NRC museum collection (codon TSRS; [Evenhuis 2021](#)). Data from both experiments were processed in the fall of 2021 when new funding allowed for an updated review of the museum collection.

For analysis, trap captures were grouped as total buprestids, genus *Chrysobothris*, or *C. femorata* complex. The *Chrysobothris* and *C. femorata* complex groupings allowed a greater analysis focus on effective traps for nursery pest species. Count data are usually fitted with a Poisson or negative binomial regression. The data were fitted to both a Poisson regression and a negative binomial regression model with a Likelihood Ratio Test to determine which model had the best

fit for the data ([Lawless 1987](#), [Lewis et al. 2010](#), [Putri et al. 2020](#)). The Poisson regression had the best fit ( $P = 0.233$ ), probably due to the equality of variance to the means in the models. For analysis of buprestid attraction to trap colors, a GLIMMIX procedure was used with the Poisson distribution to analyze the effects of color, with year as a random effect on trap collections. Data were pooled from the 2001 and 2002, and the 2002 and 2003 trap periods for the multi-colored tests and red-reflectance tests, respectively. The GLIMMIX models were followed with an LSD post hoc test for differences among colors in each of the respective tests. Chi-square tests with Holm's Sequential Bonferroni correction to control Type I error rate were used for evaluations of sex ratios across the three principal groups (buprestids, *Chrysobothris* genus, and *C. femorata* complex). Total counts of adult buprestids, *Chrysobothris* genus, and *C. femorata* complex groupings were compared by color and sex using Wilcoxon Rank Sum Tests, with Holm's Sequential Bonferroni correction to control Type I error rate. Pearson correlations were performed among color attributes ( $L^*$ ,  $a^*$ ,  $b^*$ ,  $C^*$ , and  $h^*$  and peak relative reflectance) and counts of females, males, and total (female and male) for buprestids, *Chrysobothris*, and members of the *C. femorata* complex. All analyses were performed in SAS 9.3 (SAS Institute, Cary, NC).

## Results

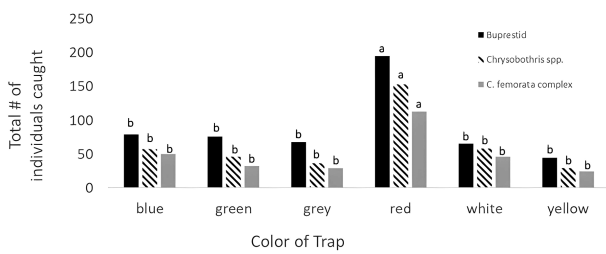
### Multi-Colored Sticky Traps

During the spring and summer of 2001 and 2002, red-colored sticky traps caught the greatest number of buprestids ([Fig. 2](#); [Tables 4 and 5](#), [Supp Tables 2–4 \[online only\]](#)), but significant differences were not detected for capture numbers by year (random effect) ([Table 4](#)). In total, 19 buprestid species were captured in middle Tennessee with these traps (see species list in [Supp Tables 2 and 3 \[online only\]](#)).

During 2001, analysis of all buprestids, *Chrysobothris* genus, and *C. femorata* complex indicated greater numbers captured on red traps than the other colors (i.e., blue, green, gray, white, and yellow;  $H = 40.4, 46.2, 34.0$ ,  $df = 5$ ,  $P < 0.001$ , respectively, also see [Supp Table 2 \[online only\]](#)). However, in the 2002 test, buprestids and *Chrysobothris* species were captured in higher numbers on red traps ( $H = 27.4$ ,  $df = 5$ ,  $P < 0.001$  and  $H = 19.0$ ,  $df = 5$ ,  $P = 0.002$ , respectively) than any other colors, but no differences were detected for *C. femorata* complex due to low trap collections ( $H = 6.9$ ,  $df = 5$ ,  $P = 0.227$ ).

