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Egg-feeding in the freshwater piscicolid leech *Cystobranchus virginicus* (Annelida, Hirudinea)

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Abstract. Leeches are common terrestrial and aquatic annelids, parasitizing or feeding on a wide range of host taxa. Here we report evidence for an unusual feeding behavior of egg-feeding in the piscicolid leech *Cystobranchus virginicus*. We identified distended specimens of *C. virginicus* in the nests of at least 4 different fish species: *Campostoma anomalum, Moxostoma carinatum, Moxostoma* sp. (either *M. anisurum* and/or *M. breviceps*), and *Nocomis leptocephalus*. We collected a total of 41 leeches from the nests of these host species and documented at least 1 leech in 19 of 55 nests (35%), with many sites containing multiple leeches. Individuals of *C. virginicus* were not identified feeding on any of the 41 adult specimens of *Moxostoma* spp. or the 635 adult specimens of *Nocomis leptocephalus* examined, and were never found in the absence of active host spawning (26 sites). These results are consistent with individuals of *C. virginicus* being an opportunistic or possibly even an obligate egg-feeder, potentially timing their own reproductive activities with the spawning of their fish hosts. The current distribution of *C. virginicus* has been expanded to include North Carolina, South Carolina, and Tennessee. The potential for leech species to induce mortality in developing fish eggs could be a concern for fish conservation and merits further investigation.

Additional key words: Hirudinea, Piscicolidae, *Campostoma, Moxostoma, Nocomis*

Leeches are well-known predators and ectoparasites, displaying a wide variety of feeding strategies. The various feeding structures and diets of leeches are vital to their basic biology and have been used to help determine evolutionary relationships among species (Sawyer 1986). Leeches belonging to the suborder Arhynchobdellida possess buccal cavities containing ridges or toothed jaws. Some species of arhynchobdellid are known to prey upon smaller annelids, devouring them whole, whereas other species parasitize larger organisms by imbibing blood (Sawyer 1986; Davies & Govedich 2001). Leeches in the suborder Rhynchobdellida possess a pharynx modified to form a muscular proboscis. Some members of this group parasitize vertebrates by draining body fluids such as blood, whereas other rhynchobdellid species feed on the soft parts of invertebrate prey. A variety of invertebrate and vertebrate taxa including molluscs (Daniels & Sawyer 1975; Klemm 1975; Sawyer 1986), fish (Paperna & Zwerner 1974; Burreson & Thoney 1991), aquatic birds (Davies & Wilkialis 1981; Oosthuizen & Fourie 1985), reptiles (Ernst 1971; MacCulloch 1981), amphibians (Brockelman 1969; van der Lande & Tinsley 1976), and mammals (Oosthuizen & Davies 1994; Hong et al. 1999) have been identified as hosts for both arhynchobdellid and rynchobdellid species. Leeches have also been known to opportunistically feed on amphibian and fish eggs; however, this feeding strategy is uncommon and is often omitted completely in reviews of leeches (Davies & Govedich 2001). Feeding on amphibian eggs has been documented for the arhynchobdellid leeches *Macrobdella decora* (Moore 1912, 1923), *M. ditetra* (Moore 1953; Beckerdite & Corkum 1973), *M. diplotertia* (Cargo 1960; Turbeville & Briggler 2003), and *Philobdella gracilis* (Viosca 1962) and the rynchobdellid leech *Desserobdella picta* (Brockelman 1969). The rhychobdellid leech

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Piscicola punctata is the only leech known to feed on the eggs of fish (Richardson 1948). To our knowledge, however, no other studies have recognized or focused on egg-feeding as a feeding strategy for leeches.

During spawning, numerous fish species either bury their eggs in gravel or construct nests in which the eggs are deposited. For example, many species of redhorse sucker (genus *Moxostoma*) bury their eggs in gravel riffles, forming shallow depressions termed redds (Jenkins & Burkhead 1994). Chubs in the genera *Nocomis* and *Semotilus* dig gravel pits and bury their eggs in large gravel mounds (Lachner 1952), and stonerollers (genus *Campostoma*) excavate pit nests in gravel deposits, sometimes within trout redds or possibly in the nests of species of *Nocomis* (Miller 1962; Jenkins & Burkhead 1994). Other cyprinid species within the genera *Clinostomus, Hybopsis, Luxilus, Lythrurus, Notropis, Phoxinus,* and *Rhinichthys* spawn as nest associates on the nests of species of *Nocomis, Campostoma,* and *Semotilus* (Johnston 1994). Male sunfish, such as *Lepomis auritus* (Linnaeus 1758), sweep away silt and sand with their tails exposing clean gravel depression nests along the quiet pool margins in slow moving water (Breder 1936).

