Display Behavior of *Ligumia* (Bivalvia: Unionidae)

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Abstract - Gravid females of *Ligumia* display marginal papillae to attract fish hosts for their parasitic larvae. In *L. nasuta* and *L. subrostrata*, the papillae move rapidly and synchronously, but we did not see *L. recta*'s papillae move. The moving displays of *L. nasuta* and *L. subrostrata* attract fish, which readily attack displaying females, causing them to release glochidia onto the fish. Display frequency in *L. nasuta* and *L. subrostrata* slows in low light and stops in the dark. *Ligumia recta* displays both in the light and in the dark. High turbidity stops the displays of *L. nasuta* and *L. subrostrata*. Displaying females of *L. nasuta* and *L. subrostrata* move more at night than during the day, perhaps allowing them to display to different fish each day.

Introduction

The life cycle of unionoid mussels includes a larva (the glochidium) that is parasitic on fish. The short life (days to weeks), non-motility, and host-specificity of larvae may subject them to enormous mortality; indeed, larval mortality rates in nature have been estimated to be much greater than 99% (Jansen et al. 2001, Young and Williams 1984). Not surprisingly, several kinds of adaptations have arisen that apparently increase a larva's chance of encountering and attaching to the correct fish host. Gravid female mussels may display lures to attract fish (Haag et al. 1999, Kraemer 1970), or release larvae in small (Hartfield and Hartfield 1996; Watters 1999, 2002) or large (Haag et al. 1995) packages that closely resemble prey items of fish hosts. Knowledge of the host-finding adaptations of unionids is incomplete, however, as many species have not yet been investigated. Such knowledge will aid in understanding evolutionary relationships among unionids and ecological relationships among unionids, host fishes, and environmental conditions. Here, we describe the display behavior of females of the genus *Ligumia*, a genus that has not been previously investigated.

The genus *Ligumia* is defined by the presence of papillae along the mantle margin of females (Burch 1975, Smith 2000). *Ligumia* contains three or perhaps four species, and is widespread and common in central and eastern North America (Burch 1975, Williams et al. 1993). *Ligumia nasuta* (Say) and *L. subrostrata* (Say) have similar shell morphologies and small marginal papillae, and live in quiet waters in northeastern and southcentral to central North America, respectively. *Ligumia recta* (Lamarck) is a much

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larger animal with very large marginal papillae, and lives in streams, rivers, and lakes over a large area of central and eastern North America. A fourth species, "*Ligumia*" *ochracea* (Say), may belong to the genus as well. This species seems not to be closely related to any other unionid species and has been difficult to place in any genus. Formerly assigned to *Lampsilis* and *Leptodea*, it was placed in *Ligumia* by Smith (2000), although its marginal papillae are minute. Its ultimate systematic placement will require further research. Centrarchids are hosts of *L. subrostrata*, and *L. recta* uses many fish species as hosts, including centrarchids, percids, cyprinids, and others, although *Sander canadensis* (Smith) (sauger) appears to be the primary host (Khym and Layzer 2000, Museum of Biological Diversity 2006). The hosts of *L. nasuta* have not been studied.

The function of *Ligumia*'s characteristic marginal papillae has not been investigated. Ortmann (1912) suggested that *Ligumia*'s papillae regulate "the aeration of the glochidia," but no functional studies have been done. The only previous work on display behavior of *Ligumia* was done by Welsh (1933), who noted only that the "mantle flaps" of *L. nasuta* contracted rhythmically, and that light intensity affected the frequency of contractions. We made a series of observations of all three accepted species of *Ligumia* to document their display behavior, interactions with fishes, and response to changing light intensity and turbidity.

Methods

Gravid females of all three recognized species of *Ligumia* were collected from Illinois and New York from May–July 1998, 1999, and 2004 (Table 1). Each species was housed separately in 38- or 76-L glass aquaria containing well water and kept in a temperature-controlled room at 19–21 °C. Temperatures were gradually increased from 19 to 21 °C during May to June. Dual full-spectrum fluorescent bulbs were hung 28 cm above the aquaria and set on a timer for a 12-h daylight cycle (0700–1900 h) for the month of May, then increased by approximately 15-min increments to a 15-h 15-min daylight cycle (0530–2045 h) by 10 June. Timers for the two light fixtures were staggered 5 min apart to mimic dawn and dusk. Each aquarium contained a 5-cm layer of mixed cobble/

Table 1. Collection information on mussels studied in captivity.

