Perception of Chromatic Cues During Host Location by the Pupal Parasitoid *Pimpla turionellae* (L.) (Hymenoptera: Ichneumonidae)

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ABSTRACT Chromatic and achromatic plant cues are expected to be particularly important for parasitoids of endophytic pupal hosts, because these stages do not feed and therefore avoid volatile emission caused by plant tissue damage. Endophytic feeding can cause discoloration or desiccation, leading to changes in color and/or brightness of infested plant parts that may be visually detected by parasitoids. The role of color cues in the host-finding behavior of parasitoids is poorly understood, and the visual system of most parasitoid species has not yet been investigated. We studied color discrimination ability and innate color preferences in the pupal parasitoid *Pimpla turionellae* (L.) (Hymenoptera: Ichneumonidae) during location of concealed hosts. Responses to combinations of yellow and blue bands of different reflectance intensities were investigated on cylindrical models of plant stems. The parasitoid's reaction to these chromatic cues was evaluated by scoring the number of ovipositor insertions into the colored bands. Female parasitoids discriminated blue from yellow irrespective of total reflectance and inserted their ovipositors significantly more often into the blue area. True color vision is demonstrated for the examined species, and responses to chromatic cues are discussed in relation to their importance for host location in parasitoids. Results of this study and of our previous work suggest that *P. turionellae* uses contrasts (chromatic or achromatic) rather than specific color characteristics in visual host location.

KEY WORDS pupal parasitoid, host location, vision, wavelength discrimination, chromatic contrast

INSECTS PERCEIVE ACHROMATIC and chromatic cues by two distinct neural pathways (Menzel and Backhaus 1991). Generally, the detection range is larger for achromatic than for chromatic targets (Hempel de Ibarra et al. 2001). Overall, however, the distance at which a target can be visually detected depends on its size, the number of ommatidia of the insects' compound eyes, and the sensitivity of the photoreceptors (Giurfa and Lehrer 2001). For example, corollae of most flower species have diameters of <5 cm, and the maximum distance from which their hue (dominant reflected wavelength) can be detected by honey bees is 45 cm (Giurfa et al. 1996). Thus, chromatic cues are involved in orientation over only a rather short range.

It is a well-established fact that floral colors are of fundamental importance for visual orientation of pollinators (e.g., Menzel and Shmida 1993, Giurfa and Lehrer 2001). Most insects possess a trichromatic color vision system with ultraviolet (UV), green, and blue photoreceptors (Menzel and Backhaus 1991, Peitsch et al. 1992, Briscoe and Chittka 2001). Also, parasitoids can use color vision during food foraging processes, because most synovigenic species need sugar sources as an energy supply (reviewed by Thompson 1999). Color vision allows parasitoids to orient toward floral color displays in much the same way as pollinators (Wäckers 1994). Besides food foraging, parasitoids also must find hosts to reproduce. In this search for hosts, chromatic cues can be employed to distinguish between green leaves and other natural objects (Chittka 1996). In addition, chromatic cues allow parasitoids to discriminate between hosts feeding on different flowering plant species or on differently colored plant structures such as flower corollae or closed buds (Wäckers and Lewis 1999). The coloration of plant structures can be altered because of herbivory, e.g., by leafmining or gallforming insects (Hawkins 1988, Faeth 1990), or by stemborers, causing "deadheart" or discoloration of stems (Smith et al. 1993). These distinct color cues could be particularly important for parasitoids of endophytic hosts. This applies even more for pupae hidden inside plant tissue, because this nonfeeding stage provides few other cues to searching parasitoids.

