Caddisfly Larvae Visual System: Response to Light

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Abstract

Understanding the behavior the caddisfly larvae (Trichoptera, Integripalpia) can have implications in a variety of areas (i.e. the fishing industry) and issues surrounding environmental impacts. This study examines the caddisfly larvae's response to a controlled light stimulus. Experiments were completed in an environment designed to mimic the larvae's natural habitat while controlling the light exposure. During experiments, the majority of the animal's tank was kept completely dark with the exception of a narrow, defined light path which resulted in three different levels of light exposure within the tank. The caddisfly larvae's location and head orientation with respect to the three light levels were recorded. These experiments suggest that caddisfly larvae migrate to lighted areas and not towards darkness. Additionally, head orientation tends to be towards the lighted areas in the tank, similar to non-aquatic insects, but not overwhelmingly toward the source of the light. Furthermore, once in a lighted condition, either direct or ambient light, caddisfly larvae tend to stop moving and remain in the lighted condition.

The larval caddisfly (*Trichoptera, Integripalpia*) is an aquatic insect species found in cool, freshwater and fast moving streams. The caddisfly larvae make up a large portion of the brook trout's diet, and thus their behaviors are of interest to anglers and the recreational fishing industry as a whole. In addition, the caddisfly larvae are used by environmental scientists to assess stream quality. Since the caddisfly larvae are intolerant of many pollutants, their survival within a stream is indication of a "good" stream rating on the WAV index chart (Morse, 1997). Thus, for a variety of reasons it is important to understand both the behavior and physiology of these insects. This paper examines the visual system of the caddisfly larvae, and more specifically, their behavioral response to light.

Literature Review

At present, limited information is available on the visual system of the larval caddisfly. Gilbert (1994) suggests they have light detecting stemmata rather than ocelli like many other larval invertebrates. In *Lepedoptera*, insects in the same phylogenetic superorder as the caddisfly, stemmata are capable of sophisticated vision and help to serve as guideposts for developing compound eyes (Morse, 1997). Indeed, studies on *Lepidoptera* indicate these animals respond positively to light and are attracted toward it, but have a "broad, but incomplete coverage of the environment" (Gilbert, 1994). Thus, they can detect light in their environment, but cannot distinguish details of their surroundings. A similar assessment of caddisfly vision has not yet been completed.

The caddisfly is a holometabolous insect, with the larvae living in freshwater habitats (Morse, 1997). The first larval instars start in the fall, remain dormant over winter, and continue their instar stages in the spring (Hart & Resh, 1980). Caddisfly larvae spend their larval stages either attached to local structures (e.g. rocks) or in motion, crawling or free-floating in the water.

Activity seems to peak at midday and decreases thereafter (Gallep, 1975). Hart and Resh (1980) described the larvae as being more sedentary during the night than during the day, consistent with Gallep's (1975) results. They spend approximately two thirds of their lives filtering (feeding) and this seems to occur while the animal is attached to a structure (Hart & Resh, 1980). Gallep (1975) found that filtering occurs most frequently during hours of darkness, while all other activities, such as case-building, being withdrawn, moving, and free-floating, happen mostly during the day. These data may suggest that the animals are drawn to darkness where their feeding routine is carried out. This study examines whether these animals are specifically attracted to dark areas in their environment or if they prefer to be in a lighted environment. In contrast to the previous studies, which examined the animals behavior infrequently (only two times in a 24 hour period), this study examines the animals' behavior in the short-term, allowing for a more detailed description of the animal's response to light.

Method

Environmental Conditions

Larval caddisfly were studied in a laboratory environment under conditions meant to mimic their natural habitat. Specimens were obtained from a western Wisconsin stream (Elk Creek, Southern Branch) which has an average temperature of 61°F. Larvae were housed in a ten-gallon glass tank. Water temperature was maintained between 58° and 63°F and a current was induced by placing the bubbler and output hose of the water chiller unit at one end of the tank and the water pump/chiller intake hose at the opposite end of the tank. Various sized rocks, collected from Elk Creek, were placed within the tank to provide natural attachment points for the caddisfly larvae. The larvae were nourished by adding crushed natural vegetation to the tank.