While studying the mating system of the river redhorse sucker *Moxostoma carinatum* (Cope 1870), the fish leech *Cystobranchus virginicus* Hoffman 1964 (Rhynchobdellida: Piscicolidae) was observed in many of the redds and was suspected of feeding on fish eggs. A subsequent mating system study of *Nocomis leptocephalus* (Girard 1856) in South Carolina also revealed the presence of this leech species in mound nests of the bluehead chub. The goals of this study were to: (1) provide evidence that individuals of *C. virginicus* feed on fish eggs, thereby recognizing egg-feeding as a viable feeding strategy for leeches and (2) provide a preliminary determination of the host specificity of egg-feeding in *C. virginicus*.

Methods

The primary study site for this project was a 10-mile section of the Valley River (tributary to Hiawasse River) upstream of Murphy, North Carolina. Collections originated across the river from the Cherokee County Sanitary Landfill (Fairview Road, off NC State Route 141) and ended at Peace Valley Campground (on Route 19, 1 mile north of 19/19 Business intersection) with the intervening stretch being accessed via canoe. The approximate latitude and longitude coordinates were 35°10′39″N, 83°53′34″W and 35°5′34″N, 83°25′45″W, for the beginning and ending locations, respectively. Sampled sites along this section of the river consisted of redds of *Moxostoma carinatum, M. erythrurum* (Rafinesque 1818), *M. anisurum* (Rafinesque 1820) and/or *M. breviceps* (Lesueur 1817), mounds of *Nocomis micropogon* (Cope 1865), and nests of *Campostoma anomalum* (Rafinesque 1820), and were chosen based upon evidence of fish spawning (disturbed substratum or active holding of territories by males). Seventy-eight sites in the Valley River were sampled on 5 different dates: 5 January 2000 (prior to any evidence of fish spawning), 23 April 2000, 14 May 2000, 24 May 2000 (active spawning dates for *Campostoma anomalum, Moxostoma* spp., *Nocomis micropogon,* and cyprinid nest associates), and 8 August 2000 (post-spawning date for most fish species with the exception of *Lepomis auritus*). For the collections on 5 January and 8 August 2000 (outside of the spawning season), sites were surveyed where spawning of species of *Moxostoma* had been documented during the previous year. During the collection on 5 January 2000, additional sites where no spawning activity had ever been observed were also surveyed.

The Savannah River System (Meyers Branch) just south of Aiken, South Carolina, was surveyed as the second study site as part of a spawning study on *Nocomis leptocephalus*. This site was located at the Savannah River Ecology Laboratory (approximate latitude and longitude coordinates were 33°10′59″N, 81°34′54″W to 33°10′05″N, 81°36′29″W). Sampling occurred from 2 to 14 June 2000 and from 8 May to 26 June 2001 at 15 mound nests of individuals of *N. leptocephalus*.

Specimens of *Cystobranchus virginicus* were collected in dip-nets from 1-m^2 sites by digging ~15–21 cm deep into the substratum of the river bed. A small shovel was used to lift the gravel near the surface of the water. The substratum was then dropped several centimeters in front of the dip-net such that the river's current carried the eggs and leeches into the net, but gravel was prevented from entering the net, thus preventing damage to either the eggs or leeches. The dip-nets were either standard 8-in aquarium dip-nets, or long-handled dip-nets (16 in, 1/16 in mesh, lined with standard bridal tulle). Without the bridal tulle, the larger mesh failed to capture all of the smaller fish eggs (i.e., species of *Nocomis* and *Campostoma*), but still successfully captured adult specimens of *C. virginicus*.

Several factors were used to identify the fish species associated with a particular site. When possible, species were identified by visual confirmation of the male(s) and direct observation of spawning activity. This was not possible for all nests and in some cases the species was deduced using nest and egg

characteristics, spawning times, and known occurrences in the stream from either published species distributions (Menhinick 1991) or direct collections (B.A. Porter, unpubl. data). In a few cases, the exact nesting species could not be determined due to numerous potential nest associate species. In the case of the genus *Moxostoma*, some species could not be differentiated because egg characteristics were too similar and spawning occurred at the same time.

