Alternative Reproductive Behaviors in Lampreys and Their Significance

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Alternative Reproductive Behaviors in Lampreys and Their Significance

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ABSTRACT

A typical lamprey mating involves a female attaching to a stone near the upstream end of the nest. A male then attaches to the back of the female's head and wraps his body around hers. Both vibrate vigorously as gametes are released. In some cases, a second male, the satellite, circles about the urogenital area of a mating pair at the moment of gamete release in what has been interpreted as an attempt to gain fertilizations. Analysis of videotapes of spawning *Lampeutra appendix* in the North Branch Whitewater River in Minnesota (Mississippi River drainage) and Jambo Creek in eastern Wisconsin (Great Lakes drainage) revealed that at both sites at least 50% of matings in nests with at least three lampreys included a satellite male. Nest associations involving more than one lamprey species in the same nest are known to involve many combinations of species, but especially relevant are cases involving closely related parasitic and nonparasitic species. For example, we have observed nonparasitic *Ichthyomyzon gagei* and parasitic *Ichthyomyzon castaneus* spawning in the same nests and have observed a male *I. gagei* attached to a female *I. castaneus*. Conventional wisdom is that the size difference between parasitic and nonparasitic lampreys prevents successful mating, but a combination of interspecific nest association and satellite male behavior could conceivably permit gene flow between paired nonparasitic and parasitic forms. This combination is displayed by at least some *Lampeutra* species.

INTRODUCTION

Each small nonparasitic lamprey species is thought to have evolved from a larger parasitic ancestor. In those cases in which the parasitic lineages are still extant, the conventional view has been that the related parasitic and nonparasitic forms are reproductively isolated, and they are referred to as paired species. If more than one nonparasitic species has been derived from the same parasitic species, the former are sometimes referred to as satellites of the latter. The conventional view, however, has not gone unchallenged. Evidence for gene flow between paired species has mounted (Schreiber and Engelhorn 1998), and some recent studies have failed to find genetic differences between paired forms (Beamish and Withler 1986, Neave et al. 2007). Moreover, the nonparasitic American brook lamprey (*Lampeutra appendix*) apparently retains within its genome the ability to produce a larger parasitic form (Cochran 2008). It is important to examine lamprey spawning behavior to reveal potential mechanisms for recombination of genetic information from parasitic and nonparasitic forms.

Lamprey spawning behavior and ecology were summarized by Manion and...
Hanson (1980) and Malmqvist (1986). Lampreys most often spawn in streams during the spring. A typical lamprey nest is a depression in gravel substrate, usually at the upstream end of a riffle (i.e., just upstream from where the water surface is broken). Males typically initiate nest construction, but females usually participate as well. Lampreys move stones or pebbles by attaching to them with their oral discs, lifting them from the bottom with thrashing motions, and letting the current help drag them downstream. They also attach to stones and sweep sediment by rapid lateral movement of their tails. Most species spawn in groups. The sea lamprey (Petromyzon marinus) is exceptional in that it is typically described as monogamous, but nests with more than two sea lampreys have sometimes been reported (e.g., Hanson and Manion 1980, Cochran and Lyons 2004).

The typical mating act involves a female attached to a stone near the upstream end of the nest. A male attaches dorsally to her head and loops his tail around her body so that their genital openings are closely aligned. The female quivers rapidly as gametes are released. Mating is brief, lasting only a few seconds. Both sexes mate repeatedly, not necessarily with the same partners. Because of the positioning of male and female during typical mating, their genital openings are most closely situated and spawning success (Beamish and Neville 1992) and fertilization efficiency (Malmqvist 1983) are greatest if they are not greatly different in size. This is the basis for the conventional view that paired nonparasitic and parasitic forms are reproductively isolated.

Groups of spawning lampreys do not always behave in the typical ways outlined above. Spawning in lakes (Russell et al. 1987) and at relatively great depths (Lamsa et al. 1980) has been reported, and some lampreys may spawn beneath cover (Cochran and Gripeptorg 1992). The sea lamprey has been observed spawning during late summer (Montgomery et al. 1983).

Individual male lampreys may display a number of alternative spawning behaviors (Malmqvist 1986). Bahr (1953) reported that small male Lampetra fluviatilis compensated by attaching farther back on the female. In some species, multiple males may attach to the same female (Bahr 1953, Dendy and Scott 1953, Malmqvist 1983, Heard 1966). In Lampetra planeri (Malmqvist 1983) and L. fluviatilis (Wüstel et al. 1996), a second male, the satellite, may circle about the urogenital area of a mating pair at the moment of gamete release in what has been interpreted as an attempt to gain fertilizations. Malmqvist (1983) recognized that this behavior is similar to “sneaking” male behavior reported among some salmonids, centrarchid sunfishes, and other teleosts (e.g., Gross 1984). Taborsky (1994 and 1997) proposed the term “parasitic” for this sort of alternative reproductive behavior, but for lampreys this term is so strongly associated with trophic behavior and life history that we prefer “satellite.”

