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Color Preference of Three Parasitoids Imported to the Americas for the Biological Control of the Coffee Berry Borer (Curculionidae: Scolytinae)

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Abstract

The African parasitoids *Cephalonomia stephanoderis* Waterston (Bethylidae: Hymenoptera), *Prorops nasuta* Betrem (Bethylidae: Hymenoptera), and *Phymastichus coffea* LaSalle (Eulophidae: Hymenoptera) are biological control agents of the coffee berry borer (Coleoptera: Curculionidae). In this study, we investigated in laboratory the female behavioral responses of these parasitoids to 14 different wavelengths (340–670 nm) against a control (570 nm, yellow). When nonchooser females were included in the analysis, none parasitoids species showed a preference between 340, 350, 370, 460, 490, 520, 540, 590, 640, and 650 nm with respect to the control wavelength. In contrast, the three species of parasitoids were more attracted to wavelengths of 380, 400, and 420 nm than the control wavelength. *Phymastichus coffea* and *P. nasuta* were more attracted to the wavelength of 400 and 420 nm compared to *C. stephanoderis*. At 380 nm, *P. coffea* and *C. stephanoderis* wasps showed the higher responses in comparison to *P. nasuta* females. When nonchooser wasps were excluded from the analysis, we observed other differences among the parasitoid species. For instance, *P. coffea* were more attracted to 490–540 nm than to 570 nm, whereas the bethylids did not discriminate between 490–540 nm or 570 nm. Our results are discussed in relation to possible implications associated with the vision of these parasitoid species.

Resumen

Los parasitoides africanos *Cephalonomia stephanoderis* Waterston (Bethylidae: Hymenoptera), *Prorops nasuta* Betrem (Bethylidae: Hymenoptera), y *Phymastichus coffea* LaSalle (Eulophidae: Hymenoptera) son agentes de control biológico de la broca del café (Coleoptera: Curculionidae). En este estudio, nosotros investigamos en laboratorio la respuesta comportamental de las hembras de esos parasitoides a 14 diferentes longitudes de onda (340–670 nm) contra un control (570 nm, amarillo). Cuando las hembras que no eligieron fueron incluidas en el análisis, ninguna de las especies de parasitoides mostró una preferencia entre 340, 350, 370, 460, 490, 520, 540, 590, 640, and 650 nm con respecto a la longitud de onda control. En contraste, las tres especies de parasitoides fueron más atraídos a longitudes de onda de 380, 400 y 420 nm que a la longitud de onda control. *Phymastichus coffea* y *P. nasuta* fueron atraídos a la longitud de onda de 400 y 420 nm comparado a *C. stephanoderis*. A 380 nm, las avispas *P. coffea* y *C. stephanoderis* mostraron la más alta respuesta en comparación con las hembras de *P. nasuta*. Cuando las avispas que no eligieron fueron excluidas del análisis, nosotros observamos otras diferencias entre las especies de parasitoides. Por ejemplo, *P. coffea* fue más atraído a 490–540 nm que a 570 nm, mientras que los betylidos no discriminaron entre 490–540 nm o 570 nm. Nuestros resultados son discutidos en relación a posibles implicaciones asociadas con la visión de estas especies de parasitoides.

Key words: wavelength, attraction, vision, Bethylidae, Eulophidae

Herbivorous and carnivorous insects may use chemical, visual, acoustic, or vibrational stimuli during the host-searching process (Schmidt et al. 1993). In most cases, the research to date has tended to focus on the role of chemical cues during host searching

by parasitoids. However, it is known that parasitoids can use visual cues (e.g., color, shape, brightness, or patterns of feeding damage) as well as other physical characteristics (e.g., surface structure, vibration) alone or in combination with chemical cues during host

location (Battaglia et al. 2000, Morehead and Feener 2000, Fischer et al. 2001, Graziosi and Rieske 2013). It is known that the sensitivity of the insect to the visible spectrum depends on a system of color photoreceptors (Menzel and Backhaus 1991). Therefore, a comparative study of color perception is required to determine the spectral properties, as an initial step in the analysis of insect vision. Most insects possess green (max 530 nm), blue (max 440 nm), and UV (max 350 nm) receptors (Briscoe and Chittka 2001). Chittka (1996) has suggested that the set of UV, blue, and green photoreceptors is an ancestral condition in the insects and that some lineages have lost or added receptors, presumably, as a result of different selection pressures.

