Vision is Important for Plant Location by the Phytophagous Aquatic Specialist *Euhrychiopsis lecontei* Dietz (Coleoptera: Curculionidae)

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Abstract The aquatic milfoil weevil *Euhrychiopsis lecontei* Dietz (Coleoptera: Curculionidae) is a specialist on *Myriophyllum* spp. and is used as a biological control agent for Eurasian watermilfoil (*Myriophyllum spicatum* L.), an invasive aquatic macrophyte. We show evidence that visual cues are important for plant detection by these weevils. Weevils had difficulty locating plants in dark conditions and were highly attracted to plant stems in the light, even when the plant sample was sealed in a vial. However, weevils were equally attracted to both *M. spicatum* and another aquatic macrophyte, coontail (*Ceratophyllum demersum* L.) in vials. Turbidity (0–100 NTU) did not significantly influence visual plant detection by the weevils. This work fills a void in the literature regarding visual plant location by aquatic specialists and may help lead to a better understanding of when and where these weevils will find, accept, and damage their target host-plants.

Keywords Host-plant location \cdot insect vision \cdot insect behavior \cdot biological control \cdot aquatic

Introduction

The aquatic milfoil weevil (*Euhrychiopsis lecontei* Dietz; Coleoptera: Curculionidae) is used as a biological control agent for Eurasian watermilfoil (*Myriophyllum spicatum* L.), a widespread invasive aquatic macrophyte (Sheldon and Creed 1995; see Newman 2004 for a review of weevil life history and use as a biological control agent). *E. lecontei*, native to northern North America, is a specialist on native *Myriophyllum* spp., but has expanded its host range to include *M. spicatum* (Newman 2004) since the plant was introduced circa 1940 from Eurasia (Sheldon

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and Creed 1995). In fact, *E. lecontei* has been used to control *M. spicatum* not only because of its negative effects on the plant, but also because weevils were observed to prefer water-borne chemical attractants produced by *M. spicatum* over other *Myriophyllum* spp. (Marko *et al.* 2005; Solarz and Newman 1996), and because weevils develop faster on *M. spicatum* than on native *Myriophyllum* spp. (Newman *et al.* 1997; Roley and Newman 2006).

There are several details of the weevil life cycle important to the research described below. First, during the spring and summer, weevils remain fully submerged, foraging, mating and laying eggs on *Myriophyllum* stems. Eggs are laid on the apical meristems of the plants, after which larvae mine the plant stem and pupate inside it (Newman 2004). The damage caused by adults foraging on leaf tissue and especially by larvae can cause host watermilfoil to fall from the water column and die back. The weevils overwinter as adults in terrestrial leaf litter along lake shorelines, from which they must enter the water or fly to find new host-plants in the spring (Newman *et al.* 2001).

Marko *et al.* (2005) studied the chemosensory abilities of *E. lecontei*. They found that glycerol and uracil were attractive to *E. lecontei*, and that *M. spicatum* exuded these chemicals at higher concentrations than native *Myriophyllum* spp. This work is clearly important in understanding the role of chemosensory capabilities in weevil selection of individual plants or plant species. However, since weevils overwinter on land and re-enter water bodies to find host-plants during the spring, chemical cues are unlikely to play a role in initial host-plant location. Thus, our aim in this study was to evaluate the importance of vision in *E. lecontei* for plant location in the water. Newman (2004) notes that "virtually nothing" is known about plant location by submersed macrophyte specialists (but see Marko *et al.* 2005), so this work is also intended to contribute to the understanding of host-plant location by aquatic specialists.

When compared with the role of chemical cues in host-plant detection/selection, visual plant detection by phytophagous insects has received relatively little attention (Prokopy and Owens 1983). However, vision is important in plant location by many terrestrial insect groups, including Heteroptera (Cook and Neal 1999), Hemiptera (Gish and Inbar 2006; Patt and Setamou 2007; Vargas *et al.* 2005), Diptera (Serandour *et al.* 2006; Drew *et al.* 2003; Aluja and Prokopy 1993), and Coleoptera (Egusa *et al.* 2006; Hausmann *et al.* 2004; Stenberg and Ericson 2007). In the above studies (which do not represent an exhaustive list), only Serandour *et al.* (2006) examined host-plant detection by an aquatic organism. They found that the mosquito larva *Coquillettidia richiardii* Ficalbi uses environmental light cues to locate the roots of its emergent aquatic macrophyte host-plants. However, *C. richiardii* is merely lucifugous (negatively phototactic), thus this work does not represent a strong case for the use of visual cues in host-plant detection.