Interspecific nest associations occur when more than one species spawn in the same nest. Those involving bony fishes, especially teleosts, have received substantial attention (e.g., Goff 1984, Vives 1990, Johnston and Page 1992, Johnston 1994a and 1994b, Shao 1997). Indeed, a description of a nest association among minnows dates back as far as the 18th century, although it wasn’t recognized as such at the time (Cochran 2000). Lampreys, however, have not been included in previous reviews.

The purposes of this report are to review and provide new information about interspecific nest associations among lampreys and to report our observations of alternative spawning behaviors in male L. appendix, with an emphasis on satellite behavior.

METHODS

The American brook lamprey was observed at two locations where the species has been studied previously. Jambo Creek is a tributary to the East Twin River (Lake Michigan drainage) in Manitowoc County, Wisconsin (Cochran et al. 1993). The North Branch Whitewater River (Mississippi River drainage) is located in Winona County,
Minnesota (Mundahl and Sagan 2005, Mundahl et al. 2006). Spawning groups were videotaped in Jambo Creek in 1993 on 28 April and 3 May, and supplemental observations were made in 1994. Spawning groups were videotaped in the North Branch Whitewater River on 23 and 25 April 2003 and 16 April 2004. Videotaping was conducted through glass-bottomed buckets with dark interior walls; a black cloth was positioned over the head and shoulders of the camera operator to reduce glare.

We recorded observations of interspecific nest associations involving lampreys during field studies in Wisconsin (e.g., Cochran 1987, Cochran and Gripentrog 1992, Cochran and Lyons 2004).

RESULTS AND DISCUSSION

Alternative spawning behaviors of male Lampetra appendix

In spawning groups of at least three American brook lampreys, alternative male behaviors were observed at both study sites (Table 1). In fact, fewer than half of the matings at either location involved the "typical" situation of a single male attached to a female. At Jambo Creek, 50% of the 22 matings in 1993 included at least one satellite male, and three included two satellites; spawning was not videotaped in 1994, but we noted satellite behavior during brief observations of spawning groups. During three matings in 1993, two males attached to the female, including one mating that also involved a satellite male. In the North Branch Whitewater River, 66% of the 47 matings during the two years included at least one satellite male, and 10 of these included two. Seven matings involved multiple attachments.

Our observations of alternative male behaviors in American brook lampreys from two major drainages suggest that these behaviors are widespread within this species. Relative frequencies of matings with and without satellite spawning did not vary significantly between the two sites (Fisher's exact test, $p = 0.290$). Similarly, relative frequencies of matings with and without multiple attachments did not vary significantly between the two sites (Fisher's exact test, $p = 1.00$).

It was not always possible to follow the behavior of individual lampreys within spawning groups because individuals moved into or out of groups and did not always remain within the camera's field of view. However, we isolated one segment of videotape in which a male lamprey successively engaged in satellite behavior and typical spawning with the same female. Thus, satellite and typical behaviors in individual

Table 1. Alternative spawning behaviors by male American brook lampreys (Lampetra appendix) videotaped at two locations. Also indicated are the number of spawning groups videotaped, the range of group sizes, the duration of time the groups were taped, and the total number of spawning events recorded.

<table>
<thead>
<tr>
<th></th>
<th>Jambo Creek, Wisconsin - 1993</th>
<th>North Branch Whitewater River, Minnesota - 2003</th>
<th>North Branch Whitewater River, Minnesota - 2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of groups</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Group sizes</td>
<td>3-13</td>
<td>4-10</td>
<td>4-9</td>
</tr>
<tr>
<td>Tape duration (min:sec)</td>
<td>18:48</td>
<td>32:56</td>
<td>26:05</td>
</tr>
<tr>
<td>Spawning events</td>
<td>22</td>
<td>32</td>
<td>15</td>
</tr>
<tr>
<td>Satellite behavior</td>
<td>11</td>
<td>22</td>
<td>9</td>
</tr>
<tr>
<td>Multiple satellites</td>
<td>3</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Multiple attachments</td>
<td>3</td>
<td>5</td>
<td>2</td>
</tr>
</tbody>
</table>

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American brook lamprey males are not mutually exclusive. Taborsky (1994) noted that male reproductive strategies in some teleost fishes may be fixed for life within individuals, regardless of whether their causes are genetic, environmental, or some combination. However, he also stated that the reproductive strategy of individual males is conditional upon circumstances in most teleosts that have been studied.

