

BEHAVIOR

Visual Orientation of Overwintered *Anthonomus pomorum* (Coleoptera: Curculionidae)

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ABSTRACT Vision is considered to be an important component of the sensory system used by herbivorous insects to locate host plants. We investigated preferences for transmissive colors and contrasts in the apple blossom weevil, *Anthonomus pomorum* L., which colonizes apple trees, *Malus domestica* Borkh., in early spring. The main components of the supposed visual system, green, blue, and UV light, were offered to the weevils versus black or versus each other in a dual choice arena. Furthermore, silhouettes of two different achromatic contrasts were offered in front of the colors blue and green. We also tested whether visual preferences change with time, i.e., 2, 4, and 6 d after termination of diapause in early spring. Female weevils chose UV, green, and blue over black, whereas males only chose UV over black in a series of dual choice experiments. Both sexes preferred blue to green. Weevil response to silhouettes of different contrasts was influenced by the background color, i.e., the silhouette with the higher contrast was preferred in front of green, whereas the silhouette with the lower contrast was preferred in front of blue. The preferences during visual orientation did not change with time after diapause. The more discriminating response of females may reflect a greater visual acuity or a greater visual responsiveness in females than in males because of a higher affinity for the host plant. Our findings indicate that weevils might have a trichromatic visual system and that they are able to include visual cues for the location of host plants in the field.

KEY WORDS *Anthonomus pomorum*, colors, vision, host finding, host plant

ALL HERBIVORE INSECTS SHOW some degree of selectivity in terms of host plants, and vision represents an important component of the sensory system involved during this process, often combined with olfaction (Prokopy and Owens 1983, Judd and Borden 1991, Kogan 1994). Accumulated evidence suggests that a distant plant at the horizon is detected by an insect herbivore primarily on the basis of a gross silhouette against a brighter, more uniformly lit, sky, with little if any perception of the dominant reflected wavelength or details of form (Prokopy and Owens 1983, Jermy et al. 1988). When an herbivore is in close proximity of a plant, it seems that the spectral quality of the light emitted by the plant becomes the predominant cue eliciting detection and alightment (Prokopy and Owens 1983). The visual response of an insect may be investigated by its behavior and by electroretinogram studies, but spectral sensitivity does not imply discrimination of dominant wavelengths, and thus, behavioral evidence is necessary to prove true color vision.

Most insects studied for their visual systems possess green receptors maximally sensitive at ≈ 530 nm, UV receptors ($\lambda_{\max} \approx 350$ nm), and blue receptors ($\lambda_{\max} \approx 440$ nm) (Briscoe and Chittka 2001). Chittka (1996) suggested that this set of UV, blue, and green photoreceptors is ancestral to Insecta and that some lineages have since lost or added receptors, presumably as a result of different selection pressures.

True color vision has only been shown for a limited number of insect species and has not yet been shown in coleopterans (Menzel and Backhaus 1991, Briscoe and Chittka 2001). By far the most studied insect in this regard is the honey bee, *Apis mellifera* L., because of its importance in agriculture and because it is amenable to training. Proof of color vision requires, for example, differentiated behavioral response of a species to wavelength cues in combination with results from physiological studies or that the species can be trained for color cues (Menzel and Backhaus 1991). It is therefore difficult to show color vision in many insect species. Therefore, lack of proof of true color vision in coleopterans does not mean that they cannot distinguish colors. On the contrary, electroretinograms have shown differential wavelength sensitivity in the eyes of at least eight coleopteran species: A trichromatic visual system with UV, blue, and green

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receptors was found in *Photuris lucifrescens* Barber (Lall et al. 1982) and in *Coccinella septempunctata* L. (Lin and Wu 1992). Two peaks of spectral sensitivity, in the UV and green region, were found in six other beetle species, i.e., *Liocola brevitarsis* (Lewis), *Cicindela japonica* (Tunberg), *Cicindela specularis* (Chaudoir) (Lin and Wu 1992), *Photuris versicolor* F. (Lall 1981), *Photuris pyralis* L. (Lall et al. 1980), and *Leptinotarsa decemlineata* (Say) (Mischke 1981). Studies on the visual ecology of two weevil species report that *Anthonomus grandis* Boheman showed color preference for blue-green in a Y-shaped test chamber in the laboratory (Hollingsworth et al. 1964), and the plum curculio, *Conotrachelus nenuphar* (Herbst), oriented preferentially to tall sticky green rectangles (Butkewich and Prokopy 1997). Taken together, these studies suggest that beetles have the physiological capability for, at least, dichromatic vision and that colors may affect behavior.