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Despite the potential importance of color cues, there are only three electrophysiological studies addressing the spectral sensitivity of hymenopteran parasitoids. A trichromatic visual system was found in *Trybliographa rapae* (Westwood) (Cynipidae) (Brown et al. 1998). Two peaks of spectral sensitivity, in the UV and green-yellow region, were found in *Encarsia formosa* (Gahan) (Aphelinidae) (Mellor et al. 1997), and only a green receptor was detected in *Ichneumon stramentarius* Gravenhorst and Ichneumon sp. (Ichneumonidae) (Peitsch et al. 1992). Some studies on the visual ecology of parasitic Hymenoptera report responses to colored sticky traps in the field (Weseloh 1972, 1986, Romeis et al. 1998), to differently colored hosts (Takahashi and Pimentel 1967, Michaud and Mackauer 1994), or to colored models in the laboratory (Schmidt et al. 1993, Battaglia et al. 2000). However, the results obtained need not necessarily indicate true color vision, i.e., the sensation of chromatic contrast, because differences in the intensity of reflected light could have elicited the responses of parasitoids. No conclusion on color discrimination ability can be drawn from experiments with *Pimpla instigator* F. (Ichneumonidae), which was tested only in a single trial where yellow had a much stronger total reflectance than blue (Schmidt et al. 1993). Similarly, *Diachasmimorpha longicaudata* (Ashmead) (Braconidae) was suggested to discriminate among hues, but an influence of overall light intensity on the wasps' responses was detected (Messing and Jang 1992). Besides innate color discrimination abilities, associative learning can modify the color preferences of parasitoids. Several parasitoid species learned to discriminate rewarded from unrewarded colors (Arthur 1966, Wäckers and Lewis 1999, Oliai and King 2000). However, these studies also did not evaluate the potential effect of achromatic cues on the choices of the parasitoids. Wardle (1990) showed that *Exeristes roborator* (F.) (Ichneumonidae) failed to learn reflectance intensity of light and dark gray host microhabitat models while succeeding in wavelength learning. Evidence for true color vision in hymenopteran parasitoids is scarce. The few electrophysiological studies that have been performed with members of different families suggest diverse visual systems among the species. Most behavioral studies so far have not evaluated the effect of total reflectance of the colored surfaces used.

Pimpla turionellae (L.) (Ichneumonidae), an endoparasitoid of concealed lepidopteran pupae (Sandlan 1982), is known to orient toward strong contrasts in total reflectance during host location (Sandlan 1980, Fischer et al. 2003). We hypothesized that *P. turionellae* additionally uses chromatic cues to locate its hidden host. In three different bioassays, we offered *P. turionellae* a choice between yellow and blue bands, which had a constant hue and varyied total reflectance. With this trial design, we are able to attribute the observed responses unambiguously to either wavelength or total reflectance.

Materials and Methods

Parasitoid Rearing. The laboratory strain of *P. turionellae* originated from insects obtained in 1994 from the Forest Research Institute of Baden-Wuerttemberg, Germany. Subsequently, parasitoids were reared on pupae of the wax moth, *Galleria mellonella* L. Adults were kept in Plexiglas (Röhm, Darmstadt, Germany) containers ($25 \times 25 \times 25$ cm) at 15°C, 70% RH, and a photophase of 16 L:8 D. They were fed with honey and water and were allowed to mate. Starting at an age of 5–7 d, host pupae hidden in white paper cylinders were offered to the parasitoids for oviposition and host-feeding. After having been exposed to the wasps for 3–5 h, parasitized pupae were stored at 24°C, 60% RH, and a photophase of 16 L:8 D until emergence of adults, which typically occurred after 3 wk. Female wasps had a lifespan of 1–2 mo.

Colors. The color space L*a*b*, defined by the Commission Internationale de L'Eclairage (CIE 1986), was used for color selection. The two chosen colors have distinct reflectance spectra: blue has a peak reflectance at 450 nm and reflects to a lesser extent in the green-yellow and UV range. Yellow reflects in the UV wavelength range and beyond 520 nm but only slightly in the blue range. Reflectance maxima of the colors correspond to the peak sensitivity ranges of the blue and green photoreceptors. Color hue was kept constant by controlling the coordinates a* and b*. Small deviations caused by the color specification system cyan, magenta, yellow, black (CMYK) used by respective printers are negligible. Because the L*a*b* system is defined for the human visual system, we determined the total reflectance as an independent spectral parameter. This measure represents the proportion of light that is reflected in a certain range of the spectrum and may be used as a signal by a hypothetical receptor.