The African parasitoids *Cephalonomia stephanoderis* Waterston (Bethylidae: Hymenoptera), *Prorops nasuta* Betrem (Bethylidae: Hymenoptera), and *Phymastichus coffea* LaSalle (Eulophidae: Hymenoptera) were imported into the American continent for biological control of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae) (Barrera et al. 1990, Infante et al. 1994a). The bethylid wasps search for their host inside the coffee berries and lay their eggs on *H. hampei* larvae and pupae (Barrera et al. 1990). In contrast, *P. coffea* is a free-living endoparasitoid because its adults never enter to the coffee berries and parasitizes to *H. hampei* adult just when the female colonizes the coffee berries (Infante et al. 1994a). Previous studies on host searching of these parasitoids have shown that bethylid species are attracted to full-grown larvae, pupae, and dust/frass (coffee berry powder mixed with coffee berry borer's feces) of *H. hampei* volatile compounds, while *P. coffea* is only attracted to mechanical damaged coffee berries and host dust/frass volatiles (Rojas et al. 2006, Chiu-Alvarado and Rojas 2008, Chiu-Alvarado et al. 2009). Nevertheless, the role of visual cues during the host location process of these three species has not been investigated.

In this study, we take the first step to understand the role of the visual cues during the host location processes of coffee berry borer parasitoids. Particularly, we compare the light color preferences of the three parasitoids in order to analyze their biological adaptations to the perception of color and to understand the way they use vision.

Materials and Methods

The Insects

Parasitoid females from the three species were obtained from stock cultures maintained at the El Colegio de la Frontera Sur laboratories. *Prorops nasuta*, *C. stephanoderis*, and *P. coffea* have been reared successively for more than 240, 300, and 220 generations, respectively, using a methodology previously described (Barrera et al. 1991, Infante et al. 1994b). These species were imported to Mexico from Africa in 1989 (*C. stephanoderis*) and 2000 (*P. nasuta* and *P. coffea*). Upon emergence, adult parasitoid females were placed together with males at a 1:1 sex ratio in plastic containers (12 cm diameter and 20 cm height) for 24 h at 27–30°C, 70–80% RH, and a photoperiod of 12:12 (L:D) h, conditioned by a fluorescent lamp (20 W). Parasitoids were fed with diluted honey. All female parasitoids used in the experiments were 2 d old. The insects were maintained in the darkness for an hour in the arena before being tested.

Light Response Measuring Device

Bioassays were conducted in a glass 'T' olfactometer (20 mm internal diameter), which were an adaptation of Brown et al.'s (1998) design (Fig. 1). The main arm of the apparatus was 30 mm long, with a side arm 50 mm long placed at the center. The main arm was divided into three equal sectors of 10 cm and secured horizontally to a wooden base. Band pass filters 20 nm (Andover Corp., Salem, NH) were placed at the ends of the main arm. The light was provided by two halogen lamps with the same intensity (150 W, OSRAM, Fiber-Lite PL-750, Munich, Germany). Light passing through the band pass filters was delivered to one end of the main arm via a fiber optic cable that was mounted outside the box. The intensity of both light sources in each fiber optic cable was adjusted to 2.3 mV using a solar cell and measured with a digital multimeter (Master Brand, Mod. MAS830L, Pittsburgh, PA), assuming that equal current will give equal intensity was used in all bioassays. The measures were performed controlling a power supply from a digital multimeter (Master Brand, Mod. MAS830L).