The apple blossom weevil, *Anthonomus pomorum* L., is a univoltine herbivore of apple trees, *Malus domestica* Borkh. Most adults overwinter in leaf litter of forests or hedgerows. Early in the season, weevils immigrate into orchards and colonize apple trees (Toepfer et al. 1999, 2002). Orientation of the weevils toward the host tree may include plant-derived chemical cues (Kalinova et al. 2000), although experimental evidence on the behavioral effect of single or combined compounds is lacking. Thus far, nothing is known about the weevil's perception of visual cues.

The aim of this study was to investigate the behavioral response of overwintered apple blossom weevils to visual cues. Weevil orientation toward transmissive colors and UV light was tested in a dual choice arena. The main components of the hypothesized visual system, green, blue, and UV light, were offered to the weevils versus black and versus each other. Furthermore, the response of the weevils toward silhouettes of different achromatic contrasts in front of the colors blue and green was investigated. In addition, we studied the influence of the physiological state of overwintered weevils on color preference by testing their response at different days after termination of diapause. Such an endogenous effect would modify the weevil's success in locating host plants during orchard colonization.

Materials and Methods

Insects. Capped brown blossoms bearing *A. pomorum* pupae were collected in May 2002 in northern Switzerland. On emergence, weevils were kept in plastic boxes (28 by 20 by 24 cm) and were fed with fresh apple leaves and pieces of apple fruit until the onset of aestivation (3–4 mo after emergence). The adults were sexed by the characteristic differences in the dorsal part of the last abdominal plates (Duan et al. 1999). The weevils were overwintered in a cooling chamber (SR Kältetechnik, Winterthur, Switzerland) at $4 \pm 1^\circ\text{C}$ in plastic boxes (19 by 9 by 8 cm). Strips of corrugated cardboard were offered as shelter. Even during aestivo-hibernation, the weevils were provided

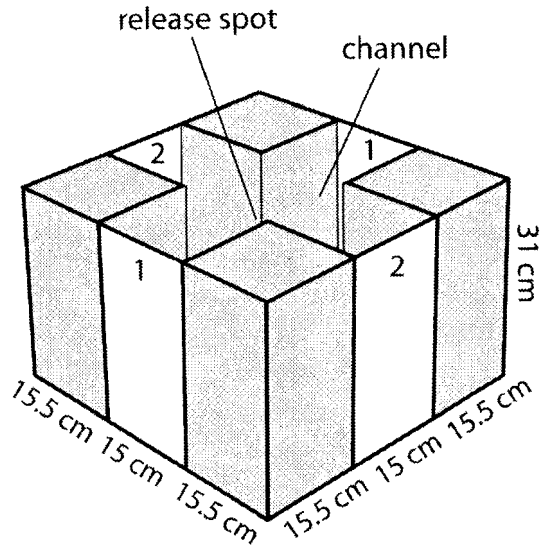


Fig. 1. Visual test arena: two perpendicular chambers bisected each other in the center forming a cross. Each of the four arms (15 by 15 by 30 cm) led to one of two visual cues, 1 or 2.

with fresh pieces of apples and sprayed with water at weekly intervals. Weevils were kept in diapause for a minimum of 20 wk, because Ctvrtecka and Zdarek (1992) showed that 65% of *A. pomorum* females showed initiation of ovarian development after a 5-mo cold treatment ($3\text{--}4^\circ\text{C}$).