Species (# of individuals)	Collection date	Water body	Days in captivity
L. nasuta (1)	19 June 1998	Lake Taghkanic, Taghkanic, NY	35
L. nasuta (2)	22 June 1998	Webatuck Creek, Dover, NY	25
L. nasuta (4)	19 May 1999	Webatuck Creek, Dover, NY	32
L. nasuta (6)	16–18 June 2004	Webatuck Creek, Dover, NY	43–45
L. subrostrata (7)	25 May 1999	Horse Creek, Sangamon County, IL	20
L. recta (2)	22 June 1999	Allegheny River, Portville, NY	7

gravel/sand substrate, a Whisperlite® powerfilter to filter the water, and a Renaissance 400® air pump for aeration. We changed ≈ 25% of the aquarium water every 2 d. In 1998, we used well water for water changes. In 1999 and 2004, we used water from a unionid-free pond or brook in Millbrook, NY, hoping that its plankton content would encourage the mussels to feed normally.

We used a Sony LE Handycam camcorder mounted on a tripod to record mussel behavior. If the mussel could not be filmed properly from the tripod, the camcorder was handheld and maneuvered into position. We marked the shells of displaying mussels with spots of Liquid Paper™ to distinguish among them. We filmed *L. nasuta* for 380 min over 9 d, *L. subrostrata* for 277 min over 13 d, and *L. recta* for 40 min over 2 d. In addition, we made extensive but unvideotaped observations of mussels at various times of the day and night from 19 June–26 July 1998 and 24 May–27 June 1999 for *L. nasuta*, 27 May–27 June 1999 for *L. subrostrata*, and 23–27 June 1999 for *L. recta*.

Interactions between mussels and fishes

We introduced fish to displaying mussels during trials in 1998–99 (Table 2). Small *Lepomis macrochirus* (Rafinesque) (bluegill) were seined from a unionid-free pond in Millbrook, NY, and *Luxilus cornutus* (Mitchill) (common shiner) were seined from the unionid-free East Branch of Wappinger Creek in Millbrook, NY, for observations with mussels in June 1998. For the 1999 studies, we obtained bluegill, *Lepomis gibbosus* (Linnaeus) (pumpkinseed), *Micropterus salmoides* (Lacépède) (largemouth bass), and *Micropterus dolomieu* Lacépède (smallmouth bass) from Northeast Aquatics hatchery in Rhinebeck, NY. None of the fish used in these studies had previous exposure to unionids. The bass were housed together in a 78-L glass aquarium filled with 20–21 °C well water, and were fed frozen chironomid larvae and live earthworms daily. The bluegill and pumpkinseed were housed in small groups in 38-L aquaria filled with well water, and were fed frozen brine shrimp, frozen chironomid larvae, or granulated fish food daily. Animals were kept in accordance with the State University of New York's IACUC regulations.

Fish were netted out of their aquaria and placed into the mussels' aquarium for observation and videotaping periods. Eighteen observation periods were conducted, ranging from 4–67 min (Table 2). If a fish attacked a mussel and was infected with glochidia, we removed it from the aquarium. We also removed fish that were obviously agitated when introduced to the mussels' tank.

We touched the mantles of displaying mussels with the end of a glass pipette to test whether a simple tactile stimulus would cause females to release glochidia. We touched each individual mussel twice.

Sensitivity of displays to light and turbidity

We filmed and observed *L. nasuta* under eight light intensities and *L. subrostrata* under six light intensities, as measured by an Olympus camera light meter. A lamp with one fluorescent bulb was placed directly over an aquarium and light intensity readings were taken with the light meter at the water's surface directly over a single displaying mussel of each species. The lamp was maneuvered until the desired light intensity was reached. We counted the number of display cycles for 5–22 min at each light intensity using a stopwatch. Trials were run in the following order: 43, 97, 323, 646, 1076, 22, 97, 161, and 2959 lux (*L. nasuta*, 1–2 June 1999), and 22, 75, 140, 430, 1076, and 2959 lux (*L. subrostrata*, 8 June 1999).