Bioassays Procedure

The behavioral responses of the parasitoids were evaluated by offering the females a choice of two wavelengths of equal quanta flux in a T-tube olfactometer (Brown et al. 1998). The bioassays were performed without airflow in a dark room, so the only sources of light consisted of the two light sources at each end of the main arm. During each bioassay, one end of the chamber was illuminated with a control wavelength (570 nm), as most insects possess photoreceptors to yellow color (Briscoe and Chittka 2001) and other parasitoid species are attracted to this color (Vargas et al. 1991, Brown et al. 1998, Ferreira et al. 2012), while the other was illuminated by one of 14 wavelengths ranging between 340 and 670 nm chosen in a random order (Table 1). A group of five females were chosen at random and introduced individually with a fine paintbrush into the side arm of the olfactometer, which was then sealed with a plastic strip. After starting each bioassay, the wasps were allowed to move freely inside the chamber for 5 min. At the end of the test, the room lights were switched on and the numbers of wasps near of both filters (control and treatment) were recorded. Those insects that remained in the central area of the T-tube (or the insects that did not cross the line that delimited the central area) were considered not attracted. The females were used only once and then discarded. For each wavelength tested, 10 replicates were performed. After five replicates, the position of the filters was exchanged, and after two wavelengths had been tested, the olfactometer was washed out with water and acetone and dried in oven at 100°C for at least 30 min in order to remove any scent traces left by the insects. In addition, the stimuli and the T-tube were changed alternately after each replicate to avoid positional bias. The bioassays were conducted between 1200 and 1600 h (local time) inside a room with a temperature of 26 ± 2°C and a RH of 60 ± 10% during the bioassays.

Statistical Analysis

Firstly, the responses of the three species toward the tested colors, toward the control, and nonchooser across all experimental wavelengths were compared with a chi-squared test using a 3 × 3 contingency table. In addition, excluding the nonchooser wasps, the number of females attracted to each wavelength was compared with those attracted to the control using a log-likelihood ratio test (*G*-test) with Williams's correction (Sokal and Rohlf 1995). All analyses were performed with R statistical software package version 3.6.2 (R Core Team 2019).

Results

When the responses (i.e., wavelength test, wavelength control, and nonchooser) of the three species were compared at each wavelength, the analysis showed that none parasitoids species made a
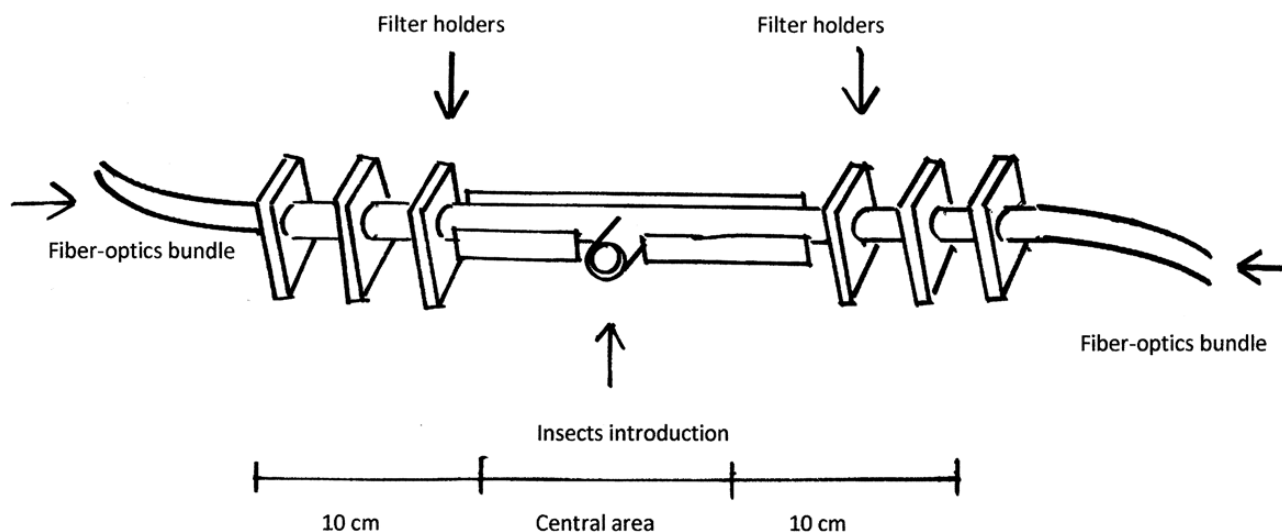
Fig. 1. T-tube olfactometer used in testing phototactic response of three species coffee berry borer parasitoids to selected wavelength regions of colored light (modified from Brown et al. 1998).

choice between treatment (340, 350, 370, 460, 490, 520, 540, 590, 640, and 650 nm) or control wavelength (570 nm). The analysis also showed that the three species of parasitoids only preferred wavelengths of 380, 400, and 420 nm over the control wavelength (Table 1). *Phymastichus coffea* and *P. nasuta* were more attracted to the wavelength of 400 and 420 nm compared to *C. stephanoderis*. At 380 nm, *P. coffea* and *C. stephanoderis* wasps showed the higher responses in comparison to *P. nasuta* females.