In order to study specific light responses of these animals, it was necessary to control the light level within the tank. Light was blocked from the sides and top of the tank with 2mm thick black panel board. Light entry through the bottom of the tank was eliminated by the use of a removable black fabric looped under and attached to the sides of the tank with Velcro. It was necessary for this lower panel to be removable in order to mark the location and orientation of the animals on the bottom surface (see *Data Collection and Analysis*). Finally, an additional black canopy tent was used to completely enclose the experiment along with the investigators during data collection. All light exposure experiments were done with the overhead room lights off and the investigator was completely dark-adapted for the course of the experiment. On one of the small faces of the tank, a 2.5 x 2.5 cm square was cut in the lower corner. This was the entry point for the controlled light exposure into the tank.

Experimental Parameters

A full spectrum bulb (wavelength ~315nm-700nm) was used to replicate natural light during the data collection portion of the experiments. Light was shown through the square opening in the corner of the tank. The light source caused different areas of the tank to experience varying levels of light exposure as observed by looking down from the top opening. The different light levels were categorized as *light path*, *ambient light* and *darkness*. The *light path* consisted of the observed distinct beam of light along the bottom of the tank. *Ambient light* were those areas outside the distinct light path, but where general shapes could be distinguished by looking without the use of a flashlight. For example, if it was possible to see a caddisfly larvae sitting on a rock out of the distinct path, the animal was considered as having an ambient light exposure. The transition between the light path and the ambient light was somewhat subjective, because the light path did not have a defined edge. In cases where an animal was on the border between these two areas, it was considered to be in ambient light. *Darkness* was defined as areas where shape could not be distinguished without the use of a flashlight.

The process for each experiment was as follows. First, in all but one experiment (light control, see below), the animals were placed in total darkness for 36-48 hours before data was collected (the cover was placed on top of the tank, the black sheet was placed under the tank, the canopy was draped over the experimental set-up and the overhead room lights were turned off). At the start of data collection, the light source was turned on. Immediately following, the caddisfly larvae were placed in specific locations within the tank. The locations were chosen for specific light exposure of the animals. Some animals were placed in the light path, others were placed in ambient light locations and still others were placed in the dark. The location, head orientation, and light exposure level of the animals were recorded every five minutes for approximately two hours. A flashlight was used briefly to locate the animals within the tank.

Two variations of the above parameters were used as controls. In the first, the light source was not turned on after the 36 hour dark period (dark control). The specimens remained in the dark during the entire two-hour data collection period, with the exception of when a flashlight was turned on briefly to observe their location and head orientation. This experiment indicated how the animals responded to strict darkness. In the second control experiment, the room lights, but not the full spectrum bulb, were turned on 41 hours before and during data collection (light control). The canopy did not cover the experimental set-up and the top and bottom covers for the tank were removed. Only the sides of the tank were kept covered. This experiment indicated how the animals respond in full light.

Data Collection and Analysis

To differentiate between caddisfly larvae, four specimens were marked by wrapping different colored orthodontic rubber bands around the outside of the larval case (orange, blue, yellow and green). If the rubber bands fell off in between experiments, a new specimen was chosen for marking. The bands did not appear to deform the case nor did they restrict the animals' mobility. Previous studies indicate that the immediate response of caddisfly larvae when handled is to withdraw into their case, but if little to no handling occurs, the behavior is close to that of unmarked larvae (Gallep, 1975). Even with marking, there is no significant difference in behavior (Hart & Resh, 1980). This also seemed to be the case in the study described here. The marked specimens seemed to move in a manner consistent with their unmarked counterparts. Attached to the bottom of the tank was a removable glass panel on which the location and head orientations of the animals were marked with a washable pen. The animals were observed by briefly removing the top panel and looking into the tank from above. A flashlight was used to provide brief, directed light in order to locate the animals in the tank for each observation. Furthermore, the light path, rocks, bubbler, pump and tubing were drawn in their relative locations. A single colored line, matching the color of the rubber band for a given specimen, was used to indicate the location of the animal. The direction of the line matched the angle of the caddisfly larva's case. Head orientation was indicated using a small perpendicular line at the head position. The position and head orientation was recorded every five minutes. In addition to the markings on the glass panel, light exposure, whether or not the animal was moving, and the direction of that motion was recorded for each observation.