Supporting the idea that *E. lecontei* may use vision in host-plant detection, evidence exists that some specialists may be more visually oriented than generalist counterparts. For example, in at least one study, a specialist aphid was shown to visually locate host-plants better than a generalist counterpart (Vargas *et al.* 2005). Further, it appears that vision is more important than olfactory cues for plant detection in the monophagous chrysomelid beetle species *Altica engstroemi* J. Sahlberg (Stenberg and Ericson 2007). On top of this, *Anthonomus pomorum* L., a

terrestrial curculionid, may have a trichromatic vision system for host plant detection (Hausmann *et al.* 2004). Thus, evidence exists of specialists visually locating plants, and beetles that show vision to be important in host-plant location, so demonstrating the importance of vision in plant location by *E. lecontei* will add an excellent aquatic example to this relatively undocumented topic.

Since *E. lecontei* overwinters on land, vision is likely important for host-plant location, given that they are unlikely to detect plant exudates from host-plants while flying over lakes to locate host-plants. Similarly, weevils are unlikely to detect exudates from plants that may be tens of meters away if they randomly entered the water from shore while searching for plants. As further evidence for the role of visual host-plant detection, *E. lecontei* also has relatively large eyes (Fig. 1). For *E. lecontei*, finding host plants quickly seems extremely important, as they are poor swimmers, with their legs being adapted to holding onto plant stems rather than swimming. Thus, vision may ultimately help *E. lecontei* find their host-plants and get to the relative safety of a milfoil stem as quickly as possible.

The goal of this study was to gain a better understanding of the role of visual cues in plant detection by the specialist herbivore *E. lecontei*. Understanding the process of plant location and selection may eventually enhance our ability to predict where and when *E. lecontei* will be able to find, select, accept, and damage *M. spicatum*. This study also contributes to the relatively small body of literature regarding visual plant detection by phytophagous insects, particularly those in aquatic systems.

Methods

The *E. lecontei* weevils used for these experiments were donated by EnviroScience, Inc. (Stow, OH, USA). They were housed as same-sex pairs (one individual was

Fig. 1 Photograph of an adult *Euhrychiopsis lecontei* head. Note large eye size relative to head size.



marked on back with nail-polish for identification purposes) in small, clear plastic, sealed $18.9 \times 10.1 \times 10.1$ cm aerated tanks filled with dechlorinated tap water. The weevils were kept on a 14 hL/10 hD cycle using broad-spectrum fluorescent light. Prior to use in these experiments, weevils were given at least two days in their holding tanks to become accustomed to the conditions and light cycle. Each tank was stocked with two *M. spicatum* stems (~12 cm long) that were replaced as necessary throughout the experimental period. *M. spicatum* used in this experiment was collected from various lakes/reservoirs in Portage County, OH, USA. All experimental trials took place between 10:00 A.M. and 2:00 P.M. to help control for any behavioral differences at different times of day.

The behavioral arenas used in these experiments were round 6.5 cm tall, clear glass dishes with an inside diameter of 17 cm at the bottom of the dish. Each arena was filled to a depth of ~2.5 cm with dechlorinated water, which was replaced after every one to two behavioral trials to reduce the presence of chemical cues in the water. The arenas were placed on a level surface atop circular grids (17 cm diameter; Fig. 2) with 12 segments (30° each) radiating from the center to the edge of the arena. Each segment was broken up into five bands (1.7 cm each) from the center to the edge of the arena to quantify how far from the arena center each weevil traveled in a segment by the end of each trial.

Initial observation confirmed, as Solarz and Newman (2001) noted, that *E. lecontei* is positively phototactic. To empirically test this, a dissecting scope light (~9,300 lux) was aimed at a random location along the edge of the experimental arena and a weevil was released in the arena's center. Nineteen of 22 weevils swam directly to the light within 5 min, with the remaining three orienting themselves toward the light. The weevils would even follow the light around the arena when the light was moved haphazardly. To control for this phototaxis during experimental trials, a small fluorescent light bank was placed directly above the experimental arenas. The light

Fig. 2 Grid used to track weevil movement in experimental arenas. Segments (1-12) were used to track weevil direction and plant placement, while bands (*labeled* 1-5) were used to track distance traveled. Plants and/or vials were always placed in band 5 against the arena wall.



bank consisted of two 59 cm bulbs (~90 lux) that were 21 cm apart and elevated ~22.5 cm. The side walls of the arenas were wrapped with aluminum foil to prevent light from entering from the side and in some trials, the arena tops were covered with white 21.6×27.8 cm paper to diffuse light entering the arena.