Depending on the time treatment after diapause, 2, 4, or 6 d before the experiments, weevils were kept for 24 h in a climate chamber (BK 6160; Heraeus, Balingen, Germany) with a constant temperature of 10°C (L:D = 12:12, $\approx 80\%$ RH, 3,000 Lux), and then they were placed in a climate chamber with a constant temperature of 15°C (L:D = 12:12, $\approx 80\%$ RH, 3,000 Lux). Such acclimatization treatment reduced their initial mortality of 80–90% to $<10\%$ (Ctvrtecka and Zdarek 1992). The adults were fed with pieces of apple fruit and provided with water.

Visual Test Arena. The visual test arena (Fig. 1) consisted of a cross made of Plexiglas (5 mm thick; Plexiglas XT, Röhm, Darmstadt, Germany). The center of the arena consisted of a rectangular chamber (15 by 15 by 30 cm). Four arms (15 by 15 by 30 cm) produced channels in each direction. At the end of each channel, the arena had an opening (15 by 30 cm) for a frame to hold color filters. The inner walls of the arena were covered with mirrors to avoid biases caused by diffuse reflection of the light falling into the arena. The floor of the arena was coated with black paper (Mi-Teintes, Pastel; Canson, Annonay, France). The Plexiglas top of the arena was covered with gray transparency (acetate sheet, Tektronix Phaser 850, 50% gray) and was provided with a 20-cm-diameter lid to insert the weevils. The color filter at the end of each channel was lit from the outside with a lamp. The intensity of each lamp was regulated with a dimmer to achieve radiation energy of 150 W/m^2 in the center of

the test arena. Filters were made of high-quality color transparencies (Göttinger Farbfilter, Göttingen, Germany) with narrow wavelength bands and maximum wavelengths of 350 (UV), 455 (green), and 550 nm (blue). Black paper (Mi-Teintes, Pastel; Canson) was used instead of the filters to provide the black cue. The green and blue color filters were illuminated with a Tungsten-halogen lamp (78 mm-R7s-150 W, Halotone; Royal Philips Electronics, Roosendaal, Holland); the UV filter was illuminated with a UV lamp (HPW-125TS-125W/E27; Royal Philips Electronics). The black paper was also illuminated with a Tungsten-halogen lamp to provide the same temperature in each channel of the arena. Spectral analyses of the color filters and measurements of radiation energy to set the intensity of lamps were made by placing a fiber optics reflective spectrometer (SD 2000 UV-VIS; Ocean Optics, Dunedin, Florida, USA) at the point where the weevils were released i.e., 22.5 cm from the cues. The white reference for the spectral analyses was measured on a commercial reference standard (WS 1; Ocean Optics).

To test the effect of silhouettes of different achromatic contrasts, a light or a dark gray transparency (Tektronix Phaser 850, 6% gray, 30% gray, 4.5 cm wide by 30 cm tall) was placed vertically in front of the green or blue filter. The coefficient of transmission of the light gray silhouette was 0.75, i.e., 75% of the radiation penetrated the transparency (low achromatic contrast). For the dark gray silhouette, the coefficient of transmission was 0.33, i.e., 33% of the radiation penetrated the transparency (high achromatic contrast).

Bioassay. All bioassays were carried out in a climate chamber (Conviron PVG 36; Controlled Environment, Winnipeg, Canada). To have a temperature of $\approx 18\text{--}20^\circ\text{C}$ in the center of the visual test arena, the temperature in the climate chamber during the experiments was adjusted between 10 and 15°C (70% RH). Within the test arena, a choice of two different visual stimuli was presented at the same time. Opposite channels were equipped with the same color filter to avoid an influence of radiation reflecting from the channels. One weevil at a time was introduced through the lid on the top and placed in a small white plastic dish (1.7 cm diameter) in the middle of the arena. As soon as the weevil crawled into one of the channels, it was scored as choosing a particular visual stimulus, and the weevil was removed. Each weevil was only tested once, and the black paper on the floor was exchanged for a new unused one after each trial. To exclude possible unexpected influences from the arena or the climate chamber, the colors were changed between the channels after every tested weevil. Each weevil was observed for a maximum time of 30 min. If the weevil did not enter a channel within this time, it was removed and not scored. All experiments were carried out in the afternoon between 1200 and 1500 hours, i.e., $\approx 5\text{--}8$ h after the beginning of the photophase, because in the field, it was found that the maximum colonization of apple trees by flight and by

crawling occurred during this time (Hausmann et al. 2004).