From the glass panel data it was possible to extrapolate overall motion with respect to both the light path and the light source. To do this, the observations for each animal were divided into trial blocks. A trial block included all observations between the time a specimen was placed in a specific location in the tank and the time the animal remained still for at least three observation periods (15 minutes). During the course of a normal experiment, each marked caddisfly larvae was placed in a specific location approximately 2-3 times. Subsets of data were obtained for each of these trial blocks, including light exposure and head orientation at the beginning and end of each trial block.

Results

General Animal Behavior

Marking the animals with colored rubber bands did not seem to affect their mobility as compared to their unmarked counterparts, which is consistent with previous studies (Gallep, 1975; Hart & Resh, 1980). Thus, it is unlikely that marking the animals influenced the light response behavior. Furthermore, it is unlikely that the artificial environment in which the animals were observed influenced their natural tendencies. Indeed, Hart and Resh (1980) found that various factors of the physical stream parameters, such as turbidity or current, among others, do not affect behavior.

Preferred Ending Locations

When free to move throughout their environment, caddisfly larvae tend to gravitate toward a lighted area over a short time period (Figure 1). Regardless of whether animals were initially placed in the dark, ambient light or direct light, generally within one hour the animals repositioned themselves so they were exposed to light. There is not a clear preference, however, for animals to locate in direct light as compared to ambient light.

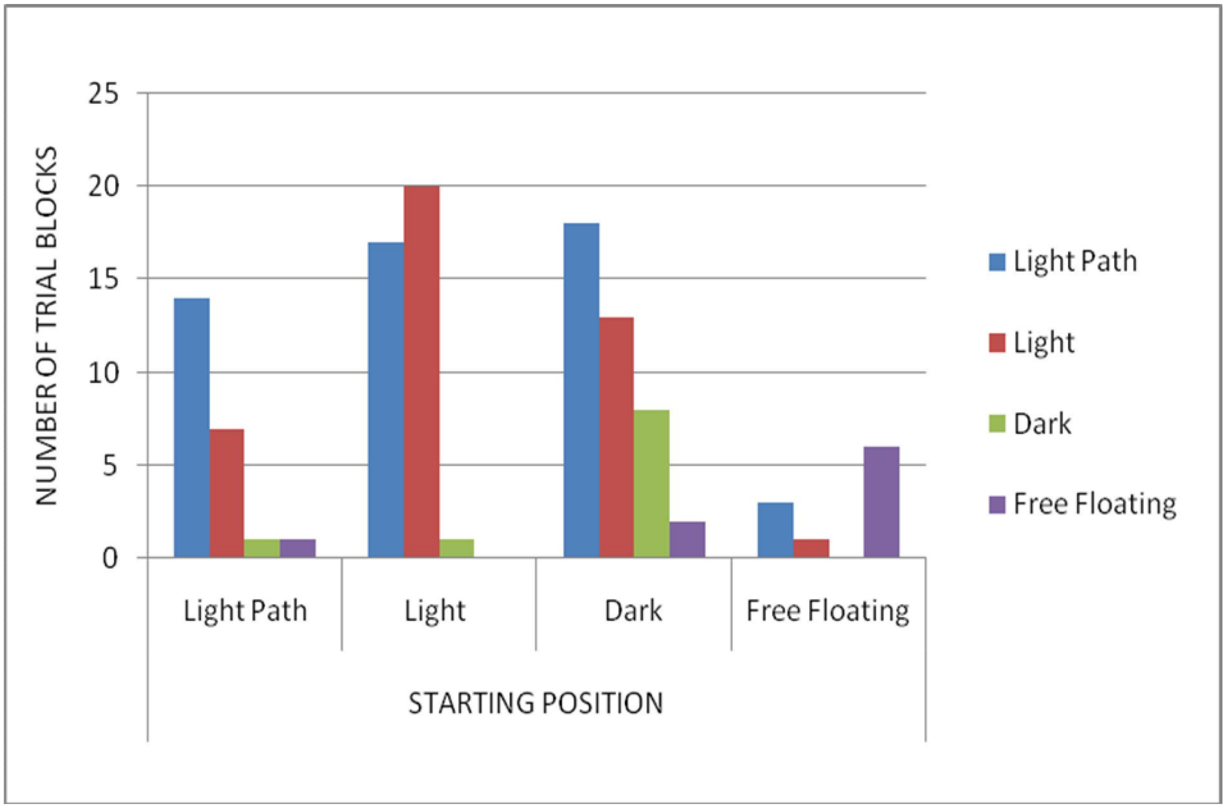

Figure 1: Starting and ending locations for total trial blocks. Different starting locations are shown on the horizontal axis. Ending locations are represented by the colored bar, as indicated in the legend. The vertical axis represents the number of trial blocks.