The L*a*b* values were measured with a GretagMacbeth Spectrolino spectrophotometer, and the total reflectance spectra were determined with an Ocean Optics PC2000-UV-VIS spectrometer (Ocean Optics, Dunedin, FL) using an ISP-REF integrating sphere (Table 1; Fig. 1). The paper used in the experiments (see below) served as white reference for spectrometer calibration. Thus, the deviations of total reflectance values from 100% reflectance (i.e., 1.0) directly represent the contrast that can be used to discriminate the cues on the model. For the colored bands and the white paper, integrated values of the total reflectance coefficient (r) were calculated for the wavelength ranges 340–360 nm (UV), 430–450 nm (blue), and 520–540 nm (green). These ranges were chosen according to the peak spectral sensitivities of the three basic visual receptor types in hymenopterans (Peitsch et al. 1992, Briscoe and Chittka 2001). Discussion of results in this paper is based on the reflectance coefficients (r). This allows an estimate of the color contrasts, receptor-specific contrasts, and intensity contrasts that the parasitoid is likely to perceive on the model.

Experimental Set-up. One yellow and one blue band (width: 15 mm), separated by 20 mm of white space, were printed on airmail paper (45 g/m^2; ELCO

Table 1. Spectral characteristics of printed blue and yellow bands and the white background paper used in the experiments

	r UV (340–360 nm)	*r* Blue (430–450 nm)	*r* Green (520–540 nm)	*L** (%)	*a**	*b**
Treatment 1						
Light blue	0.57	0.83	0.53	75	−1.8	−16
Dark yellow	0.36	0.08	0.19	55	−2.1	56
Treatment 2						
Medium blue	0.44	0.76	0.39	65	−1.3	−29
Medium yellow	0.44	0.08	0.28	65	−1.7	69
Treatment 3						
Dark blue	0.34	0.69	0.30	55	−0.01	−39
Light yellow	0.55	0.08	0.42	75	−0.4	82
White (paper)	1.00	1.00	1.00	94	−0.2	6.3

L a* b* values and integrated values of total reflectance (coefficient *r*) for the peak sensitivity ranges of the three basic photoreceptors in insects (UV, blue, green) measured against the paper as calibration standard.

Atlantic Clipper, Allschwil, Switzerland) with a Tektronix Phaser 840 (Xerox, Wilsonville, OR). The banded paper was formed into a hollow cylinder (length: 70 mm; diameter: 8 mm) with both ends left open (Fig. 2). The response of *Pimpla* spp. to such models can be easily assessed by scoring the ovipositor penetrations of the paper.

We used three different treatments with yellow and blue bands of equal hue but varyied total reflectance (Fig. 1). Treatment 1 (light blue/dark yellow) offers strong achromatic contrast between the two colors, with blue reflecting stronger. In treatment 2 (medium blue/medium yellow), the two test colors differ strongly in their blue contrast but reflect to the same extent in the UV and green-yellow wavelength ranges. In treatment 3 (dark blue/light yellow), yellow has a similar total reflectance in the UV and green-yellow wavelength ranges as blue has in the blue wavelength range.

During the trials, female parasitoids were placed individually into Plexiglas containers (18.5 × 8.5 × 7.5 cm) and exposed to one of the three treatments for a period of 20 min. To quantify the behavioral response, the paper cylinder was subdivided into 28 sections (width: 2.5 mm; Fig. 4). At the end of the experiment, the frequency and location of ovipositor insertions was scored.