To determine how displaying mussels responded to the onset of light and dark, we observed *L. subrostrata* (n = 4) and *L. nasuta* (n = 2) in the early morning and at night, before and after the lights came on or were shut off. On 9 and 11 June 1999, we observed *L. nasuta* and *L. subrostrata* for 60 min after the timer lights had shut off at 2045 h. On 9 and 10 June 1999, we observed the same mussels for 10 min before and 20 min after the lights turned on at 0530 h. Observations were made with the aid of a small red-lensed penlight for a light source. On 27 June 1999, we videotaped the mussels' behavior using the camera's night-vision feature before and after the lights shut off for the night.

To test whether the light response of *L. nasuta* was cued by a circadian rhythm or a direct response to light, we observed the responses of two displaying females when lights were turned on at 0200, 0600, 0730, 1315, 1835, 2100, and 2210 h on various days in 2004. We also observed the responses of these displaying females when lights were turned off at 0230, 0652, 1239, 1520, 1545, 2035, 2132, 2217, and 2248 h.

Table 2. Fish that were exposed to displaying mussels in 1998–99. Fish that are known or suspected hosts of each mussel are marked with an asterisk.

Mussel species	Fish species (# of individuals)	Date of observations (length of observation period, in minutes)
L. nasuta	Bluegill (8)	24 June (67) and 26 June 1998 (36); 15 June (48), 16 June (48), 19 June (20), and 23 June 1999 (17)
	Largemouth bass (2)	14 June (26) and 23 June 1999 (11)
	Smallmouth bass (1)	14 June 1999 (21)
	Pumpkinseed (1)	8 June 1999 (37)
	Common shiner (1)	26 June 1998 (56)
L. subrostrata	Pumpkinseed (6)	27 May (24), 30 May (33), 31 May 1999 (4), and 8 June 1999 (20, 26, 27)
L. recta	Bluegill* (2)	23 June 1999 (17, 48)
	Largemouth bass* (2)	23 June 1999 (11, 26)
	Smallmouth bass (1)	23 June 1999 (21)

We conducted turbidity experiments with displaying *L. nasuta* and *L. subrostrata* on 20 June 1999. A plexiglas sheet was glued into a 38-L aquarium to divide it into a treatment and control side. Each side of the tank was filled with 5 cm of mixed gravel substrate and ≈ 15 L of 21 °C well water. Bentonite clay was stirred into the water of the treatment side of the divided aquarium to increase turbidity. We placed one displaying mussel into the turbid tank and another into the clear-water tank, and observed and videotaped their behavior. *L. nasuta* was subjected to two turbidity levels: 0.27 and 0.8 g/L of bentonite. Mussels in the high-turbidity treatment were moved between treatments after 13 min. We subjected *L. subrostrata* to 0.8 mg/L of bentonite.

Diel movements of displaying mussels

We compared the diel movements of males and displaying females of *L. nasuta* in 2004 by periodically observing the positions of four males and two displaying females in the laboratory. Each mussel was housed in a 36-L aquarium containing ≈ 5 cm of sand and washed gravel, as described above. We used a Sony Mavica digital camera to photograph the mussels as the lights came on in the morning at 0600 h and just before the lights went off at night at 2100 h (similar to day length in the field during the display season). We placed a 2.5- by 5-cm grid on top of the aquaria to allow us to compare the positions of mussels at different times, and calculated a minimum distance moved between photographs. We collected movement data on six days and seven nights.

In addition to the laboratory observations, we observed females of *L. nasuta* displaying in nature in Webatuck Creek and Lake Taghkanic, NY, and females of *L. recta* displaying in the Allegheny River, NY. All mussels used in the 1999 studies were deposited as vouchers in the University of Massachusetts Zoology Museum in Amherst, MA, and subsequently transferred to the collections of the Illinois Natural History Survey.