When the nonchoosers were excluded from analysis, we found *P. coffea* females were more attracted to range 380 nm (UV), 400–420 nm (violet-blue), 460 nm (blue), 490–540 nm (blue-green), and 590 (orange) than to the control (570 nm). In contrast, *P. coffea* females were more attracted to wavelength control than to the wavelengths of 340–350 (UV) and 640–670 nm (red). Unexpectedly, no difference in the responses to the wavelength control and 370 nm wavelength was observed (Fig. 2).

Prorops nasuta females were more attracted to wavelengths within the ranges 380 nm (UV), 400–420 nm (violet/blue), 460 nm (blue), 520–540 nm (green), and 590 nm (orange) compared to 570 nm (yellow, control). In contrast, *P. nasuta* females were more attracted to 570 nm than to wavelengths of 340–370 (UV) and 640–670 nm (red). Wasps did not show any preference for the wavelength of 490 nm (green) or the control wavelength (Fig. 3).

Cephalonomia stephanoderis females showed preference for 380 (UV), 400–420 (violet/blue), and 540 (green) wavelengths over the 570 nm wavelength (control). In contrast, wasps were more attracted to the control wavelength compared to wavelengths of 340–370 (UV) and 640–670 nm (red). Females did not show any preference for 490–520 nm (blue-green) wavelengths or the wavelength control (Fig. 4).

Discussion

Color vision has relatively been demonstrated in a limited number of insect species (Briscoe and Chittka 2001), but little is known about the role of color cues in the behavior of parasitoids in relation to the host (Fischer et al. 2004). This is the first report on color preference of three coffee berry borer parasitoids. The color preference for these parasitoids, reported here, is probably an adaptation associated with the need to feed their adult state (i.e., parasitoid attraction to flower color). Consistently, including or excluding nonchoosers from analysis, the three parasitoid species preferred the 380 (UV), 400 (violet), and 420 nm (blue) wavelengths to the wavelength control. However, *P. coffea* and *P. nasuta* were more attracted to the wavelength of 400 (violet) and 420 nm (blue) compared to *C. stephanoderis*, while *P. coffea* and *C. stephanoderis* wasps showed the higher responses at 380 nm (UV) in comparison to *P. nasuta* females. When nonchoosers were excluded from the analysis, we observed other differences among the parasitoid species. For instance, *P. coffea* were more attracted to blue-green (490–540 nm) than to yellow (570 nm), whereas the bethylids did not discriminate between blue-green or yellow. *Prorops nasuta* and *C. stephanoderis* are taxonomically related and have a similar natural history.

Prorops nasuta and *C. stephanoderis* females spend a lot of time living inside coffee berries (Infante et al. 1994b; Infante 1998), searching for host larvae and pupae to lay their eggs. Instead, *P. coffea* females display a free life, because adults never enter to the berries (Infante et al. 1994a), parasitizing the coffee berry borer adults outside the berries (Espinoza et al. 2009). However, our results suggest that the activity of these three species of coffee berry borer parasitoids are mainly diurnal and that they have the ability to orient themselves toward light, especially at wavelengths of 380 (UV), 400 (violet), and 420 (blue). Generally, parasitoids fly toward vegetation to increase the chance of finding their hosts (Goff and Nault 1984). However, parasitoids may also use the contrasts between sky and vegetation during host location, as reported for *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae) (Goff and Nault 1984), *Ichneumon stramentarius* Gravenhorst *Ichneumon* sp. (Hymenoptera: Ichneumonidae) (Peitsch et al. 1992), *Trybliographa rapae* Westwood (Hymenoptera: Cynipidae) (Brown et al. 1998), and *Campoletis perdistinctus* Viereck (Hymenoptera: Ichneumonidae) (Hollingsworth et al. 1970). If this type of contrast between sky and vegetation is used by coffee berry borer parasitoids, a more likely occurrence is to be found in *P. coffea* because this species has a high dispersal capacity (Castillo et al. 2006) and a greater range of color preference than that exhibited by the bethylids.