Experiments were performed in a climate chamber at 20°C and 60% RH with 13- to 21-d-old individuals that had been provided with ad libitum food. The parasitoids were given at least 1 h to adjust to the climatic conditions. One or 2 d before the test session, parasitoids had access to paper-covered host pupae (see Parasitoid Rearing). Under the white fluorescent bulbs, the human-perceived light intensity in the plastic box was 6,750 Lux (TES-1334 lightmeter). The radiation energy flux was 17 W/m^2 (Pyranometer; Thies Clima, Göttingen, Germany; and radiation indicator CC20; Kipp & Zonen, Delft, The Netherlands).

Data Analysis. The sample size for each of the three treatments consisted of 30 females that inserted their ovipositor at least once into the model during the trial period. All parasitoids were used for one trial session only. The general responsiveness of the wasps in the different treatments, i.e., the number of individuals inserting their ovipositor versus the inactive ones, was analyzed for significant differences using χ^2-tests. Absolute numbers of ovipositor insertions on the yellow and blue, as well as the white, areas between the colored bands were quantified by counting the insertions in the respective cylinder sections. The insertions in these three scored areas were compared for each treatment using the nonparametric Friedman test for *k* related samples. The 5% level of significance with two degrees of freedom resulting from our setup is reached at $\chi^2_R = 5.99$. As a second step, Paired *t*-tests were applied for comparisons of the mean number of insertions on the yellow and blue bands.

Results

General Responsiveness. Calculated over the three treatments of the experiment, 90 ± 8% (mean ±SD) of tested female *P. turionellae* inserted their ovipositor at least once. Treatment 2 (medium blue/medium yellow) elicited a significantly higher responsiveness than treatment 1 (light blue/dark yellow; χ^2 test; $\chi^2 = 4.0$, df = 1, $P < 0.05$). No significant difference was found between treatment 1 and treatment 3 (dark blue/light yellow; χ^2 test; $\chi^2 = 1.4$, df = 1, $P = 0.2$) or between treatment 2 and treatment 3 (χ^2 test; $\chi^2 = 0.9$, df = 1, $P = 0.3$).

Response to Different Hues. The absolute number of ovipositor insertions was significantly different among the three areas "yellow," "blue," and "center" (white) in all treatments (Friedman test; treatment 1: $\chi^2_R = 42.3$, df = 2; treatment 2: $\chi^2_R = 44.0$, df = 2; treatment 3: $\chi^2_R = 50.0$, df = 2). The strongest response to the blue band was recorded in treatment 3 (dark blue/light yellow) with 4.4 ± 0.5 (mean ± SE) insertions per individual female wasp. The strongest response to the yellow band was recorded in treatment 1 (light blue/dark yellow) with 0.3 ± 0.1 insertions (Fig. 3), which was still lower than the blue band with 3.3 ± 0.3 insertions.

The mean number of ovipositor insertions is significantly different between the yellow and blue bands in all treatments (paired *t*-tests; treatment 1: $t = -8.2$, df = 29, $P < 0.0001$; treatment 2: $t = -8.5$, df = 29, $P < 0.0001$; treatment 3: $t = -8.7$, df = 29, $P < 0.0001$). In all treatments, blue yielded a higher mean number of ovipositor insertions than yellow. The spatial distribution of total numbers of ovipositor insertions into