The study also found differences in male and female sex ratios and response to trap colors. In both 2001 and 2002, females were caught in greater numbers than males (2001: 189 females vs 91 males; and 2002: 91 females vs 44 males;  $\chi^2 = 16.02$ ,  $df = 0.36$ ,  $P =$

0.002 [2001 and 2002 pooled data]). For female and male buprestid beetles, *Chrysobothris*, and members of the *C. femorata* complex, a negative relationship to color lightness was found ( $r = -0.56, P = 0.039$ ;  $r = -0.55, P = 0.021$ ;  $r = -0.51, P = 0.022$ , respectively, Table 6). There was also a negative relationship between female buprestids, and females in *C. femorata* complex and lightness ( $r = -0.62, P < 0.001$ ;  $r = -0.61, P < 0.001$ , respectively, Table 6), indicating that less reflective colors were preferred. Male beetles from the three categories did not share this relationship (all  $r$  range  $-0.36$  to  $-0.43$ ,  $P = 0.246$ , Table 6). Additionally, a strong positive correlation with  $a^*$  (green to red color space axis) was found between buprestids (total, female, and male), *Chrysobothris* spp. (total, female, and male), and individuals in the *C. femorata* complex (total, female, and male) (all  $r > 0.69, P < 0.05$ , Table 6), indicating a strong preference for red over green.



**Fig. 2.** Total counts of buprestids, *Chrysobothris* spp., and members of the *Chrysobothris femorata* complex caught in each color trap pooled from the 2001 and 2002 multi-color trapping tests. Each color was replicated 25 times (see Table 2 for color attribute qualities) from stock wall liner (see Methods for details). Different letters represent significant differences between numbers caught in a specific group, determined by an LSD post hoc analysis.

**Red-Reflecting Sticky Traps**

As in the multi-colored trap test, buprestid trap collections varied among trap colors (Table 4). However, overall numbers of buprestids collected were greater than in the multi-colored test. In both years, purple traps (i.e., traps that reflected in the violet range with reflectance peaking at 405 nm on the electromagnetic spectrum) caught the greatest number of total buprestids, *Chrysobothris*, or *C. femorata* complex species (Fig. 3; Table 7; Supp Table 5–7 [online only]), but there were significantly greater numbers of buprestids, *Chrysobothris*, and members in the *C. femorata* complex caught in 2002 than in 2003 (Supp Tables 5 and 6 [online only]). Using various shades of red sticky traps, significantly more female buprestids were caught than males in 2002 and 2003 (2002: 339 females and 195 males; 2003: 266 females and 102 males;  $\chi^2 = 100.12, df = 0.38, P = 0.009$  [2002 and 2003 pooled data]).

The strength of the correlation changed from year 2002 to 2003 in the relationship between individual color attributes and the number of beetles caught (Table 8). However, the total number of buprestids (total, female, and male), *Chrysobothris* spp. (total, female, and male), and members in the *C. femorata* complex (total, female, and male) had a strong negative correlation with  $b^*$  (yellow to blue color axis) ( $r$  range  $-0.60$  to  $-0.88$ , all  $P < 0.05$ , Table 8), indicating a preference for more blue reflectance. The strength of this relationship was greater for males than females of all three groups (males:  $r$  range  $-0.70$  to  $-0.76$ , all  $P < 0.05$ ; female  $r$  range  $-0.60$  to  $-0.72$ , all  $P < 0.05$ ). Additionally, strong positive correlations were found for male buprestids and total count (females and males) from the *C. femorata* complex with  $b^*$  (hue) ( $r = 0.67, P = 0.001$  and  $r = 0.58, P = 0.003$ , respectively, Table 8), indicating a preference for violet base colors (Tables 7; Supp Tables 5–7 [online only]). Males from the *C. femorata* complex also were positively correlated with peak reflectance ( $r = 0.62, P = 0.024$ ).