Satellite male behavior is now known in three species of Lampetra, and we predict it will be found to be widespread within the clade. Efforts should be made to survey other lamprey taxa for this behavior. Attempts should also be made to verify that satellite males achieve fertilizations, and, if possible, with what efficiency relative to typically spawning males.

**Interspecific nest associations**

Lampreys have not been included in previous reviews of nest associations, but nest associations involving lampreys may be widespread. We use as an example the upper Midwestern United States, where six species of lampreys, including the exotic sea lamprey, are known to occur. Taking into account their known geographic distributions (e.g., Lyons et al. 1997 and 2000) to exclude cases involving species with disjunct ranges, there are eleven possible nesting associations involving pairs of species. Nine have been reported to occur in at least one locality (Table 2): two involve paired parasitic and nonparasitic forms. In two cases, a third species, the sea lamprey, was also present, resulting in lampreys of three genera spawning in the same nest.

Additional examples of nest associations among lampreys in other areas have been reported. Huggins and Thompson (1970) found *L. planeri* and *L. fluviatilis* spawning together in Great Britain. Cooper (1983) stated that the mountain brook lamprey (*Ichthyomyzon greeleyi*) tended to occur farther upstream than the Ohio lamprey (*Ichthyomyzon bellioum*) in Pennsylvania, but he observed both species in the same spawning pit on three occasions. Western brook lampreys (*Lampetra richardsoni*) were observed building nests in the center of Pacific lamprey (*Lampetra tridentata*) nests, sometimes when the larger species was still spawning (Bruno 2006). Savvaitova and Maksimov (1979) and Kucheryavyi et al. (2007) did not consider them to be separate species, but they observed large, anadromous parasitic Arctic lampreys (*Lampetra camtschaticum*) spawning in the same nests with an anadromous praecox form of intermediate size and a small, nonanadromous nonparasitic form.

Lamprey species participating in nesting associations may mutually benefit from their collective effort in nest construction, but it has been suggested that smaller species may benefit more than larger species (Morman 1979, Cochran and Lyons 2004). Because larger lampreys can move larger rocks, they may be able to create nests in areas with deeper, swifter water and coarser substrate than would normally be usable by smaller lampreys. Cochran and Lyons (2004) reported that silver lampreys spawned at significantly greater depths in the presence of sea lampreys. Bruno (2006) suggested that western brook lampreys might use the low-flow refuge created within a Pacific lamprey nest and be able to manipulate the smaller gravel left after the larger lampreys removed the coarser gravel.

Some potential benefits of nest associations involving teleosts (Johnston and Page 1992) may also be applicable to lampreys. These include a reduction in predation on adults or eggs through the selfish herd effect. Our observations of hornyhead chubs (*Nocomis biguttatus*) feeding on eggs from the nests of chestnut and southern brook lampreys in Wisconsin support the potential importance of predation as a selective agent.

Some authors have implied that nest associations among lampreys would be maladaptive by emphasizing facets of lamprey biology that would permit sympatric species to avoid them. Scott and Crossman (1973), in accounts of several lamprey species, mentioned the potential for competition for spawning grounds. Schwartz (1959)
noted that the mountain brook lamprey and the least brook lamprey (*Lampetra aepyptera*) occurred together in some stream systems, but he suggested that they were separated by habitat and spawning season. Trautman (1981) also mentioned the separation of spawning times. Although these authors were not explicit about the negative effects of sharing spawning sites, potential negative effects of nest association proposed for teleosts (Johnston and Page 1992) may have applicability to lampreys; these include increased risk of predation due to the increased conspicuousness of a larger group, disruption of spawning due to interruption by the nest associates, and hybridization.

Recent work has provided evidence for the role of sex pheromones in lamprey reproduction (Li et al. 2002). Yamazaki and Goto (2000) suggested the possibility that pheromones facilitated reproductive isolation in two sympatric forms of nonparasitic *Lethenteron* that overlapped in body size and spawning times but were found only in separate nests. It would be desirable to test whether the pheromones produced by a given species are attractive to other species. If smaller lamprey species in nest associations benefit asymmetrically, it might be expected that they would be more attracted by the pheromones of larger species than vice versa. Comparisons of interspecific responses by nonparasitic and parasitic members of species pairs might prove especially enlightening.