Importance of Light in Plant Location

To test if light is important for *E. lecontei* in locating *M. spicatum*, our first experiment was to place a single *M. spicatum* meristem (~3 cm long) in a randomly chosen location along the periphery of an arena (multiple plant stems were used across trials and were soaked in dechlorinated water between uses). In each trial, a single weevil was released into the center of the arena and given 10 min to find the plant. For each weevil, paired trials were conducted both in the light and in the dark (n=28 trials per lighting treatment). We hypothesized that if the weevil found the plant in the light but not the dark, visual (light) cues may be driving plant location by the weevils.

For each set of paired trials, the first lighting treatment was randomly selected and the remaining light or dark trial was immediately performed upon the conclusion of the first trial. Using the same weevil, the same plant stem was moved into the same relative location (i.e., band five in same segment) in a fresh arena for the remaining trial according to the grid in Fig. 2. For dark trials, arenas were placed into cardboard boxes with corners and seams covered with aluminum foil. The boxes in which the arenas were placed were at least four times taller than the arena to prevent light from entering through the sides. The arenas were then also covered with smaller cardboard boxes close to the same size of the arena, again with corners and seams covered with aluminum foil. After the 10-min movement period, weevil location was recorded. For statistical analysis of this light–dark experiment, a McNemar test was used to compare the number of weevils that found the plant only in the light vs. only in the dark.

Weevil Attraction to Plants in Vials

To further isolate the importance of visual cues in *E. lecontei* plant location by eliminating the role of chemical cues, the remaining experiments focused on weevil response to *M. spicatum* meristems that were sealed in water-filled, clear glass, one-dram vials. Prior to vial use in these experiments, vials were filled with food coloring, capped, and submerged in water to confirm that no food coloring (used as a surrogate for plant chemical cues) escaped from the vials. Finally, all vials were rinsed between trials.

Vials containing *M. spicatum* meristems were placed at random locations around the arena's edge, as in the light–dark experiment. However, preliminary experiments showed weevils would often swim to the vial containing the plant but then swim away after a short time of not being able to get onto the plant. This did not happen when exposed plants were used in the light–dark experiment, where all weevils that found the plant had to be physically removed from the plant by the experimenter at trial's end. Because the weevils would not stay on the vials, the paper light diffuser was not used and weevils were observed directly. Since the light bank used in these experiments consisted of two bulbs running horizontally above the experimental arenas, few (if any) directional light cues existed, as weevils showed no tendency to swim in any particular direction during initial observation. Since no plant chemical cues could be present in these experiments, and results of the light–dark experiment were so convincing relative to the role of vision in plant detection, all vial experiments were only conducted in the light.

The first vial experiment was conducted in order to eliminate the possibility that weevils were attracted to the vials alone. For this experiment, we placed a vial at a random location along the periphery of the arena. The weevils (n=15) were run though paired trails with *M. spicatum*-filled vials and empty (filled only with fresh tap water) vials, in random order, one immediately after the other. The time it took the weevil to contact each vial was recorded. Vials were placed in the same randomly selected location for each treatment and arenas and water were changed between each treatment. Weevils were given 10 min to contact the vial in each trial, and the trial was stopped if the weevil did not find the vials in the allotted time (this protocol was followed for all experiments that follow). For this experiment, a two-tailed paired *t*-test was used to compare the time to vial for each treatment type.

Visual Plant Differentiation

This experiment involved determining if weevils can visually differentiate between plant species. Using the methods described for the previous vial experiment, each weevil (n=17) went through paired trials with either *M. spicatum* or coontail (*Ceratophyllum demersum* L.) meristems in sealed vials, in randomly chosen order. *C. demersum* was chosen for use in this experiment because it is similar in overall color and form to *M. spicatum* but has different leaf and branch formation. The time it took the weevil to contact the vial containing a given species was recorded for each trial. The location of the vials along the arena wall was again randomly assigned and stayed the same for each trial pair. For this experiment, a two-tailed paired *t*-test was used to compare the time to vial for each treatment type.