Results

Ligumia nasuta

Field conditions. We saw five females in nature exhibiting similar display behavior. One female was displaying in 1 m of water in an open patch of soft sediment between patches of submersed vegetation in Lake Taghkanic, Columbia County, NY, on 19 June 1998. She was nearly unburied, her valves were widely parted, and a tiny white spot moving up and down the mussel's mantle edge could be seen under water at a distance of > 0.5 m. On 19 May 1999, we saw two displaying females in the shallows of Webatuck Creek, Dutchess County, NY. One female was at the end of a 3-m long trail in the silt produced by recent movement. Both females were nearly unburied with their valves widely parted. The moving spots on their mantle edges were detectable from above the water's surface. The display

cycle (described in more detail below) took ≈ 7 s. An *Etheostoma olmstedi* Storer (tessellated darter) approached and attacked the mantle edge of a displaying mussel, then retreated with its gills flared. The female mussel continued to display after the attack. Two displaying females observed in Webatuck Creek in June 2004 exhibited similar behavior.

Captive conditions. We watched five animals of *L. nasuta* display in captivity. Displaying females positioned themselves almost completely upright in the substrate and exposed more than half of their shells out of the substrate (Fig. 1A). Almost the entire mantle margin was exposed. The mantle edges separated and papillae along each margin fluttered in synchrony up and down the mantle margin (see supplementary video file 1 at http://dx.doi.org/10.1656/N580.s1). As the mantle edges parted, the light-colored interior was exposed and contrasted sharply with the darkly pigmented mantle edges. This light-colored patch appeared to move along the mantle margin as well, giving the illusion of a moving white dot. This spot moving along the mantle margin resembled a small swimming invertebrate, such as an amphipod.

Display behavior was persistent and difficult to disrupt. Displaying *L. nasuta* began to display within 1 h of transition from the wild into an aquarium. The *L. nasuta* female from Lake Taghkanic exhibited the same display behavior in captivity as in the lake and continued to display for 36 d before being released back into the lake. The four displaying mussels collected from Webatuck Creek in 1999 and 2004 continued to display in captivity for 21–43 d. Mussels slowed or paused their mantle movements when a shadow passed, or after a fish attacked their mantle edge and glochidia were ejected. Strong surges of water from refilling the aquarium temporarily slowed or stopped displays, but the displays resumed quickly after the water settled. Eight non-displaying animals of *L. nasuta* (presumably males or non-gravid females) collected from Webatuck Creek during 1998–99 did not display in captivity either, but remained mostly buried in the aquarium sediment.

Fish were strongly attracted by *L. nasuta*'s display. Fish investigated a displaying mussel by swimming over to it, facing it, and pausing to inspect the mantle edge (see supplementary video file 2 at http://dx.doi.org/10.1656/N580.s2). Fish attempted to attack the moving white spot. Three of the 13 fish exposed to displaying females (one bluegill, one largemouth bass, and one pumpkinseed) attacked the mantle edge of displaying mussels. All three of these mussels released a burst of free glochidia when attacked. Attacking fish retreated quickly with their gill covers flared. Attacked mussels appeared uninjured and resumed displaying within seconds of the attack. Fish that attacked a mussel and were exposed to glochidia approached other displaying mussels in later trials, but none of these fish attacked again. When we touched a mussel's mantle edge with a pipette, the mussel simply closed its shell and stopped displaying for a few seconds, without releasing glochidia, then resumed its display.