**Synthesis**

The conventional view that paired parasitic and nonparasitic forms are separate species is based on the difference in body size as a reproductive isolating mechanism between lampreys mating in the "typical" fashion (Malmqvist 1983, Beamish and Neville 1992). Alternative spawning behaviors provide potential mechanisms to explain evidence for gene flow between forms that differ in size. It has been suggested that nest associations involving paired parasitic and nonparasitic lampreys may permit hybridization merely through the proximity of multiple individuals releasing gametes (Huggins and Thompson 1970, Savvaitova and Maksimov 1979, Kucheryavyi et al. 2007). However, satellite male behavior in combination with nest association may provide a more direct way for a male of one form to fertilize the eggs of the other. For example, a nonparasitic male acting as a satellite might be able to fertilize some of the eggs released by a parasitic female mating with a parasitic male, or a parasitic male might be able to fertilize some of the eggs released by a nonparasitic female mating with a

<table>
<thead>
<tr>
<th>Species</th>
<th><em>P. marinus</em></th>
<th><em>L. appendix</em></th>
<th><em>I. unicuspis</em></th>
<th><em>I. fossor</em></th>
<th><em>I. castaneus</em></th>
<th><em>I. gagei</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. marinus</em></td>
<td>–</td>
<td>Michigan</td>
<td>Michigan</td>
<td>Michigan</td>
<td>Michigan</td>
<td>disjunct</td>
</tr>
<tr>
<td><em>L. appendix</em></td>
<td>–</td>
<td>–</td>
<td>Michigan with <em>P. marinus</em></td>
<td>not reported</td>
<td>Michigan with <em>P. marinus</em></td>
<td>disjunct</td>
</tr>
<tr>
<td><em>I. unicuspis</em></td>
<td>–</td>
<td>Michigan</td>
<td>–</td>
<td>not reported</td>
<td>–</td>
<td>disjunct</td>
</tr>
<tr>
<td><em>I. fossor</em></td>
<td>–</td>
<td>–</td>
<td>(Missouri)</td>
<td>–</td>
<td>Wisconsin (Arkansas)</td>
<td></td>
</tr>
<tr>
<td><em>I. castaneus</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>I. gagei</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<td>–</td>
</tr>
</tbody>
</table>
nonparasitic male. Regardless of the size of the satellite male, the observations of Beamish and Neville (1992) suggest that egg release may be greater when the male that attaches in typical fashion to a female is of similar size and can squeeze the eggs from her body.

*Lampetra fluviatilis* and *L. planeri* are the only paired species for which both nest association (Huggins and Thompson 1970) and satellite male behavior (Malmqvist 1983, Wüstel et al. 1996) have been reported. However, although Huggins and Thompson (1970) noted that male *L. planeri* frequently attempted unsuccessfully to mate with a female *L. fluviatilis*, they described no behavior consistent with the subsequent reports of satellite behavior at other locations.

Several paired species in the genus *Ichthyomyzon* are known to engage in nest associations. Cooper (1983) observed both *I. bdellium* and *I. greeleyi* in the same spawning pit on three occasions, including, in two cases, males and females of both species. No interspecific matings were observed during the few minutes of observation prior to capturing the lampreys, but Cooper (1983) recognized the potential for hybridization. We have observed *I. castaneus* and *I. gagei* in the same nests at several locations in the Saint Croix River drainage in Wisconsin but a tendency for these groups to be at least partially obscured by boulders or other cover objects (Cochran and Gripentrog 1992) has compromised our recent attempts to videotape spawning behavior. However, on 26 May 2006 in the Yellow River, Washburn County, Wisconsin, one of us observed a nest with a female *I. castaneus* (281 mm) and 25-26 *I. gagei*. Twenty-three were captured, including 15 males and eight females, and they ranged in length from 114 mm to 150 mm. During a period of approximately five minutes, four times an *I. gagei* attached to the back of the head of the *I. castaneus*, and one time another *I. gagei* attached at mid-body. No quivering or release of gametes was observed, and during this time no typical matings by pairs of *I. gagei* occurred.

ACKNOWLEDGEMENTS

Work at Jambo Creek was supported in part by the Saint Norbert College Office of Faculty Development through a grant from the Student-Faculty Development Endowment Fund. We thank the Pokorski family for access to Jambo Creek through their property. We are grateful to the many students who provided field assistance, especially Eric Golden, Kaci Hocking, Andy Kinziger, and Paul Woods at Jambo Creek and Jenny Cochran, Tiffany Schriever, Ryan Spencer, and Mark Zoller at the North Branch Whitewater River. Abel Brumo and Ginny Adams shared their observations of interspecific nest associations.

LITERATURE CITED


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