We infer that the preference of coffee berry borer parasitoids for the blue color is related to location of food as the relative attraction to near blue region (λ_{max} ~ 440 nm) is involved in flower

Table 1. Comparison of the coffee berry borer parasitoids at each wavelength by responses toward the wavelength test, wavelength control (570 nm), or nonchooser (NC)

Wavelength	Variable	Parasitoid			χ^2	P-value
		Phymastichus coffea	*Cephalonomia stephanoderis*	*Prorops nasuta*		
340	Test	0 (1.3)	3 (1.3)	1 (1.3)	3.9	0.409
	Control	26 (27)	27 (27)	28 (27)		
	NC	24 (21.6)	20 (21.6)	21 (21.6)		
350	Test	1 (2.0)	3 (2)	2 (2)	6.8	0.145
	Control	18 (24)	25 (24)	29 (24)		
	NC	31 (24)	22 (24)	19 (24)		
370	Test	6 (5)	3 (5)	6 (5)	14.1	0.006
	Control	8 (17.6)	21 (17.6)	24 (17.6)		
	NC	36 (27.3)	26 (27.3)	20 (27.3)		
380	Test	37 (33)	39 (33)	23 (33)	21.1	<0.001
	Control	0 (4.6)	3 (4.6)	11 (4.6)		
	NC	13 (12..3)	8 (12.3)	16 (12.3)		
400	Test	48 (41.6)	31 (41.6)	46 (41.6)	25.6	<0.001
	Control	0 (2.6)	7 (2.6)	1 (2.6)		
	NC	2 (5.6)	12 (5.6)	3 (5.6)		
420	Test	50 (41.3)	32 (41.3)	42 (41.3)	23.6	<0.001
	Control	0 (2)	5 (2)	1 (2)		
	NC	0 (6.6)	13 (6.6)	7 (6.6)		
460	Test	18 (19)	15 (19)	24 (19)	3.67	0.452
	Control	6 (5.3)	6 (5.3)	4 (5.3)		
	NC	26 (25.6)	29 (25.6)	22 (25.6)		
490	Test	16 (13.3)	9 (13.3)	15 (13.3)	8.17	0.085
	Control	5 (10)	11 (10)	44 (10)		
	NC	29 (26.6)	30 (26.6)	21 (26.6)		
520	Test	15 (16)	14 (16)	19 (16)	9.7	0.045
	Control	6 (6)	11 (6)	1 (6)		
	NC	29 (28)	25 (28)	30 (28)		
540	Test	20 (22)	25 (22)	21 (22)	1.21	0.874
	Control	4 (4)	4 (4)	4 (4)		
	NC	26 (24)	21 (24)	25 (26)		
590	Test	14 (16.3)	17 (16.3)	18 (16.3)	1.46	0.832
	Control	5 (6)	7 (6)	6 (6)		
	NC	31 (27.6)	26 (27.6)	26 (27.7)		
640	Test	3 (2)	3 (2)	0 (2)	11.9	0.017
	Control	16 (14.6)	7 (14.6)	21 (14.6)		
	NC	31 (33.3)	40 (33.3)	29 (33.3)		
650	Test	0 (1.9)	5 (1.9)	0 (1.9)	8.78	0.066
	Control	16 (18.5)	21 (18.5)	19 (18.5)		
	NC	33 (29.4)	25 (29.4)	31 (29.4)		
670	Test	0 (1.3)	4 (1.3)	0 (1.3)	9.58	0.047
	Control	17 (19)	21 (19)	19 (19)		
	NC	33 (29.6)	25 (29.6)	31 (29.6)		

Number in parentheses denotes expected frequencies.

discrimination in Hymenoptera (Chittka and Menzel 1992). Our results suggest that floral nectar could be more important for *P. coffea* than for *P. nasuta* and *C. stephanoderis* because the former species has a preference for violet color (López-Vaamonde and Moore 1998). However, bethylids require ingestion of floral nectar to feed themselves because their longevity increase when feeding with honey (Lauziére et al. 2000, Bacca et al. 2012). The need for food in adults seems to be lower in *P. nasuta* and *C. stephanoderis* than in *P. coffea* because bethylids live longer (30 d) than the latter species (4 d). In addition, it is known that bethylids require ingestion of the hemolymph of coffee berry borer larvae and pupae to produce offspring (Lauziére et al. 2001).