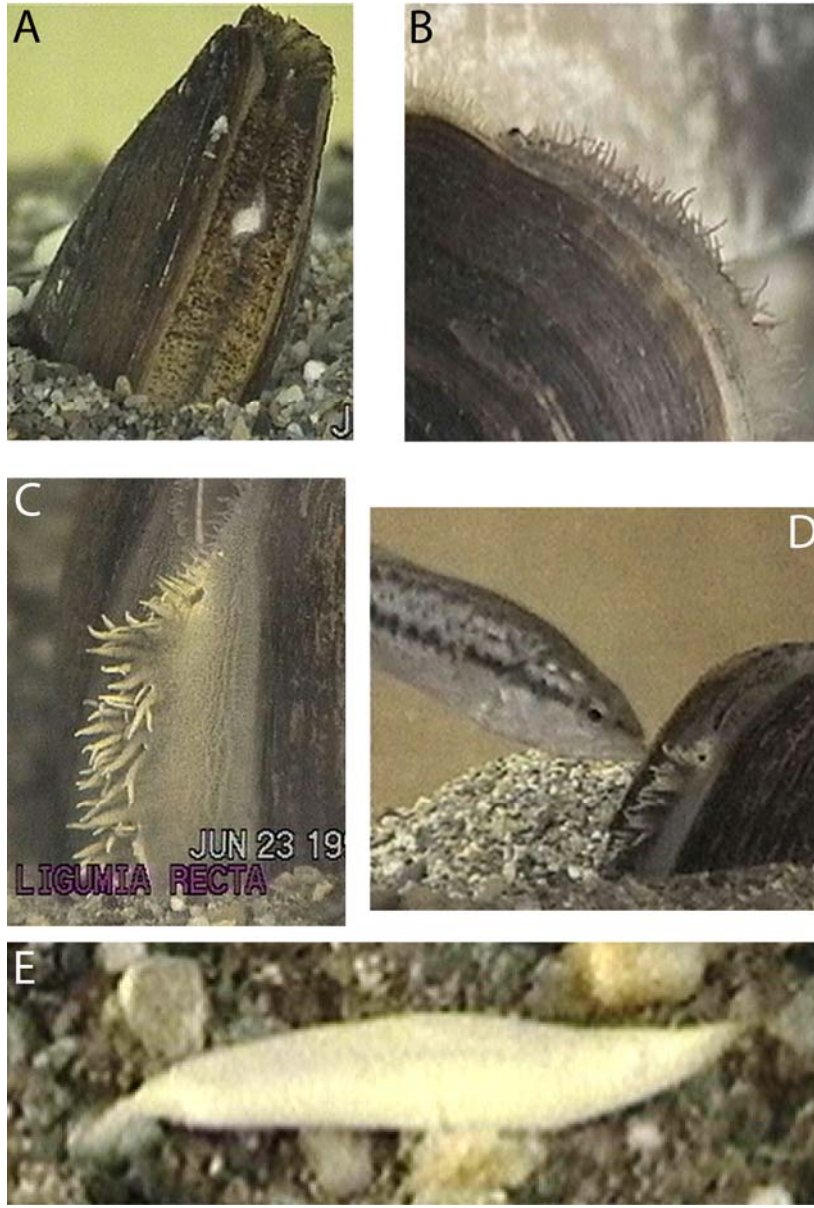

Figure 1. A. Display of *L. nasuta*. The light spot near the center of the mantle margin moves rapidly along the mantle margin. B. Lateral view of the mantle margin of a displaying *L. subrostrata*, showing the eyespot. C. Mantle margin of a displaying *L. recta*. D. Largemouth bass investigating the mantle margin of a displaying *L. recta*. Note the prominent eyespot on the mantle margin. E. Conglutinate of *L. recta*; actual length is 20–25 mm.

The frequency of display movements increased with increasing light intensity (Fig. 2), but then leveled off at high light intensities (the slope of the log-log plot of frequency vs. light intensity was 0.055 (SE = 0.0098, r^2 = 0.84), showing that the increase was far less than linear). Displays stopped in the dark and resumed in the light, regardless of the time of day. Mussels observed before lights came on in the morning were never displaying, but had moved around within the aquarium, as shown by deep tracks in the substrate, and were in a moving position with mantle edge in the substrate. Displays began as a weak fluttering soon after lights were turned on, and reached their full extent after 11.9 ± 3.8 min (mean ± SE, n = 7). Mussels also changed their positions from buried to upright in the substrate at this time. Mussels stopped displaying 21.7 ± 3.4 min (n = 7) after lights were turned off.

High turbidity also affected displays of *L. nasuta*. In turbid water (0.27 g/L), the mussel in the turbid tank was slower to begin displaying than the one in the control tank. However, within 40 min, its mantle edge movements matched those of the mussel in the control tank. Display behavior changed markedly under very turbid conditions (0.8 g/L). The mussel in the control tank began to display after 2 min, but the mussel in the turbid tank did not display. When we exchanged mussels after 13 min, the mussel previously in the turbid tank still did not display, and the mussel previously in the control tank began to exude white mucous from