Of the 112 total trial blocks (all animals and experiments), 41 trial blocks (36.6%) started in the dark, 38 trial blocks (33.9%) started in ambient light, and 23 trial blocks (20.5%) started in direct light. There was a small collection of trial blocks (10 trial blocks, ~9%) where animals were not directly contacting a structure or the bottom of the tank and were either floating freely through the tank or attached to a structure via their silk and moving under the control of the current. These 10 trial blocks are included in Figure 1 but not in the detailed analysis below.

When animals were placed in the dark, 75.6% of trial blocks ended in a lighted condition whereas only 19.5% ended in the dark. There was a small collection of animals placed in the dark that ended free floating (4.9%). While the animals shifted their position towards a lighted condition, there was only a minimal preference specifically toward direct light as compared to ambient light (43.9% vs. 31.7%, respectively). When animals were placed in ambient light, they tended to either remain where they were initially placed (52.6%) or shift to direct light (44.7%). Only 2.6% of trials resulted in the animals shifting towards darkness. A similar result occurred when animals began in direct light. Although most (60.9%) of the trial blocks resulted in the animals staying within direct light, in 30.4% of the trial blocks the animals shifted towards ambient light, and in only 4.3% (1 of 23 trial blocks) did an animal move from direct light to darkness. Taken together, these data suggest that the caddisfly larvae have a strong tendency to position themselves in a lighted area over a short time period. However, there does not seem to be a strong tendency for these animals to be located in direct light, but rather direct or ambient light is sufficient. Furthermore, the caddisfly larvae do not gravitate towards darkness.

Head Orientation Behaviors

Since the caddisfly larvae prefer to be in a lighted environment, it might be expected that animals would orientate their heads towards the light path or the light source. Since the stemmata are located lateral on the head, the caddisfly larvae may also orientate their head parallel to the light path or light source. When the animals were in the dark, their heads were orientated towards or parallel to the light path in 75.3% of observations (Table 1). Animals in ambient light showed a tendency to orientate towards or parallel to the light path in 67.3% of observations. Since animals located within the light path are, by default, orientated toward the path, they were not considered in this analysis.

Table 1

Caddisfly Head Orientation Relative to Light Path

	Towards/Parallel to Light Path	Away from Light Path

Animals in Darkness	75.3%	24.7%
Animals in Ambient Light	67.3%	32.7%
OVERALL	71.3%	28.7%

In addition to orientation towards the light path, the orientation towards the light source was also examined for each observation, including those where the animal was located within the light path (Table 2). Animals in the dark orientated specifically towards or parallel to the light source in 72.6% of observations. When animals were in ambient light, they orientated towards or parallel to the light source in just over half of the observations (55.2%). Similarly, when animals were within the light path, they again orientated towards or parallel to the light source in nearly half of the observations (44.7%).

Table 2
Caddisfly Head Orientation Relative to Light Source

	Towards Light Source	Away from Light Source
Animals in Darkness	72.6%	27.4%
Animals in Ambient Light	55.2%	44.8%
Animals in Light Path	44.7%	55.3%
OVERALL	57.5%	42.5%

Taken together, these data suggest that while the animals position themselves so they are orientated toward the light path, they show only a slight preference towards the source of that light, particularly when they are already in a lighted area.

Observed Movements

For some of the observations (70 of 798), the specimen was moving during the observation time. In these situations, the direction of motion was recorded with respect to the light path and the light source (Tables 3 & 4).

Light Path: Only observations while the animals were located outside the light path were considered (49 of 70). A large majority (91.4%) of these observations showed motion towards the light path (Table 3). Of these 49 observations, 14 were of animals located in the dark and all these animals showed movement towards the light path. Of the remaining 35 animals, which were located in ambient light, 91.4% showed motion toward the light path.