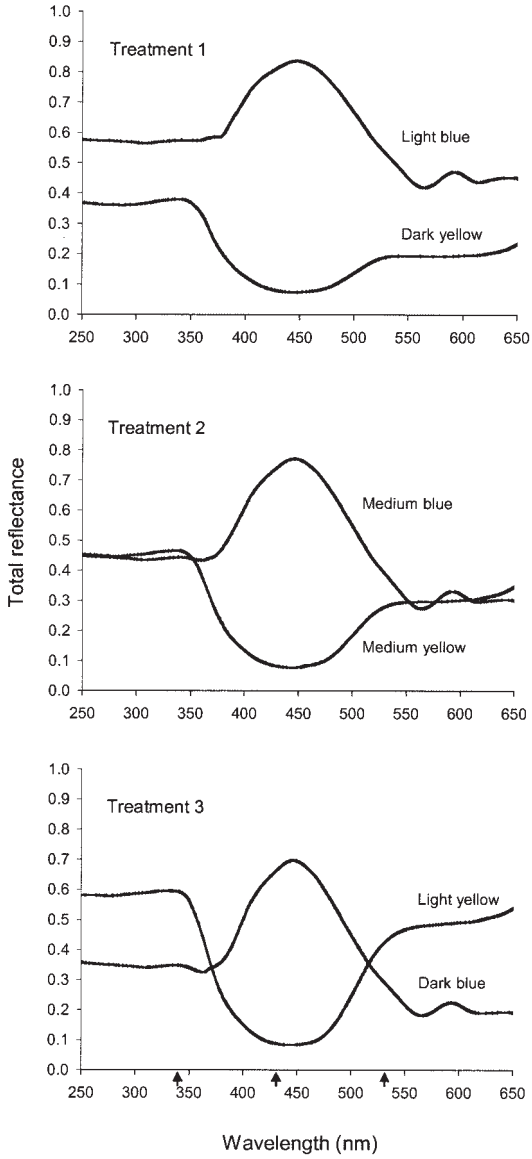

Fig. 1. Total spectral reflectance of the light, medium, and dark yellow and blue shades used in the three treatments of the experiment relative to the white paper background. Arrows on the x axis indicate maximal sensitivity of UV (340 nm), blue (430 nm), and green (530 nm) photoreceptors in Hymenoptera (Peitsch et al. 1992).

different sections of the paper cylinders shows a concentration of insertions on the blue bands, which is most pronounced in treatment 3 (dark blue/light yellow; Fig. 4). The response peaked at the center of the blue bands in all treatments.

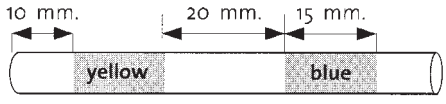

Fig. 2. Experimental set-up using paper cylinder models with yellow and blue bands as visual cues.

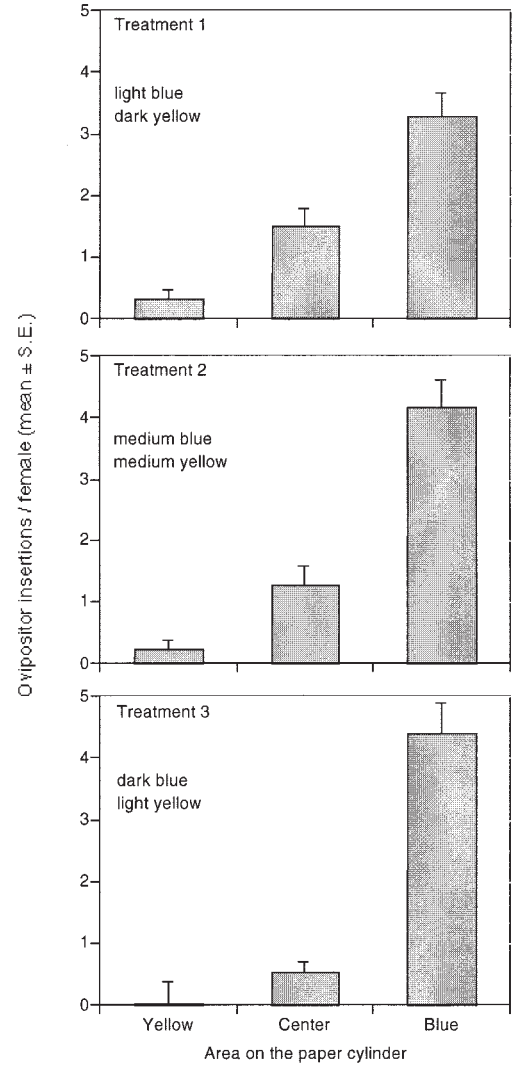

Fig. 3. Individual number of ovipositor insertions of *P. turionellae* on the yellow band, blue band, and the white center area of the paper cylinders in treatments 1–3 (mean ± SE; $n = 30$).