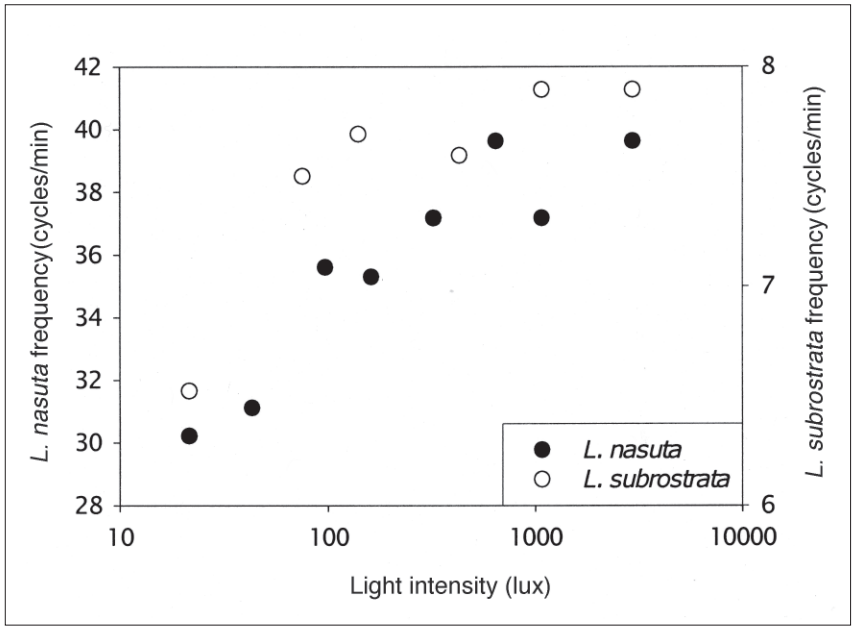

Figure 2. Effect of light intensity on the frequency of the displays of *L. nasuta* and *L. subrostrata*. Note that the x-axis is logarithmic.

the middle of its mantle margin. Both mussels resumed their displays within 8 min of being returned to the aquarium in which they were held between experiments.

Two captive *L. nasuta* ejected conglutinates at night when no fish were present. They expelled 5–20 conglutinates, buried themselves in the substrate, and did not display any longer. Conglutinates were elongate, cream-colored, and ≈ 10 mm long.

Displaying females were more active at night than males (Fig. 3). One displaying female that had been moving an average of 36 cm/night, stopped displaying after discharging her conglutinates in the middle of the trial, and did not move after that time.

Ligumia subrostrata

Four of the seven *L. subrostrata* displayed while in captivity (we did not observe this species in the field). Displaying *L. subrostrata* positioned themselves upright in the substrate with widely gaping valves. Whitish papillae along the posterior 2/3 of the mantle edge were delicate and feathery (Fig. 1B) and were waved or fluttered during the display (see supplementary video file 3 at http://dx.doi.org/10.1656/N580.s3). Darkly pigmented eyespots present beneath the inhalant siphons also moved during the display. Two dark lines under the papillae and border-

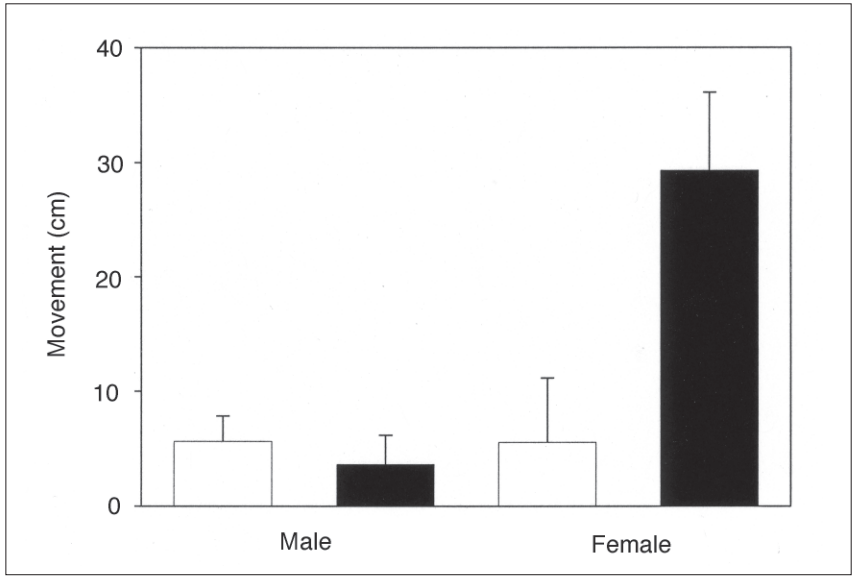

Figure 3. Movement of four males and two displaying females of *Ligumia nasuta* in laboratory aquaria during a 15-h day (white bars) and a 9-h night (black bars). Error bars show 1 SE. The nighttime movements of displaying females are significantly greater than those of females during the day or males ($p = 0.0001$; ANOVA, planned comparison).