The weevils were given the choice between the following pairs of visual stimuli: UV versus green, UV versus blue, UV versus black, green versus blue, green versus black, and blue versus black. Also compared were silhouettes of low and high achromatic contrast in association with green and with blue filters. Forty-five male and 45 female weevils (15 individuals each 2, 4, and 6 d after termination of diapause) were tested per treatment combination. All choice experiments were analyzed by χ^2 tests, with the zero hypothesis of homogeneity in the distribution of individuals responding to the choices offered in the bioassays (Zar 1998).

Results

Female weevils show a preference for UV, green, and blue over black (UV versus black: $\chi^2 = 15.21$, $df = 1$, $P < 0.001$, green versus black: $\chi^2 = 8.02$, $df = 1$, $P = 0.005$; blue versus black: $\chi^2 = 8.02$, $df = 1$, $P = 0.005$; Fig. 2). Male weevils show a preference for UV over black (UV versus black: $\chi^2 = 10.79$, $df = 1$, $P = 0.001$), but they show no preference when the colors green versus black or blue versus black were offered (green versus black: $\chi^2 = 0.20$, $df = 1$, $P = 0.655$; blue versus black: $\chi^2 = 3.76$, $df = 1$, $P = 0.053$; Fig. 2). The time after diapause did not influence the color choice of the males and females (UV versus black: females: $\chi^2 = 1.68$, $df = 2$, $P = 0.431$, males: $\chi^2 = 2.81$, $df = 2$, $P = 0.245$; green versus black: females: $\chi^2 = 0.22$, $df = 2$, $P = 0.898$, males: $\chi^2 = 3.75$, $df = 2$, $P = 0.153$; blue versus black: females: $\chi^2 = 1.51$, $df = 2$, $P = 0.469$, males: $\chi^2 = 3.10$, $df = 2$, $P = 0.212$).

When green or blue was offered versus UV light, females and males show no preference (green versus

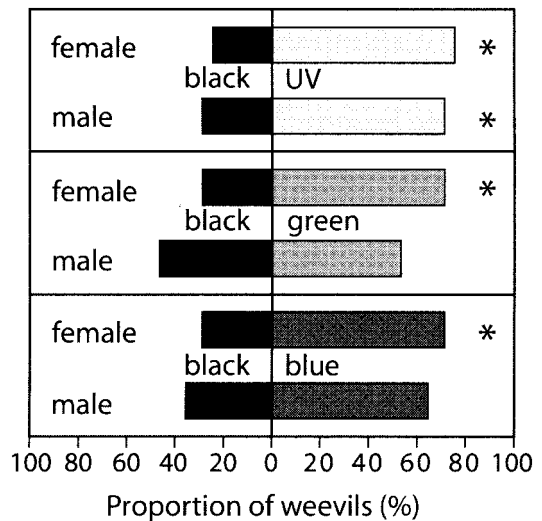


Fig. 2. Color choice of overwintered female and male apple blossom weevils in the visual test arena when green, blue, and UV are offered versus black ($n = 45$). * Significant difference (χ^2 test, $P < 0.05$).

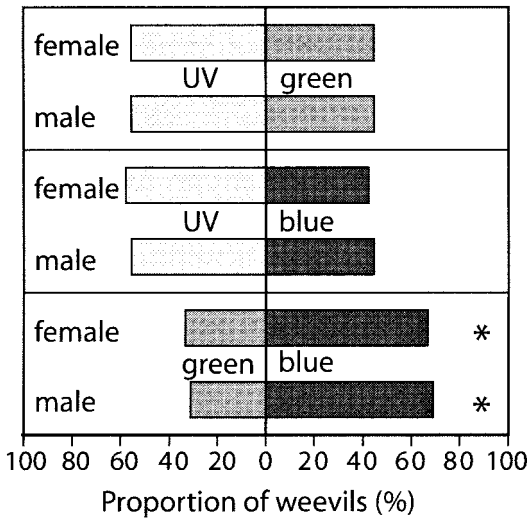


Fig. 3. Color choice of overwintered female and male apple blossom weevils in the visual test arena when blue, green, and UV are tested against each other ($n = 45$). * Significant difference (χ^2 test, $P < 0.05$).