Effect of Water Turbidity on Plant Location

The final experiment was conducted to determine how water turbidity affects visual plant location by the weevils. For this experiment, each weevil (n=11) was run through three levels of turbidity: clear (unaltered, dechlorinated tap water), 40 NTU (nephelometric turbidity units, an arbitrary unit of turbidity measured by a nephelometer; 40.87 ± 1.70 NTU [mean ±1 SD across treatment replicates]), and 100 NTU (101.09 ± 2.48 NTU [mean ±1 SD across treatment replicates]). Turbidity was manipulated by varying the concentration of bentonite clay suspended in the arena water. These relatively high turbidity values were selected after initial trials demonstrated that much lower turbidity levels had no negative effect on plant location by weevils. Each weevil was run through the three turbidity treatments in random order, with the vial containing an *M. spicatum* meristem placed randomly in the same position along the arena periphery in each trial. Once more, time elapsed until contact with the vial was recorded. For each weevil, the slope of the relationship between turbidity level and time to the vial was estimated. Then, a one-

tailed, one sample *t*-test was performed on these slopes with the expectation that there would be a positive slope to these lines, indicating that weevils generally found vials more quickly at lower turbidity levels. This regression slope approach was used so we could keep track of individual weevils' performance, as there is much variation in individual weevils' ability to swim.

Overall, variation in sample size across this series of experiments was a result of high levels of within-lab weevil mortality. Also, weevils that could not move from arena center (e.g., weevils that got stuck on their backs on the arena bottom) in experiments were not included in analyses. For all vial experiments, weevils that did not contact a vial within the allotted 10 min were excluded from the analyses as well.

Results

Importance of Light in Plant Location

In the light–dark experiment, weevils found the *M. spicatum* meristem in the light significantly more frequently than in the dark (McNemar P < 0.0001; n=28), with 19 out of 28 weevils finding the plant in the light but not the dark. Of the remaining nine weevils, one weevil found the plant in the dark but not the light, four found the plant in the light and dark, and four never found the plant (Fig. 3). It should be noted that weevils still moved in the dark, as 20 of 23 weevils that did not find the plant in the dark were in the fourth or fifth band of the arena at the trial's end, with many swimming vigorously into or along the arena's edge.

Weevil Attraction to Plants in Vials

The weevils were significantly more attracted to sealed vials containing an *M.* spicatum stem than to empty vials (paired *t*-test P=0.0138; t=-3.0478; n=10; Fig. 4). Those weevils that contacted the empty vials appeared to do so through random movement around the experimental arena and showed no tendency to stay at





the vial after initial contact. In contrast, for vials containing an *M. spicatum* meristem, weevils swam directly to the vial when it entered their field of view and swam against the vial for several seconds seemingly to get to the plant (data were not recorded relative to time spent attempting to get to plant meristem, as trials were ended shortly after vial contact). Four weevils were excluded from this analysis for not contacting the empty vial during the allotted time (i.e., 10 min) for the trials, while one weevil was excluded for not contacting the *M. spicatum* vial during the allotted time.

Visual Plant Differentiation

The weevils were not more attracted to *M. spicatum* than *C. demersum* in vials (paired *t*-test P=0.7216; t=0.3631; n=16). The average time to vial for the *M. spicatum* treatment was 50.7 s, while the average time to vial for *C. demersum* treatment was 46.6 s. One weevil was excluded from this analysis for not contacting the vial within the allotted time in a *C. demersum* trial.

Effect of Water Turbidity on Plant Location

Turbidity did not significantly affect weevil ability to locate *M. spicatum*-filled vials (one-tailed, one sample *t*-test P=0.3179; *t*=0.4883; *n*=11). In this analysis, six of the eleven weevils had positive slopes for the relationship between their time to vial and turbidity, with the remaining five weevils having negative slopes. Slopes ranged from -17.215 through 10.52, with an average slope of 1.065. None of the individual slopes were significantly different than zero.

Discussion

These experiments demonstrated that vision plays an important role in *M. spicatum* location by *E. lecontei*. Not only did weevils find plants much more easily in the

light than in the dark, the weevils also showed attraction to plants in vials sealed to prevent any chemical cues associated with *M. spicatum* from influencing their behavior.