Discussion

The current study shows that females of the pupal parasitoid *P. turionellae* can distinguish between the colors blue and yellow solely on the basis of hue (wavelength) differences. Blue is innately preferred over yellow, irrespective of total reflectance. This demonstrates true color vision in this parasitoid species. In previous experiments, it was shown that the response of *P. turionellae* increased along with the achromatic contrast. Three times more ovipositor insertions were scored on medium and dark gray bands than on light gray bands on cylindrical models iden-

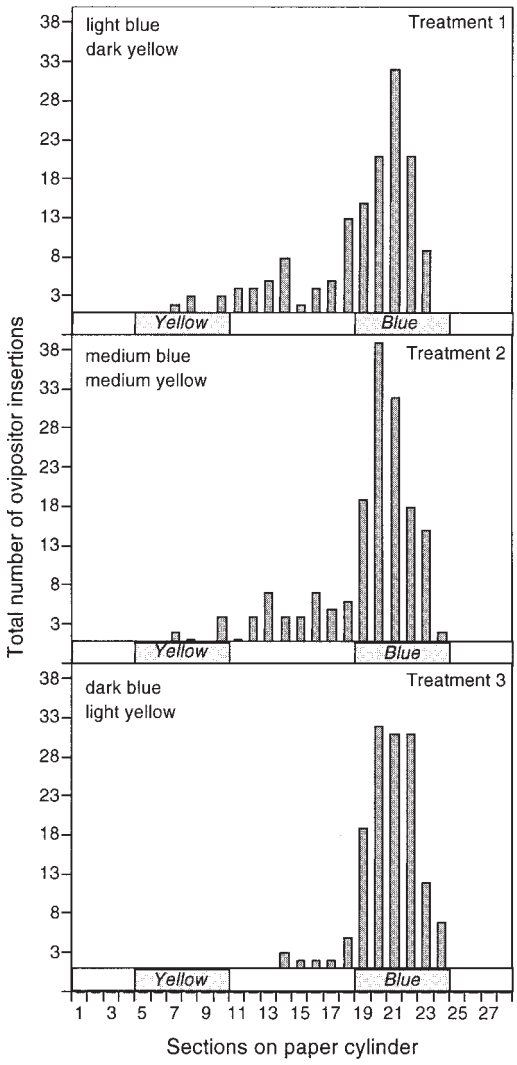

Fig. 4. Spatial distribution of total number of ovipositor insertions of *P. turionellae* on the paper cylinders with yellow and blue bands in treatments 1–3 ($n = 30$). The paper cylinder was divided into 28 sections of a standard length of 2.5 mm (x axis).

tical to those used in this study (Fischer et al. 2003). Accordingly, in the absence of chromatic vision, the "darker" color should be preferred, and discrimination of colors of similar total reflectance should not be possible. Because of the selection of the test colors on the basis of parameter lightness, treatment 2 (medium blue/medium yellow) offers colors of equal lightness values. However, total reflectance values as measures independent of the visual system are most similar in treatment 3 (dark blue/light yellow). In treatments 1 and 2, the total reflectance of yellow is lower and thus offers the higher reflectance contrast. Nevertheless, blue was strongly preferred over yellow in all treatments. Our results clearly demonstrate wavelength discrimination because the preference for blue was significant, both when blue represented a lower contrast than yellow (treatments 1 and 2) and when blue and yellow had a similar total reflectance (treatment 3). Total reflectance had just a minor effect on the color choice: when yellow provided a much stronger contrast to the background than blue (treatment 1), the parasitoids' attraction to blue was slightly reduced. An interaction of hue and achromatic cues in responses of *Diachasmimorpha longicaudata* (Ashmead) (Braconidae) to colored sticky traps was also emphasized by Messing and Jang (1992). However, the magnitude of reaction to chromatic cues in *P. turionellae* on the close range is striking. The species' general responsiveness toward model cylinders with colored bands in the current study (90 ± 8%) was significantly higher than to models offering bands with only achromatic contrast to the background (56 ± 3%; χ^2 test; $\chi^2 = 29.0$, df = 1, $P < 0.0001$) (Fischer et al. 2003). In the experiments with both achromatic and chromatic cues, the response peaked at the center of the favored cue areas.