**Table 4.** Regression summary for GLIMMIX model of effect of color, year, and the interaction of color and year on buprestid, *Chrysobothris*, and members of the *C. femorata* complex

	Buprestid			<i>Chrysobothris</i>			<i>C. femorata</i>		
	df	F	P	df	F	P	df	F	P
<i>Multi-colored tests</i>									
Color <sup>a</sup>	5	31.78	<0.001	5	23.04	<0.001	5	9.68	<0.001
Year	1	3.58	0.06	1	0.03	0.87	1	1.03	0.31
Color*Year	5	3.95	0.002	5	3.45	0.01	5	5.48	<0.001
<i>Red-reflecting tests</i>									
Color <sup>b</sup>	9	23.38	<0.001	9	8.21	<0.001	9	3.18	0.001
Year	1	15.74	<0.001	1	75.67	<0.001	1	90.49	<0.001
Color*Year	9	6.57	<0.001	9	2.67	0.01	9	1.37	0.20

<sup>a</sup> Each color was replicated 25 times.

<sup>b</sup> Each color was replicated 9 times.

**Table 5.** Mean ( $\pm$ SE) buprestids, *Chrysobothris*, and members of the *C. femorata* complex caught in multi-colored sticky traps in 2001 and 2002

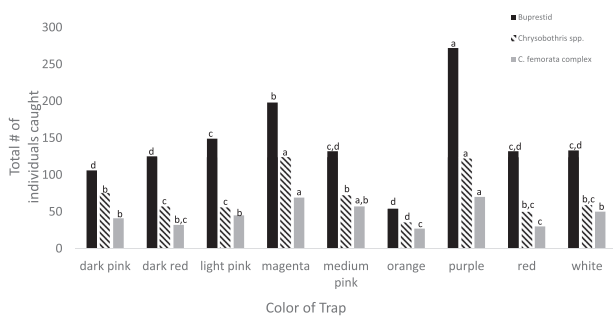
Taxonomic Group	Mean ( $\pm$ SE) Trapped					
	Red	Green	Blue	White	Yellow	Grey
Buprestids	5 $\pm$ 0.34a	2 $\pm$ 0.39b	2 $\pm$ 0.38b	1 $\pm$ 0.00b	1 $\pm$ 0.00b	1 $\pm$ 0.00b
<i>Chrysobothris</i>	5 $\pm$ 0.41a	1 $\pm$ 0.51b	2 $\pm$ 0.46b	1 $\pm$ 0.46b	1 $\pm$ 0.00b	1 $\pm$ 0.49b
<i>C. femorata</i> complex	4 $\pm$ 0.47a	0 $\pm$ 0.63b	1 $\pm$ 0.50b	1 $\pm$ 0.51b	0 $\pm$ 0.00b	1 $\pm$ 0.54b

Different letters represent statistically different means within rows. Each color was replicated 25 times. Because exact means indicate partial beetles, averages were rounded to the nearest whole number.

**Table 6.** Pearson correlations ( $r$ ) between color attributes red to green ( $a^*$ ), blue to yellow ( $b^*$ ), chroma ( $C^*$ ), hue ( $h^*$ ), lightness ( $L^*$ ), and peak reflectance ( $PR$ ) and sex of buprestids, *Chrysobothris* spp., and members of the *C. femorata* complex in the multi-color trapping test

	Buprestids			<i>Chrysobothris</i> spp.			<i>C. femorata</i> complex		
	F	M	T	F	M	T	F	M	T
$a^*$	<b>0.77*</b>	<b>0.75*</b>	<b>0.78*</b>	<b>-0.51*</b>	<b>0.74*</b>	<b>0.77*</b>	<b>0.79*</b>	<b>0.73*</b>	<b>0.78*</b>
$b^*$	-0.09	-0.30	-0.17	<b>-0.62*</b>	-0.31	-0.23*	-0.20	-0.37	-0.29*
$C^*$	0.23	0.02	0.15	<b>0.77*</b>	-0.01	0.09	0.17	-0.07	0.06
$h^*$	<b>-0.57*</b>	<b>-0.25*</b>	<b>-0.47*</b>	-0.18	<b>-0.24*</b>	<b>-0.41*</b>	<b>-0.50*</b>	-0.14	-0.34
$L^*$	<b>-0.62*</b>	<b>-0.43*</b>	<b>-0.56*</b>	0.15	<b>-0.43*</b>	<b>-0.55*</b>	<b>-0.61*</b>	<b>-0.36*</b>	<b>-0.51*</b>
$PR$	-0.48	-0.27	-0.40	<b>-0.55*</b>	-0.22	-0.42	<b>-0.50*</b>	-0.33	-0.25