Results

Across 6 different collection dates and 2 drainages, we surveyed a total of 93 sites. Evidence of active fish spawning was found at 67 of these sites (43 redds of *Moxostoma* spp., 5 nests of *Campostoma anomalum,* 3 potentially mixed cyprinid nests, 15 mounds of *Nocomis leptocephalus,* and 1 depression nest of *Lepomis auritus;* Table 1). We positively identified specimens of *Cystobranchus virginicus* from both the Valley River (Hiwassee River System) in North Carolina and Myers Branch (Savannah River System) in South Carolina. From these 2 river systems, we documented the presence of individuals of *C. virginicus* in the redds, nests, or mounds of at least 4 different fish species from 3 distinct genera (Table 1). From the Valley River, we found individuals of *C. virginicus* in 2 nests of *Campostoma anomalum,* 12 redds of *Moxostoma carinatum,* and 3 redds of an unidentified *Moxostoma* spp. (either *M. anisurum* and/or *M. breviceps*). From the Savannah River, we identified individuals of *C. virginicus* in 2 mounds of *Nocomis leptocephalus*. We collected a total of 41 leech specimens from 19 of 67 active sites (28%), with a maximum of 7 specimens taken from a single redd of *M. carinatum*. Leeches were not found from any of the 8 redds of *M. erythrurum,* 3 mounds of mixed cyprinid species, or 1 depression nest of *L. auritus*. Excluding these sites, individuals of *C. virginicus* were present in 35% (19 of 55) of the redds, mounds, or nests of the identified host species. Specimens collected on 24 May 2004 were deposited (by E.M. Burreson and W.E. Moser) as voucher specimens at the Smithsonian Institution's National Museum of Natural History (USNM 1024419).

When collected, specimens of *C. virginicus* were highly distended and of the same translucent yellow color as the fish eggs (Fig. 1). Broken egg casings were often found in the presence of leeches, but rarely in their absence. In one instance, a specimen of *C. virginicus* was observed actually attached to an egg of *M. carinatum*. Two specimens were kept alive in an aquarium for several days in the presence of eggs of *M. carinatum* but no direct feeding was observed. One individual did initiate cocoon deposition but died shortly thereafter (Fig. 2). Although we were not explicitly searching for individuals of *C. virginicus* at the time, we neither observed them attached to any captured specimens of adult redhorse suckers [39 *M. carinatum,* 1 *M. duquesnei* (Lesueur 1817),

Table 1. Occurrence of individuals of *Cystobranchus virginicus* in the nests of potential fish hosts.

Date	Fish species	Number of sites	Number of sites with leeches	Number of leeches found
5 Jan 2000	No activity[a]	14	0	0
23 Apr 2000	*Campostoma anomalum*	5	2	7
	Moxostoma spp.[b]	12	1	5
14 May 2000	*Moxostoma carinatum*	7	1	1
	Moxostoma erythrurum	8	0	0
	Moxostoma spp.[b]	2	2	6
	Unidentified cyprinids[c]	3	0	0
24 May 2000	*Moxostoma carinatum*	14	11	19
8 Aug 2000	*Lepomis auritus*	1	0	0
	No activity[d]	12	0	0
8 May 2001	*Nocomis leptocephalus*	15	2	3
	Total	93	19	41

[a] Seven sites had spawning by individuals of *Moxostoma* during the previous season and seven sites did not support spawning in the previous season.
[b] *Moxostoma* spp. could be either *Moxostoma anisurum* and/or *M. breviceps* (B. Jenkins, pers. comm.).
[c] Nest of *Nocomis micropogon* and/or *Campostoma anomalum* that may have contained eggs from several other cyprinid nest associates.
[d] All 12 sites had spawning of individuals of *Moxostoma* during the previous season.

Fig. 1. A specimen of *Cystobranchus virginicus* and fish eggs. Dorsal view exhibiting the yellow color the leech obtains after feeding on fish eggs. Note the white appearance of the intestines indicating the beginning stages of digestion. The anterior end of the leech is located at the bottom right-hand side of the figure. Photograph provided by E.M. Burreson.