Although the attraction to UV light is common in nocturnal insects (Stark and Tant 1982), this type of response can also be observed in diurnal parasitoids such as *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) (Mellor et al. 1997) and *C. perdistinctus* Viereck (Hymenoptera: Ichenumonidae) (Hollingsworth et al. 1970). UV light (Chittka and Menzel 1992) commonly induces an escape response (Brown et al. 1998). This behavior has been observed in *A. ervi* Haliday (Goff and Nault 1984), *Trybliograpa rapae* Westwood (Hymenoptera: Figitidae) (Brown et al. 1998), and *Phyllotreta striolata* (F.) (Coleoptera: Chrysomelidae) (Yang et al. 2003). This, however, would not be an advantage for coffee berry borer parasitoids because the *H. hampei* infestations are aggregated in the field. Nevertheless, *P. coffea* and *C. stephanoderis* wasps showed the higher responses at 380 nm (UV). Given that UV photoreceptors are clearly exploited by day-active nectar feeders (Chittka and Menzel 1992), it is possible that UV sensitivity could favor orientation to hosts or alternative food sources, such as floral nectar (Jervis and Kidd 1999). The most likely cause of this is that
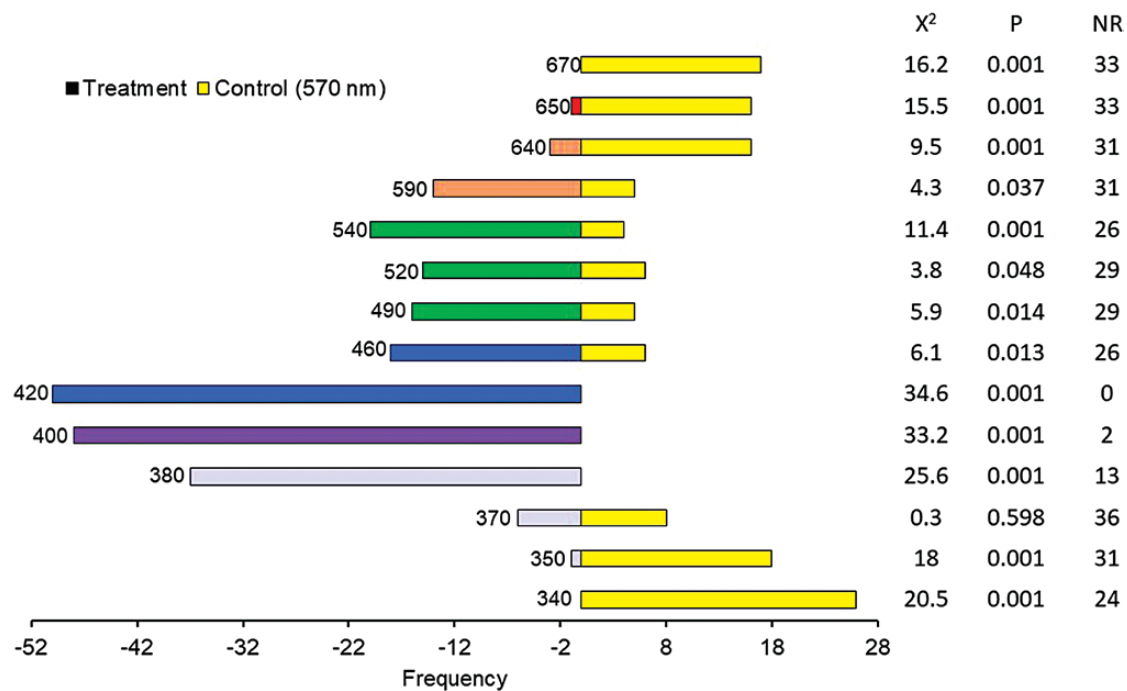
Fig. 2. Attraction response by *P. coffea* females to the light comparing 14 wavelength (nm) with a control (570 nm) inside a T-tube olfactometer. The frequency of response to each treatment and control was compared using a chi-square test, not including in the analysis the number of females without response (NR).
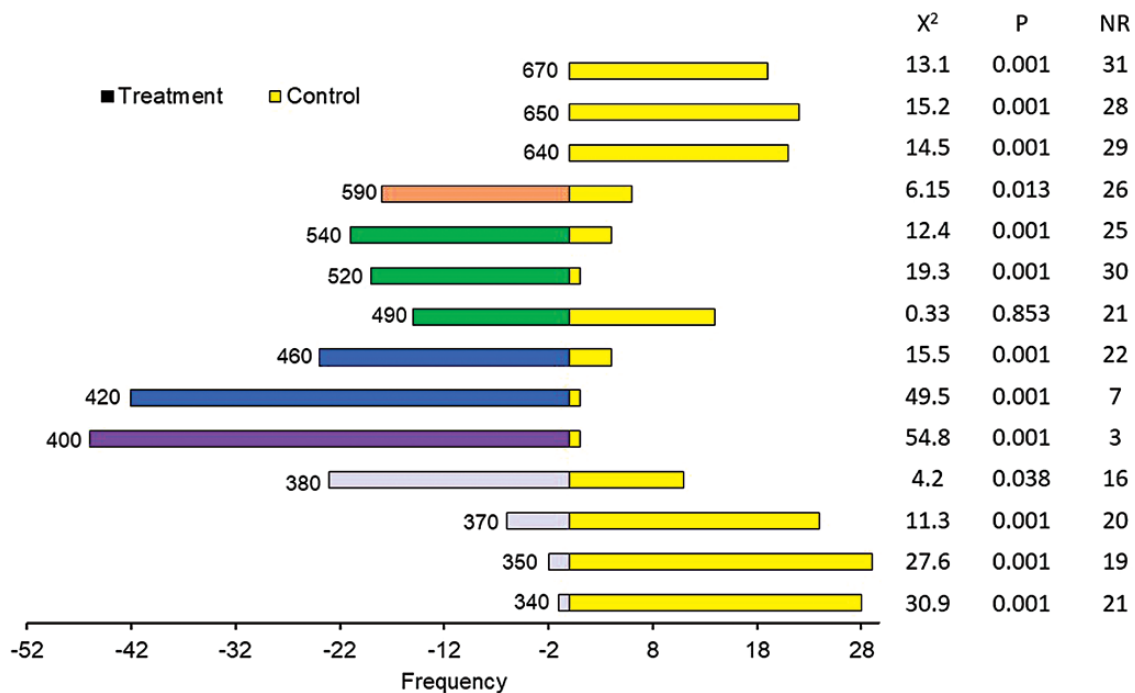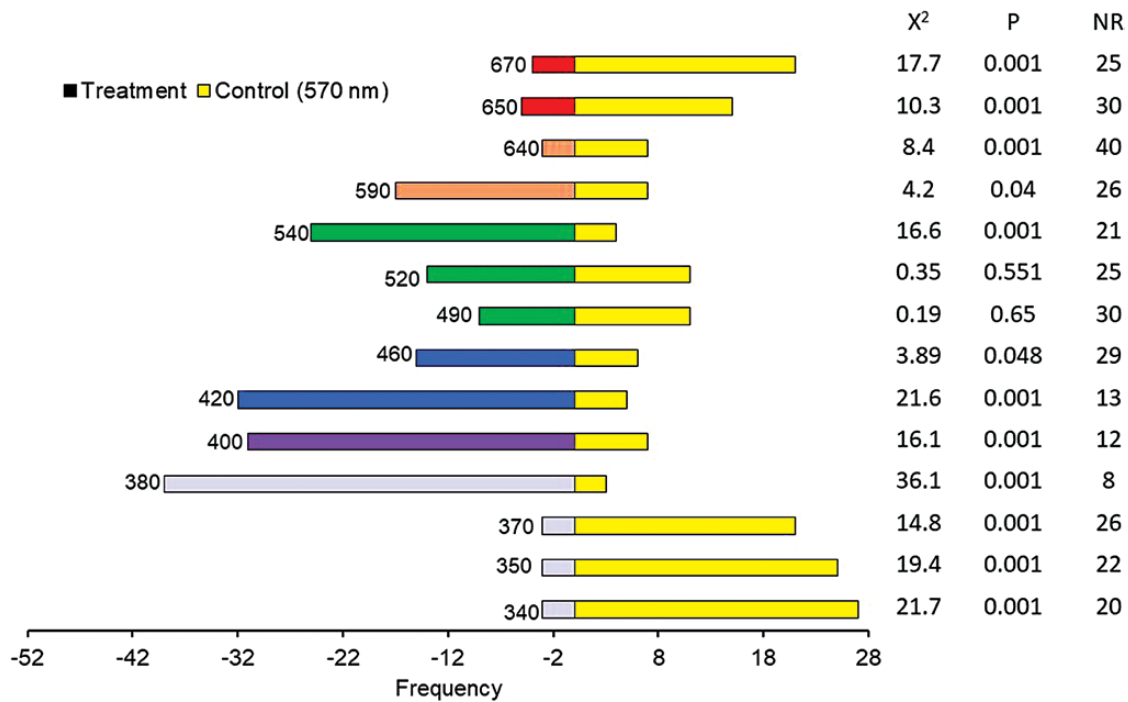