ing each side of the mantle edge undulated as the mantle edge moved in display. The mantle edge of *L. subrostrata* reminded us of two types of potential prey for host fishes. The ventral view of the fluttering mantle edge resembled the moving gills of an ephemerid mayfly. In lateral view, the eyespots and dark strip were visible, and the mantle edge looked like a small fish. The mantle edge in some individuals was parted enough to expose the glochidia-packed water-tubes of the gills. The rhythm of the display was a period of fluttering activity for several seconds followed by a rest period of several seconds. During the rest period, the papillae remained spread apart. Under normal laboratory lighting and 21 ˚C water temperature, the *L. subrostrata* averaged 8.6 displays/min.

One of six pumpkinseeds presented to displaying *L. subrostrata* (Table 2) attacked the mantle edge of a displaying mussel. The fish spent several seconds watching the fluttering of the mantle edge and then twice pecked at it. A cloud of free glochidia was then ejected and the fish retreated quickly with its gill covers flared. The mussel continued to display after a brief pause. Displaying females of *L. subrostrata* touched with a pipette did not react, or stopped their display only briefly (< 1 min).

The display of *L. subrostrata* was sensitive to light, increasing in frequency with rising light levels (Fig. 2), but leveling off again at high light intensities (the slope of the log-log relationship between light intensity and display frequency was 0.033 (SE = 0.11, $r^2 = 0.69$), showing that the effect of light was far less than linear). *L. subrostrata* did not display in the dark. Displays slowed markedly within 10 min of the lights going off (n = 4) and stopped completely after 50–53 min of darkness (n = 4). In the morning, one individual began displaying as soon as the lights came on, but it took 20–25 min for the others to begin displaying. Almost all the mussels were moving about the aquarium before the lights turned on, or were buried with mantle edges down in the substrate.

A displaying *L. subrostrata* placed in very turbid water (0.8 g/L) for 30 min did not resume its display, but the mussel in the control tank began displaying within 1 min.

We found elongate, cream-colored conglutinates in the *L. subrostrata* aquarium on the mornings of 30 May, 7 June, 11 June, and 12 June 1999. Although many conglutinates appeared to have broken apart, we estimated that they were ≈ 10–12 mm long and 3 mm wide.

Ligumia recta

Field conditions. We saw two females displaying during the day in the Allegheny River. Both were almost completely exposed on top of the gravel substrate, lying on their sides and easily visible in < 0.5 m of water. Papillae along the mantle margin were well exposed, but did not move.

Captive conditions. The same two female *L. recta* continued to display in captivity. An eyespot at the base of the inhalant siphons was visible,

and the immediate area around the eyespot was lighter in color than the rest of the mantle edge (Fig. 1C). The whitish area around the eyespot was especially noticeable under low light. The marginal papillae posterior to the eyespot were small, but larger, tentacle-like papillae ≈ 0.5 cm long occurred along the mantle edge anterior to the eyespot. We did not see the papillae wave or flutter at any time. The *L. recta* display did not change at night, and the papillae were not retracted, even if animal was moving about the aquarium.

All three fish presented to the two displaying *L. recta* in the aquarium (Table 2) inspected the mussels (Fig. 1D), but none of the fish attacked. No glochidia or conglutinates were released by *L. recta* in the presence of the fish. In response to being prodded with a pipette, *L. recta* retracted its papillae, but did not eject glochidia.

We found cream-colored conglutinates on the aquarium substrate on 24 June 1999. They were shaped like an elongate D, ≈ 22 by 6 mm (Fig. 1E), and had been expelled during the night.

Discussion

Gravid females of *Ligumia* use their distinctive marginal papillae as part of a display to attract fish hosts. The moving displays of *L. nasuta* and *L. subrostrata* attract fish, and displaying females release glochidia onto attacking fish. Because females released glochidia when attacked by fish, but not when prodded with a pipette, they can rapidly distinguish the attack of a fish from other tactile stimuli. It appears that these displays are an effective adaptation for ensuring attachment of glochidia onto potential host fish.