Innate color preferences of parasitoids have been studied in a few species of the superfamily Ichneumonoidea, and the results are inconsistent. In one case, no preference for blue over orange was found (*Exeristes roborator* F.; Wardle 1990). Other studies reported innate preferences for blue over yellow (*Itoplectis conquisitor* Say; Arthur 1966; *Pimpla instigator* F.; Schmidt et al. 1993), for yellow over green, red, black, and blue (*Diachasmimorpha longicaudata* Ashmead; Messing and Jang 1992) and for yellow over green (*Aphidius ervi* Haliday; Battaglia et al. 2000). However, in all these studies, it is unclear whether color discrimination was based on wavelength or intensity of reflected light. Nevertheless, the results of the color discrimination study of Schmidt et al. (1993) with *P. instigator* point in the same direction as our findings, and we conclude that species of the genus *Pimpla* can discriminate colors irrespective of their intensity. Briscoe and Chittka (2001) suggest a trichromatic color vision system in Ichneumonidae. With our findings, we support chromatic vision in a member of this family, but further electrophysiological studies are needed for the description of the visual system.

Explanations for innate preferences for specific colors are diverse. Food-deprived *Cotesia rubecula* (Marshall) (Braconidae) oriented toward yellow targets, whereas fed wasps concentrated their search on green leaf tissue. Wasps seemed to prefer yellow during nectar foraging and green while searching for hosts (Wäckers 1994). Other reports on an innate preference for yellow (e.g., Messing and Jang 1992, Battaglia et al. 2000) might have been caused by the hunger state of the tested parasitoids. However, yellow reflects in the same wavelength range as green foliage, but at a greater intensity. For host-seeking parasitoids surrounded by an environment appearing mostly in shades of green, a high sensitivity to reflectance contrast and particularly green contrast is important (Prokopy and Owens 1983, Lythgoe and Partridge 1989). Parts of herbivore-infested plants may turn "yellowish" when they desiccate or when they are

drained of chlorophyll, presenting a conspicuous visual contrast to the unharmed green plant surface. This raises the question of why *P. turionellae* innately prefers blue over yellow. Honey bees and bumblebees were shown to favor violet-blue shades (Briscoe and Chittka 2001), obviously as an adaptation to the high frequency of these colors in flowers visited by Hymenoptera in general (Menzel and Shmida 1993). It is not likely that the observed response to blue in *P. turionellae* is related to floral color preference during food foraging, because the tested wasps had been provided with food ad libitum, and ovipositor insertions were scored as response. During host location in a natural environment, parasitoids might respond to wavelengths offering a strong chromatic contrast against the mostly green background. Yellow wavelengths contrast less to green than blue wavelengths. In our treatments with white background, both colors offered a strong chromatic contrast, but the wasps might still have chosen wavelength ranges that differ strongly from wavelengths reflected from green foliage.

The current study and further experiments in the same species summarized above (Fischer et al. 2003) suggest that contrasts (chromatic or achromatic) rather than specific color characteristics are used by *P. turionellae* in visual host location. Furthermore, the species responds significantly stronger to chromatic cues than to achromatic cues on identical models. Considering this preference and the fact that color cues can only be used at short distance, our results are compatible with the assumption of a sequential use of achromatic and chromatic visual channels by *P. turionellae* as described for the honeybee (Hempel de Ibarra et al. 2001).

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