Significant correlations ( $P < 0.05$ ) are indicated with “\*”, and strong correlations ( $> 0.50$  or  $< -0.50$ ) are in bold. F = female, M = male, T = total female + male.



**Fig. 3.** Total counts of buprestids, *Chrysobothris* spp., and members of the *Chrysobothris femorata* complex found in each color trap pooled from the 2002 and 2003 red-reflectance trapping tests. Each color was replicated 15 times (see Table 3 for color attribute qualities, and Supp Table 1 [online only] for details on paints used on wall liner). Different letters represent significant differences between numbers caught in a specific group, determined by an LSD post hoc analysis.

## Discussion

Ornamental tree nurseries are a commonly exploited larval habitat resource by *Chrysobothris* beetles. Research indicates *Chrysobothris* prefer to oviposit on the sunny sides of trees (Oliver et al. 2010, Seagraves et al. 2012, Dawadi et al. 2019). In lab observations, *Chrysobothris* adults are generally more active in sunny weather (C.L.P. and K.M.A., personal observations) and beetles in the genus are also less responsive to traps on cloudy days (J.B.O. and D.C.F., personal observations). Nursery rows allow more sunlight to reach trunk surfaces than in forested areas (Seagraves et al. 2012, Dawadi et al. 2019), potentially making nursery trees more attractive and suitable hosts. Management strategies need to account for mechanisms of host location in *Chrysobothris* to protect nursery trees. However, identifying host selection strategies in polyphagous insects can be difficult because of their ability to shift hosts based on local plant population densities and host quality (Jaenike 1990, Mitra et al. 2021). Because nurseries often plant the same species in designated blocks, they may provide a stronger host location signal (i.e., plant apparency, *sensu* Feeny 1976) than nearby forests that often have interspersed tree species.

## Color Preference

It is important to note that the glue used may have had an impact on the reflectance and visual cues (Crook et al. 2009). However, Crook et al. (2009) found that the effect of glue was negligible. Furthermore, the spectrophotometer measurements were recorded with the SCI

function, which negates surface appearance effects to measure true color. The conclusions from this study are therefore drawn with the assumption that differences in trap success are due to the base color of traps in these studies. In the multi-colored trapping test, genus *Chrysobothris* and buprestids at the family taxonomic level preferred a red trap color (peak reflectance of 700 nm) over other colors. For both the genus *Chrysobothris* and family Buprestidae levels, there was a strong, positive correlation with  $a^*$ , indicating higher values of  $a^*$  (i.e., more red reflectance) were more attractive traps. Contrastingly, in the red-reflectance test, the amount of red reflectance (indicated by positive  $a^*$  values) in a trap color did not correlate with trap captures. Instead, trap collections indicate preferences of buprestids to purple (peak reflectance of 405 nm) and those in the genus *Chrysobothris* (including those in the *C. femorata* complex) also preferred purple in addition to other colors (i.e., magenta [peak reflectance of 670 nm] and medium pink [peak reflectance of 660 nm]).