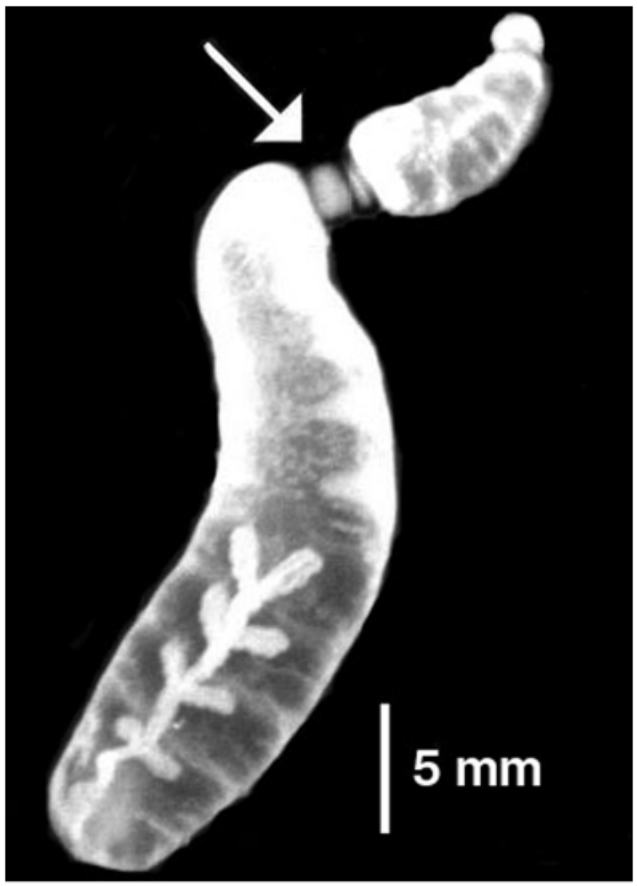

Fig. 2. A specimen of *Cystobranchus virginicus*. Dorsal view showing the constriction of the clitellum (arrow), indicating the initiation of cocoon deposition. The anterior end of the leech is to the upper right-hand side of the figure.

1 *M. anisurum*], nor have they been noted on any of the thousands of adult specimens of *Moxostoma* sp. handled by Dr. Robert E. Jenkins (pers. comm.). In association with a mating system study, we have preserved 635 samples of adult and juvenile specimens of *Nocomis leptocephalus* without noting a single attached leech.

Discussion

Piscicolid leeches are traditionally considered to be ectoparasites, feeding on the blood of fish (Meyer 1940, 1946). Although Hoffman (1964) did not document feeding from fish in his original description of *Cystobranchus virginicus,* subsequent investigators have found this leech feeding on various hosts including catfish and cyprinid fish (Putz 1972; Paperna & Zwerner 1974). These observations, however, have recently been called into question (E.M. Burreson, pers. comm.) and it is, therefore, unclear if individuals of *C. virginicus* parasitize adult fish. Here, we present evidence that this leech is likely feeding on the eggs of at least 4 different species of fish: *Moxostoma carinatum, Moxostoma* spp. (*M. anisurum* and/or *M. breviceps*), *Campostoma anomalum,* and *Nocomis leptocephalus*. Adults of these fish species are not known to be parasitized by *C. virginicus*. We collected specimens of *C. virginicus* only from sites where developing fish eggs or larvae were present and never observed them on any of the nest-attendant fishes (although exhaustive searches for leeches were not conducted). To our knowledge, the only other observation of leeches feeding on fish eggs comes from Richardson (1948). The fish leech *Piscicola punctata* was observed feeding on the eggs of *Semotilus corporalis* in southeastern Quebec (Richardson 1948). Richardson (1948), however, probably misidentified this leech because his description matches what we now know to be *C. virginicus* (Burreson et al. 2005). Therefore, while several species of leech are reported to feed on amphibian eggs

(Moore 1912, 1923, 1953; Cargo 1960; Viosca 1962; Brockelman 1969; Beckerdite & Corkum 1973), *C. virginicus* is the only leech known to exhibit this unusual behavior of feeding on fish eggs. Although potentially confounded by misidentifications, *C. virginicus* has previously only been reported from Virginia and West Virginia (Klemm 1982), and thus our collections from North and South Carolina, and recent collections in Tennessee (Spivey Creek 36°04.010′N, 82°30.145′W, May 2004; voucher specimen USNM 1024420; E.M. Burreson, W.E. Moser, J. Williams, & S. Furiness, pers. comm.), represent the identification of new localities for this species.