UV: female: $\chi^2 = 0.56$, $df = 1$, $P = 0.456$, male: $\chi^2 = 0.56$, $df = 1$, $P = 0.456$; blue versus UV: female: $\chi^2 = 1.09$, $df = 1$, $P = 0.206$, male: $\chi^2 = 0.56$, $df = 1$, $P = 0.456$; Fig. 3). Females and males showed a preference for blue when the green and blue were offered (females: $\chi^2 = 5.00$, $df = 1$, $P = 0.025$; males: $\chi^2 = 6.42$, $df = 1$, $P = 0.011$; Fig. 3). The time after diapause did not influence the color choice of the males and females (green versus UV: females: $\chi^2 = 0.72$, $df = 2$, $P = 0.698$, males: $\chi^2 = 1.26$, $df = 2$, $P = 0.533$; blue versus UV: females: $\chi^2 = 5.10$, $df = 2$, $P = 0.078$, males: $\chi^2 = 0.72$, $df = 2$, $P = 0.698$; green versus blue: females: $\chi^2 = 0.60$, $df = 2$, $P = 0.741$, males: $\chi^2 = 0.31$, $df = 2$, $P = 0.902$).

When analyzed separately, females and males showed no preference between silhouettes of a low or a high contrast in blue or green (green low versus high contrast: female: $\chi^2 = 1.09$, $df = 1$, $P = 0.297$, male: $\chi^2 = 1.8$, $df = 1$, $P = 0.180$; blue low versus high contrast: female: $\chi^2 = 2.69$, $df = 1$, $P = 0.101$, male: $\chi^2 = 1.8$, $df = 1$, $P = 0.180$; Fig. 4). When the data of females and males were pooled, the response to low and high contrast shows a significant difference when tested in blue and green ($\chi^2 = 7.20$, $df = 1$, $P = 0.007$). The higher contrast was preferred in green, whereas the lower contrast was preferred in the blue range. The time after diapause did not influence the choice of achromatic contrast in males and females (green low versus high contrast: females: $\chi^2 = 0.18$, $df = 2$, $P = 0.913$, males: $\chi^2 = 1.67$, $df = 2$, $P = 0.438$; blue low versus high contrast: females: $\chi^2 = 0.76$, $df = 2$, $P = 0.685$, males: $\chi^2 = 2.22$, $df = 2$, $P = 0.324$).

Discussion

Our laboratory results show that apple blossom weevils orient positively toward transmissive visual stimuli and show preferences between different col-

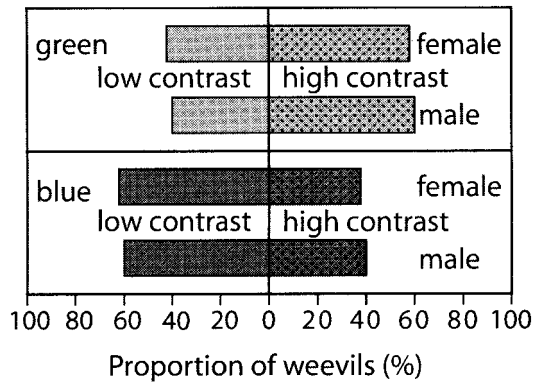


Fig. 4. Choice of overwintered female and male apple blossom weevils in the visual test arena when blue and green are offered with a vertical silhouette, resulting in a high versus low achromatic contrast ($n = 45$). Females and males separately: No significant differences. Pooled females and males: Significant difference of choice in the green versus the blue range (χ^2 test, $P < 0.05$).

ors. Furthermore, weevil response to silhouettes of different achromatic contrasts is influenced by the background color. These results indicate that weevils might include visual cues in their host plant location in the field. Physiological changes within the first 6 d after diapause did not influence the behavioral responses to the visual stimuli offered in our experiments.