There was a divergence in the importance of individual color attributes at the buprestid family, *Chrysobothris* genus, and *C. femorata* complex taxonomic levels as well as between females and males in these levels. In the red-reflectance test, all trap colors had high red reflectance (except for white) compared to trap colors in the multi-colored test. Additionally, in the red-reflectance test, all three taxonomic levels were negatively correlated with  $b^*$ , suggesting a greater preference for traps with higher red and blue reflectance (i.e., hence the attraction to violet range colors like purple that fall in between red and blue on the  $L^*a^*b^*$  color space sphere). Changes from color preferences in the two experiments have shown that the preference for blue reflectance is context-dependent on red reflectance. However, the opposite is not true, and red reflectance is consistently important, where blue alone is not. Interestingly, hue and peak reflectance become correlated with trap captures in the red-reflectance tests. Reflectance is the amount of light that is reflected off the surface of an object, whereas peak reflectance refers to the primary wavelength that is being reflected. Males from the *C. femorata* complex showed a strong, positive correlation with the peak reflectance (Table 8), indicating an attraction to reflectance at longer wavelengths (i.e., red reflectance). Males from all three groups also were positively correlated with hue (Table 8; i.e., preferred a purer red base color). Amongst females, the genus *Chrysobothris* was the only group analyzed that was not correlated with hue (Table 8). Hue refers to the origin of the color or the underlying base color. In the red-color test, the hue was red (dark pink, dark red, light pink, light red, medium pink, and red) or violet (magenta and purple) for most of the colors (excluding orange and white). *C. femorata* complex members were more attracted to violet hues, but males of this group were more sensitive to the peak reflectance from the hue red.

**Table 7.** Mean ( $\pm$ SE) buprestids, *Chrysobothris*, and members of the *C. femorata* complex caught in red-reflectance sticky traps in 2002 and 2003

Taxonomic Group	Mean ( $\pm$ SE) Trapped								
	Purple	Magenta	Light Pink	Medium Pink	Dark Pink	Dark Red	Red	Orange	White
Buprestids	9 $\pm$ 0.22a	8 $\pm$ 0.24b	3 $\pm$ 0.25c	4 $\pm$ 0.25cd	3 $\pm$ 0.27d	3 $\pm$ 0.26d	2 $\pm$ 0.27cd	2 $\pm$ 0.32e	3 $\pm$ 0.00cd
<i>Chrysobothris</i>	6 $\pm$ 0.38a	6 $\pm$ 0.38a	2 $\pm$ 0.42b	4 $\pm$ 0.42c	3 $\pm$ 0.39c	2 $\pm$ 0.41b	2 $\pm$ 0.43bc	2 $\pm$ 0.49d	3 $\pm$ 0.00bc
<i>C. femorata</i> complex	4 $\pm$ 0.50a	4 $\pm$ 0.51a	2 $\pm$ 0.53b	3 $\pm$ 0.55ab	2 $\pm$ 0.52b	2 $\pm$ 0.56bc	1 $\pm$ 0.57c	1 $\pm$ 0.60c	3 $\pm$ 0.00b

Different letters represent statistically different means within rows. Each color was replicated 15 times. Because exact means indicate partial beetles, averages were rounded to the nearest whole number.

**Table 8.** Pearson correlations (*r*) between color attributes red to green (*a*\*), blue to yellow (*b*\*), chroma (*C*\*), hue (*h*\*), lightness (*L*\*), and peak reflectance (*PR*) and sex of buprestids, *Chrysobothris* spp., and members of the *C. femorata* complex in the red color trapping test

	Buprestids			<i>Chrysobothris</i> spp.			<i>C. femorata</i> complex		
	F	M	T	F	M	T	F	M	T
<i>a</i> *	0.09	0.00	-0.33*	0.20	-0.01	0.13	-0.01	-0.22	-0.10
<i>b</i> *	<b>-0.66*</b>	<b>-0.70*</b>	<b>-0.88*</b>	<b>-0.60*</b>	<b>-0.70*</b>	<b>-0.65*</b>	<b>-0.72*</b>	<b>-0.76*</b>	<b>-0.76*</b>
<i>C</i> *	0.03	-0.05	-0.37*	0.11	-0.06	0.05	-0.09	-0.31*	-0.19*
<i>h</i> *	<b>0.51*</b>	<b>0.67*</b>	<b>0.67*</b>	0.37*	<b>0.65*</b>	<b>0.48*</b>	<b>0.56*</b>	<b>0.57*</b>	<b>0.58*</b>
<i>L</i> *	-0.32*	-0.33*	-0.17	-0.30	-0.28	-0.31*	-0.01	0.14	0.05
<i>PR</i>	-0.29	-0.37	<b>-0.52*</b>	-0.16	-0.33	-0.24	-0.04	<b>0.62*</b>	-0.04