Individuals of *C. virginicus* appear to prefer habitats with gravel substratum and moderate flows. In the Valley River, specimens of *C. virginicus* were restricted to areas with mixed gravel, large gravel and small cobbles in runs, glides and adjacent pool tails with moderate to heavy flows. The 3 fish species that were associated with individuals of *C. virginicus* spawn in this same habitat. We did not find specimens of *C. virginicus* in areas with finer substrata associated with lower flows along the periphery of the stream. Although the one nest of *Lepomis auritus* sampled was constructed of gravel, it was located along the periphery of the stream, surrounded by finer substrata, and did not contain specimens of *C. virginicus* [nor did any of the 25 nests of *L. auritus* surveyed from Fourmile Creek in the Savannah River system by DeWoody et al. (1998); (J.A. DeWoody, pers. comm)]. In the Myers Branch of the Savannah River System, the substratum was dominated by sand, but specimens of *C. virginicus* were found only in the gravel nests of *Nocomis leptocephalus*.

Furthermore, these leeches may require high spawning site fidelity by the host species. For example, redhorse suckers are highly predictable in their choice of spawning locations and timing of spawning seasons, tending to use the same gravel riffles year after year (Jenkins & Burkhead 1994; R.E. Jenkins, B.A. Porter, & A.C. Fiumera, unpubl. data). These observations, combined with the apparent absence of leeches on the adult fish in either locality, might suggest an obligate egg-feeding strategy and annual life cycle for this species. Juveniles of *C. virginicus* could hatch near the time of spawning and consume eggs during their host's spawning season. Upon digestion and maturation, the adult leeches could mate, deposit cocoons in the substratum, and then die. The cocoons could over-summer and the next generation of juvenile leeches would again hatch near the time of fish spawning. This type of summer estivation has been noted for other piscicolid leeches, possibly as a response to temperature (Burreson & Zwerner 1982; Bower & Thompson 1987). We were not able to locate cocoons attached to rocks; however, our observation of initiation of cocoon deposition by the one captive individual is consistent with this strategy (Fig. 2). Recent collections of leeches (May 2004) in North Carolina (Valley River) and Tennessee (Spivey Creek; E.M. Burreson, W.E. Moser, J. Williams, & S. Furiness, pers. comm.) also support this hypothesis. In addition to finding leeches in fish nests, engorged leeches were also found attached to rocks near the river edges (usually 3–5 leeches per rock). It was clear that leeches from the Valley River had recently fed as their crops were completely distended with stored egg material. The intestines of these leeches appeared white in color against the yellow/orange egg material in the crop (Fig. 1), indicating that the Valley River leeches had not fully digested the egg material. In contrast, the specimens of *C. virginicus* collected from Spivey Creek appeared to be much further along in the digestion process than Valley River leeches (Spivey Creek leeches were collected two days after those from North Carolina). The crops of the leeches from Spivey Creek were no longer fully distended, indicating that most of the stored egg material had been digested. Furthermore, the intestines of these leeches were yellow/orange in color, evidence that food contents were being processed (unpubl. data). Similar observations were made with leeches feeding on amphibian eggs (Turbeville & Briggler 2003). Furthermore, two leeches from Tennessee were found mating. These findings are consistent with the hypothesis that these leeches time their feeding with fish spawning, then retreat under rocks to digest, mate, and deposit cocoons.

The impact of egg-feeding on fish populations remains to be investigated. High mortality and decreased fitness in frog eggs, tadpoles, and juvenile snails has been attributed to the glossiphoniid leeches *Desserobdella picta* (Brockelman 1969; Berven & Boltz 2001) and *Glossiphonia complanata* (Brönmark 1992) respectively. It is possible that obligate or opportunistic egg-feeding by individuals of *C. virginicus* could also be a significant source of mortality in developing fish eggs. Given that many fish species of conservation interest (e.g., some salmonids, other suckers and sturgeon) tend to bury their eggs in manners similar to the redhorse suckers, the potential impact of feeding by adults of *C. virginicus* on fish mortality should be investigated.

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