Visual cues are considered to be important for host plant location in insects (Prokopy and Owens 1983), and a variety of solutions have evolved to locate plant resources. For example, host plant location in *Erioischia brassicae* (Bouché) cabbage root flies involves response over a distance of several meters to host volatile compounds, presumably coupled with close range response to plant visual stimuli (Hawkes 1974). The opposite seems to occur in *Trialeurodes vaporariorum* (Westw.) whiteflies, where initial detection of host and nonhost plants from a distance is visual, and host olfactory stimuli are involved only at very close range (Vaishampayan et al. 1975).

The results from our experiments with a choice between a transmissive wavelength cue and black indicate that apple blossom weevils show positive phototaxis. The weevils orient toward light when black serves as a blank in the bioassay design. Female weevils favor UV, green, and blue wavelength cues when offered versus black, and therefore, have the ability to perceive these cues with their visual system. Males only prefer UV significantly over black. Nevertheless, this does not exclude the ability of the males to perceive green and blue, because they are able to discriminate between these two colors when offered against each other in a choice test. Both sexes favor the color blue over green, which proves that the weevils can distinguish between green and blue solely on the basis of wavelength differences.

During the colonization of apple trees in early spring, weevils encounter the visual stimuli of sky,

green vegetation, and brown or gray bark of apple trees. In this period, weevils need to recognize the dark apple trees without foliage surrounded by green vegetation. Indeed, they choose a high contrast silhouette in the green wavelength range. In the blue range, the weevils show phototaxis toward the homogeneous transmissive cue, and this difference, in response to achromatic cues in the blue and green range, is significant when analyzed for both sexes together. The necessity to orient toward other colors than green during host plant location might lead to the general preference of blue over green in the visual test arena. Nevertheless, the choice of the low contrast silhouette versus high contrast in the blue wavelength range is surprising and will require field tests for further interpretation.

The more discriminating response of the female sex in the apple blossom weevil in the visual test arena may reflect a greater visual acuity or a higher visual responsiveness in females than in males, possibly because of a higher affinity for the host plant. Females should have an advantage of a more critical choice because (1) they have to select oviposition sites and (2) their choice is final because the larvae cannot abandon the buds into which the eggs were laid. This finding coincides with the visual response of the white pine weevil, *Pissodes strobi*, to cardboard silhouettes in the laboratory: female weevils select only vertical rectangles, whereas males are less critical in their choice (VanderSar and Borden 1977). Similar evidence was found in the Colorado potato beetle, *Lepidotarsa decemlineata* (Say): females took shorter paths to attractive color stimuli, and they were less hesitant than comparable male beetles (Szentesi et al. 2002).

In another curculionid species, the plum curculio, *Conotrachelus nenuphar*, color does not seem to be a strong visual cue when foraging within the canopy of host trees (Leskey and Prokopy 2002). This is in good agreement with our findings because the apple blossom weevils showed no preference for green when this color was offered against other colors. Orientation to green occurred only when green was offered against no color, i.e., against black. During the search for apple buds in early spring, olfactory cues may contribute to female orientation (Kalinova et al. 2000), although experimental evidence on the behavioral effect of single or combined plant-derived chemical compounds is lacking yet in *A. pomorum*.

Phototaxis is considered to be one of the basic orientations in insects with the ability for visual orientation (Jander 1963). This assumption is supported by our finding that color preference remained unchanged over 1 wk after termination of diapause. In contrast, thermal choice in female weevils actually changes with time after diapause because females discontinue to prefer warmer sites at night after about 1 wk after termination of diapause (Hausmann, Samietz, and Dorn, unpublished data).

Results of our study prove that the apple blossom weevil shows positive phototaxis and a preference for the color blue. The color preference seems to be a

conservative trait that does not change during colonization of orchards in spring. Although the physiology of the receptors in curculionids, including *A. pomorum*, remains to be investigated (Briscoe and Chittka 2001), our findings support the hypothesis that the weevils have a trichromatic visual system with UV, blue, and green receptors.

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