Significant correlations ( $P < 0.05$ ) are indicated with “\*”, and strong correlations ( $> 0.50$  or  $< -0.50$ ) are in bold. F = female, M = male, T = total female + male.

### Using Ecological Theory to Understand Color Preference

Ecological theories on host selection and insect physiology can be used to inform research decisions on pest-management and trapping strategies of *Chrysobothris* in nurseries. The sequential cues hypothesis (SCH) suggests that generalist insects initially use common cues of potential hosts to locate a general host habitat (Bruce and Pickett 2011, Wang et al. 2017, Silva and Clarke 2019). Once they are within the preferred habitat, generalists may use more specific components of the common attractant cues to locate hosts or use a completely different set of cues to orient to preferred hosts (Agrawal 1998, Silva and Clarke 2019). The SCH may provide a framework to explain variations in buprestid preference for individual color attributes between the multicolor and red-reflectance tests. However, to apply host locating theory, affinity for specific color attributes must first be understood. The trap collection totals among the various colors tested provide indirect empirical evidence of affinity for certain color attributes.

General correlations exist between the ecology of beetle families and colors that provide spatial orientation within the environment (Atkinson et al. 1988, Safranyik et al. 2000, Francese et al. 2008). Many studies have been successful at trapping wood boring beetles with red lures (e.g., Kerr et al. 2017, Cavaletto et al. 2021). Congruent with SCH, red reflectance may function as a common cue for locating potential host habitats because red reflectance increases in stressed plants (Carter and Estep 2002), which are often preferred hosts of buprestid beetles (Potter et al. 1988, McCullough et al. 2009). However, once inside a potential habitat, *Chrysobothris* and buprestids in general may be using a wider range of visual cues to locate specific host plants based on their ecological niche. For example, Poland et al. (2019) found that emerald ash borer females were attracted to purple traps hung in tree canopies whereas males were attracted to green traps. Male foraging and mate seeking behaviors may explain the attraction to green because males often forage and find females in tree canopies.

The attraction to purple cannot easily be explained by naturally occurring cues such as host or mate coloration. Some studies have suggested that the reflectance of bark (common hosts of buprestids) reflects similarly to the purple color cues (see Prokopy and Owens 1983, Strom et al. 1999, Campbell and Borden 2005). Many visual stimulants are associated with mate- or host-seeking behaviors (Wynne et al. 2020, van der Kooi et al. 2021). Polyphagous insects have evolved the ability to use color as a visual cue during mate and host selection (Bernays 2001), but their ability to process visual stimuli is limited to a specific range of the optical spectrum (Chittka and Menzel 1992, Kevan et al. 1996). Insect opsins, which are protein-coupled receptors, allow for the expression of sensitivity to various wavelengths. Opsins for detecting long wavelengths (infra-reds) are commonly found in many insect orders, but opsins that produce a sensitivity to short wavelengths (ultra-violet) are much less common (Briscoe and Chittka 2001, Porter et al. 2007). Recent studies of coleopteran opsin classes show a great diversity of spectral sensitivities (Crook et al. 2009, Jiang et al. 2014, Lord et al. 2016), and the buprestid family demonstrate unique opsin expressions that allow them to detect ultra-violet wavelengths (340 nm) (Crook et al. 2009, Lord et al. 2016). Furthermore, Lord et al. (2016) found that buprestids express multiple opsin classes resulting in many peak color sensitivities, suggesting visual stimulation from multiple colors. Ecological factors that favored the evolution of opsin adaptations are still not understood but other studies have produced similar results as this study, suggesting that buprestid beetles use multiple reflectance peaks as visual stimuli (e.g., Francese et al. 2010). Francese et al. (2010) noted that a blue color in their study had similar reflectance (430 nm) to the purple paint color used in this study but concluded the 3 times higher trap capture rate of emerald ash borer on the ‘TSU purple’ color was due to an additional visible red reflectance peak in the 650–670 nm range. Thus, Francese et al. (2010) findings were similar to this study in that both red and blue colors enhanced buprestid trap response, but blue alone was much less attractive.