Fig. 3. Attraction response by *P. nasuta* females to the light comparing 14 wavelength (nm) with a control (570 nm) inside a T-tube olfactometer. The frequency of response to each treatment and control was compared using a chi-square test, not including in the analysis the number of females without response (NR).

they search for floral nectar under the protection of coffee plants and shade trees.

Coffee berry borer parasitoids evaluated in this work clearly showed response to different sections of the spectrum. Results from the present study suggest that the peaks obtained correspond to the three classes of photoreceptors commonly found in the Hymenoptera (Peitsch et al. 1992, Briscoe and Chittka 2001). However, with our results we are unable to state if there is true color vision in the coffee berry borer's parasitoids. Therefore, the visual response of these insects may be investigated in future studies. To fully understand how the insects to solve its visual problems, it is necessary to combine data from three sources: 1) the physical environment, 2) insect behavior, and 3) the physiology of the insect's visual system (Prokopy and Owens 1983).

Fig. 4. Attraction response by *C. stephanoderis* females to the light comparing 14 wavelength (nm) with a control (570 nm) inside a T-tube olfactometer. The frequency of response to each treatment and control was compared using a chi-square test, not including in the analysis the number of females without response (NR).

We found that between 40 and 50% of the parasitoids did not respond during the bioassays. A number of factors could explain this situation. It is possible that nonchoosers were not physiologically ready to respond to the light stimuli. For instance, although we offered sugar solution ad libitum to all wasps, it was not feasible to verify exactly the time of the last meal of each individual. Hunger state of wasps may affect their responses to chemical or visual cues (Wäckers 1994, Lewis et al. 1998). Starved females of *Cotesia rubecula* searched and landed more often on yellow targets, whereas sugar-fed wasps exhibited a high overall searching activity, without showing a preference for yellow targets (Wäckers 1994). It is also possible that the observed responses are those normally exhibited by the studied parasitoids. These parasitoid species exhibited higher responses (60–80%) to host chemical cues compared to observed here (Rojas et al. 2006; Chiu-Alvarado and Rojas 2008, Chiu-Alvarado et al. 2009).

The importation of these three parasitoids to the Americas has produced disappointing results for the biological control of the coffee berry borer (Infante et al. 2012), probably due to the ignorance of many aspects related to the ecology of these species, and, in turn, due to the lack of proper management at field. This study represents an initial contribution to the study of the role of vision in the coffee berry borer parasitoids. Further behavioral studies are needed to determine whether these parasitoids have true color vision, given that the spectral sensitivity does not imply discrimination of dominant wavelengths (Hausmann et al. 2004). Also, it would be necessary to investigate how factors such as age, mating, feeding regimen, and oviposition of parasitoids can affect their spectral responses.

Acknowledgments

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