Displays differ among the different species of the genus. *Ligumia nasuta* and *L. subrostrata* have rapidly moving displays that are active only during daylight. The displays of these two species resemble one another, but differ in length and color of papillae and frequency of movement. Our observations of *L. recta* are less complete. We never observed any movement in the display of *L. recta*, but displaying specimens of *L. recta* from Minnesota flutter their papillae weakly (Mark Hove, University of Minnesota, St. Paul, MN, pers. comm.). In addition, *L. recta* displayed at night as well as during the day. This may be related to the fact that sauger, perhaps the chief host of *L. recta* (Khym and Layzer 2000), is nocturnal. Haag and Warren (2000) also noted differences between two species of *Villosa* in the timing of their displays, although these species shared the same fish hosts. Further observations on the display behavior of *L. recta* would be desirable.

The displays of *L. nasuta* and *L. subrostrata* were sensitive to light in two ways. First, displays occurred only in the light. We found no evidence that the light-sensitivity of *L. nasuta* had a circadian component; light and dark could start and stop mussel displays at any time of the day.

Second, the frequency of the display was a strong, increasing function of light intensity in both species.

Females of *L. nasuta* and *L. subrostrata* stopped displaying in very turbid (0.8 g/L) water. In addition, high turbidity probably indirectly reduces the frequency, duration, and effectiveness of mussel displays by reducing underwater light intensity and thereby display frequency (cf. Fig. 2), as well as reducing the distance over which fish can see the display. Thus, the widespread, severe pollution of streams and rivers by silt and clay (Waters 1995) may have strong effects on the reproductive biology of *Ligumia* and the many other mussels that use visual displays. Suspended sediment concentrations in North American streams and rivers often exceed the concentrations used in our study (0.27 and 0.8 g/L), especially in agricultural areas of the Midwest (e.g., Walling and Webb 1996).

Females of all three species released conglutinates at night. This could be an alternative strategy to reach a host that is bottom-feeding and nocturnal, or simply a stress response to captivity.

Ligumia's display is reminiscent of displays by other lampsiline genera such as *Lampsilis* (Haag et al. 1999, Kraemer 1970), *Villosa* (Haag et al. 1999), and *Medionidus* (Haag and Warren 2003). In all of these genera, the mantle edge is elaborated into some kind of a moving lure. In *Lampsilis* and *Medionidus*, the mantle edge has been developed into a fleshy lure, while in *Ligumia* and *Villosa*, the mantle edge supports papillae or tentacles. The difference between *Villosa* and *Ligumia* may be one of degree rather than kind; *L. nasuta* and *L. subrostrata* have small papillae, *L. recta* has large papillae (or small tentacles), and *Villosa* has large tentacles. The specialized structures of the mantle edge are smaller in *Ligumia* than in *Lampsilis*, *Villosa*, or *Medionidus*, which may make *Ligumia* less susceptible to damage from fish attacks.

Displaying captive females of *L. nasuta* and *L. subrostrata* were very active at night, even though their restriction to aquaria may have limited their movements. Displaying females were more active than males (or the single non-displaying female we observed), suggesting that this nocturnal movement is related to display behavior. Further, one of the displaying females we saw in the field was at the end of a long trail, indicating extensive recent movement. This nocturnal movement may be adaptive. Fish that received a dose of glochidia were reluctant to attack again. Females may therefore need to find new audiences of fish to display to if they are going to continue to infect hosts over the whole period of glochidial release. Females of many displaying species may therefore be especially active during the display season.

Acknowledgments

This project was supported by The Nature Conservancy, the Graduate Student Organization of the State University of New York at Albany, and the Hodson Trust Internship Program at St. John's College. We thank Dr. Margaret Stewart

for encouragement and suggestions; Kevin Cummings, Mike Mesere, Ethan Nedeau, Douglas Smith, and Alan Tousignant for technical help; Janice Smith and four anonymous referees for helpful comments; and Tod and Cara Rubin, Jill Cadwallader, Gary Lovett, Janet Allison, Linda Olsen, Steve Roberts, Lee Rassnick, and Nancy Dier for support.

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