To understand why purple is an attractant, more research is needed to analyze ecological pressures that caused adaptations to specific visual cues and stimulants. It may be that purple is reflected by conspecific *Chrysobothris*. If light reflects into the ultra-violet spectra (340 nm) from *Chrysobothris* elytra, this suggests that the attraction to purple is related to mate-selecting behaviors. For example, Crook et al. (2009) found that female emerald ash borers responded to ultra-violet wavelengths (340 nm) and that the abdomens of male emerald ash borers peaked in reflectance in the same spectral region. There are no studies that have investigated the reflection of *Chrysobothris* anatomy.

### Possible Secondary Cues for Host Selection Inside the Suitable Environment

The SCH model suggests there may be additional environmental cues that are used by generalist herbivores, such as *Chrysobothris*, after locating a suitable host habitat. Other environmental cues may include plant volatile emissions (kairomones) or localized visual stimulants that are required for a beetle to orient to a potential host (Pierik et al. 2014). Several studies have had success trapping other buprestid beetles by using a combination of visual and olfactory plant stimuli (Ryall et al. 2013, Ryall 2015, Silk et al. 2020). Alternatively, these cues may not necessarily be related to host detection (Pureswaran and Poland 2009, Domingue et al. 2011, Silk et al. 2011). Beetles also may use conspecific visual, audio, and olfactory stimuli (Fenton and Maxwell 1937, Pureswaran and Poland 2009, Silk and Ryall 2015). For example, *Chrysobothris* oviposition occurs on the sunny sides of trees (Oliver et al. 2010, Seagraves et al. 2012, Dawadi et al. 2019), and groups of beetles have been observed flying above exposed wood piles. Sunlight reflected from conspecifics may act as a visual cue, guiding individuals to specific tree hosts. Additionally, *C. femorata* display an abdomen tapping behavior (Fenton and Maxwell 1937), and this audible tapping may act as a signal to conspecifics once beetles have entered a suitable habitat. Olfactory stimuli also have been observed in host-locating behaviors (e.g., Grant et al. 2011, Silk et al. 2011). Silk et al. (2011) found that a volatile pheromone emitted by emerald ash borer increased attraction to specific host foliar volatiles. Female and male emerald ash borers were successfully trapped using different combinations of visual and olfactory cues (Grant et al. 2011), indicating secondary visual stimuli may also influence beetle preference.

Additional visual or olfactory cues may be necessary to increase the attractiveness of traps monitoring *Chrysobothris* in nursery systems. Our study lays a foundation to improve trap optimization for *Chrysobothris* in nursery settings. Pest management strategies that incorporate traps with a violet base color should see improved *Chrysobothris* captures, particularly females. Further research is needed to elucidate the relationship between violet hue, female *Chrysobothris* behavior and physiology. For now, there are commercially available plastic traps that are used for emerald ash borer (as described in Francese et al. 2010; 2013a,b) that are similar in color as the purple used in the red-reflectance tests of this study. However, additional spectral analysis of hosts, habitats and conspecific anatomy may identify a source of selective pressure responsible for the observed sex differences in *Chrysobothris* visual preferences. Such information will both increase our understanding of the complex nature of color preference in wood boring beetles and aid in the development of better tools to manage them.

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### Data Availability

Data will be made available upon acceptance of manuscript.

### Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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