Table 3
Caddisfly Movement Relative to Light Path

	Towards/Parallel to Light Path	Away from Light Path
Animals in Darkness	100%	0%
Animals in Ambient Light	91.4%	8.6%
OVERALL	95.7%	4.3%

Light Source: All 70 observations where motion occurred during the recording were assessed to determine the direction of motion relative to the light source (the small 2.5 x 2.5 cm square at the corner of the tank; Table 4). Larvae located in the dark moved towards the light source in 75.0% of trials. Specimens in ambient light moved towards the light source 72.7% of the time. Finally, the animals within the light path moved 61.9% of the time toward the light source. These data suggest the animals do show a slight tendency for motion towards the light source.

Table 4

Caddisfly Movement Relative to Light Source

	Towards Light Source	Away from Light Source
Animals in Darkness	75%	25%
Animals in Ambient Light	72.7%	27.3%
Animals in Light Path	61.9%	38.1%
OVERALL	69.9%	30.1%

Taken together, the motion data is consistent with the location data presented previously, such that the animals prefer to locate in light areas. Although Table 4 suggests that the animals have a preference to move towards the light source, since the light source is within the light path, it is difficult to distinguish between these two.

Control Experiments

Darkness: When animals were placed in complete darkness, their behavior did not follow a specific pattern. For example, one specimen orientated its head in a variety of directions with very little translational movement. Another specimen remained orientated in one direction with linear movement but, when relocated, orientated in a variety of directions with little movement. The last specimen remained free-floating for the majority of the experiment. These data suggest that when the insects are in complete darkness, they do not orientate their heads or move in a distinguishable pattern.

Complete Light: The overall behavior of animals in total light is much more sedentary, with only 7 changes in location per animal during the entire 2 hour experiment. This is in contrast with the roughly 14-21 location changes per animal that occurred during the light exposure experiments. This limited movement in a lighted environment is consistent with the suggestion that once animals are within a lighted environment, they tend to remain stationary.

Discussion

Caddisfly larvae prefer exposure to light (Figure 1). When specimens are placed in darkness, they gravitate to either direct or ambient light. When the specimens are placed in either the direct light or ambient light, they tend to remain in a lighted condition either by staying in their current light exposure or moving between the two types of light exposure. Given that the animals relocate themselves in both direct light and ambient light with similar frequency, there does not seem to be a preference for one light condition over the other. For all three starting conditions, the animals did not tend to remain in or gravitate toward darkness (only 2 of 61 trials starting in either direct light or ambient light moved to darkness and in only 8 of 41 trials starting in darkness the animals remained in darkness).

While the animals did not seem to gravitate differentially toward direct light as compared to ambient light, they did orientate their heads toward the light path (Table 1), but not necessarily toward the light source (Table 2). Similarly, when animals were moving during the observations, they seemed to move towards or parallel to the light path (Table 3), and with a slight preference toward the light source (Table 4). However, since the light source is within the light path, it is difficult to determine whether the preference was toward the source specifically.

If the animals gravitate towards lighted areas (direct and ambient) but not specifically towards the direct light (and thus the light path), then why is there a slight tendency for both their head orientation and observed movements to be toward the light path? It is possible that the physical size of the aquarium limited the animals' ability to differentiate between direct light and ambient light, particularly since there was not a clear distinction between these two adjacent areas in the tank. Even with this possibility, a strong tendency for these animals to position themselves in a lighted area is evident.

While it appears to be common knowledge that non-aquatic insects gravitate toward light, prior to this study, little has been known about aquatic insects' response to light. Further, as the first of its kind, this paper describes a methodology that is effective for studying specific short-term light responses in aquatic insects. Knowing whether or not an aquatic insect gravitates toward light might aid environmental scientists and others in various pursuits. For example, by artificially controlling the light exposure within the stream, it may be possible to manipulate where a specific aquatic insect locates. Further, knowing valuable information about the caddisfly larvae will aid researchers examining behaviors of brook trout in a stream, since during feeding times, brook trout may tend to mimic behaviors of the caddisfly larvae.

This study describes the first examination of the visual system in the caddisfly larvae. It will be valuable to expand these ideas and techniques to look at more complex visual processing such as the threshold of light detection and color distinguishing capabilities. One might expect minimal color capabilities since stemmata serve as guideposts for the more sophisticated compound eye in phylogenic orders such as *Lepidoptera*, and it has been shown that even the larvae of *Lepidoptera* have "green sensitive photoreceptors" (Gilbert, 1994). Even though the stemmata are only light and dark detectors, there could be other factors involved which cause a preference towards a particular wavelength, and thus color, of light.

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