Given that weevils did not differentiate between *M. spicatum* and *C. demersum*, or at least were not more attracted to one than the other, vision is likely not the ultimate determinate of how these specialist weevils select their host-plants. Prokopy and Owens (1983) note that the historically accepted phases of host plant selection by phytophagous insects include: host habitat location, host location, host recognition/acceptance, and host suitability. Since these weevils over-winter on land and must crawl into or fly over water to find their host plants (Newman et al. 2001), vision is likely used for at least the host habitat location and host location phases. Chemical cues (Marko et al. 2005) may explain host-plant selection by E. lecontei and how the weevils differentiate among macrophyte species and select appropriate plants. It is possible that vials used in these experiments distorted the image of the plants they contained, so it should not be concluded that weevils cannot visually differentiate between plant species based solely on these data. The weevils are also poor swimmers and may have been trying to get to the first plant they could to cling onto, especially in the novel and potentially stressful environment of the experimental arena.

It seems from these data that color and/or shape contrast may be important for the weevils to visually identify potential plant hosts, supporting the appropriate/ inappropriate landings hypothesis whereby insects may land haphazardly on green objects and use other (chemical) cues to discern appropriate hosts (Finch and Collier 2000). The results of the turbidity experiment may further support this notion. Even in highly turbid water, the weevils still easily found the plant-containing vials. The sample size for the turbidity experiment was small (n=11), but it seems clear from the data that the weevils can discern and become attracted to the form and/or color of a plant at a distance of at least 8.5 cm (the distance from the center of the arena to its edge). Even under highly turbid conditions, all weevils contacted the vials via direct swimming paths from the release site, not random movement. These data may be promising to lake managers utilizing *E. lecontei* as a control for *M. spicatum*, as the weevils seem to not be highly affected by turbid water. The water was well illuminated for the turbidity experiment, however, so the weevils may react differently under field conditions

Beyond visual attraction to the plants, the positively phototactic tendencies of the weevils may also prove interesting relative to navigational abilities. Initial pilot experimentation using the light–dark methods involved undiffused, ambient laboratory lighting. The weevils still tended to find the plants more in the light than in the dark. However, the weevils seemed to be swimming to the top of the water column in the direction of the closest ceiling light in the laboratory. Given this anecdotal result, we hypothesize that the weevils may use light cues to navigate to appropriate locations on their host plants (e.g., meristems for oviposition).

The aphid *Sitobion rosaeiformis* Das is positively phototactic and may use sunlight as a directional cue to move upward onto plants for safety and food, especially after dropping off their host-plant for predator escape (Hajong and Raghu Varman 2002). Similarly, if *E. lecontei* becomes dislodged from its host-plant, the weevils may very well use sunlight at the water surface to reorient, particularly given

that adult weevils feed on the top portions of the plants. Supporting this notion, Solarz and Newman (2001) note that *E. lecontei* tends to swim upward. Females may use sunlight to guide them to the floating apical meristems where oviposition occurs. Further, we speculate that males may potentially even use sunlight to help them locate these females.

When considering host-plant selection in phytophagous insects, more attention is paid to chemical cues than visual cues (Prokopy and Owens 1983; see Bernays and Chapman 1994 for comprehensive information on chemical cues). However, flying insects do use visual cues to find host-plants (Prokopy and Owens 1983). This work adds to the small body of literature on visual host plant location by aquatic insects, showing that they too use vision to find host-plants. The data presented in our study clearly indicate the importance of vision in plant location for these specialist aquatic weevils and provide another example of an insect that uses visual cues in locating its host-plant.

Gaining an understanding of what affects host-plant location and selection by biological control agents such as *E. lecontei* can be of critical importance. Having knowledge of factors influencing weevil behavior, particularly relative to host-plant detection, should lead to a better understanding of when and where they will be most effective as a biological control agent. For instance, if *E. lecontei* adults that overwintered cannot find *M. spicatum* because of factors such as wave action, low light conditions, plants with unattractive morphology, etc., they cannot attack or control the plant. Research is warranted, then, regarding how well the weevils can detect submerged plants from the air if they are flying to find their host-plants, or how far they may be able to see underwater if they entered a lake. These questions should also be answered relative to the potential plant location influences noted directly above.

While the work presented here is not a comprehensive study of cues used by E. *lecontei* to find M. *spicatum*, it does provide strong evidence that vision is important and justifies further research. For example, experiments could be devised to test how well weevils can find M. *spicatum* in mixed stands, or if weevils are visually more attracted to certain morphologies (i.e., size, branch number, color etc.) of M. *spicatum* over others. An understanding of factors such as these will ideally allow for better prediction of biological control efficacy not only of E. *lecontei*, but any biological control agent for which vision is important in host-plant location.

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