

Spawning Behaviors in *Luxilus albeolus* and *Luxilus cerasinus* (Cyprinidae)

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ABSTRACT

With our descriptions of spawning activities in *Luxilus albeolus* and *Luxilus cerasinus*, the reproductive behaviors of all nine species in *Luxilus* have been documented. Based on these accounts of behaviors there are two lineages in the genus (furrowing species where females rise to the water surface after the clasp, and non-furrowing species where females do not rise to the surface after the clasp). Reproductive behaviors in *L. albeolus* and *L. cerasinus*, each chronologically resolved into a sequence of six categories (Interim, Approach, Alignment, Run, Clasp and Dissociation) exemplified a successful spawn as defined by the clasp.

INTRODUCTION

With the exception of *Luxilus albeolus* and *Luxilus cerasinus*, the breeding behaviors of the nine species of the cyprinid genus *Luxilus* have been documented (Johnston and Birkhead, 1988; Kendall and Goldsboro, 1908; Miller, 1967; Outten, 1957; Pflieger, 1975; Raney, 1940; Robison and Buchanan, 1988; Smith, 1979). For this study the spawning behaviors in *L. albeolus*, which forms a furrow (equals hollow of Kendall and Goldsboro, 1908), are described and compared to those in the surface substrate spawner, *L. cerasinus*.

MATERIALS AND METHODS

Breeding behaviors of 12 *L. albeolus* and 11 *L. cerasinus* were observed over four nests of *Nocomis leptcephalus* in Pumpkin Creek (Dan-Roanoke River drainage), St. Rt. 86, 1 km N of St. Rt. 205, Pittsylvania Co., Virginia, 15 May 1987 (16.5 C) and 8 May 1993 (18.9 C). Behaviors were filmed above the surface of the water with Nuvi-con-tube and CCD cameras equipped with zoom macrolenses and polarizing filters. Three hours of videotapes were played repeatedly, and frame by frame to establish spawning behaviors for each species. The categories, which identify a chronological sequence of spawning behaviors, follow Sabaj (1992): Interim (male only), Approach (female only), Alignment (orientation of a male and female), Run (female initiated), Clasp (flexure of male's body around the female), and Dissociation (separation following clasp). Behaviors other than those associated with the spawning sequence were considered disruptive of a successful spawn.

RESULTS

Descriptions of spawning behaviors over one nest on 15 May 1987, representative of activities seen on all nests, are presented by species and category.

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Luxilus albeolus

Interim: Six male *L. albeolus*, one after another, swimming against the water current, established territories in depressions in the irregular surface on the upstream slope of clean mound nests of *N. leptocephalus* that were not occupied at the time by attending males. Male *L. albeolus* either bulldozed or flicked pebbles aside with their snouts (mouths closed) or their cheeks to form spawning furrows (≤ 2 cm deep) that eventually equalled the total length of a male.

Approach: The female approached the male in the spawning furrow either from the side or from downstream. Females did not approach a furrow when the male was engaged in territorial defense.

Alignment: As the female moved into the furrow, the male shifted laterally (1-2 cm) away, allowing her to position herself in the center of the furrow. Then the male, coordinating his swimming to that of the female, aligned alongside, and pressed his snout to hers.

Run: The Run was initiated by the female. The female swam forward with the ventral portion of her body appressed to the substrate of the furrow. Her forward movement did not exceed more than one-half the length of her body. The male followed the female, keeping his snout firmly affixed to hers. The female then arched her head upwards (≤ 30 degrees) as she turned her body away from the male. As her snout came up, she twisted so that her dorsum was appressed to the male's anterior flank, and her caudal peduncle to the substrate.

Clasp: The male initiated the spawning clasp. As the female arched her head upwards, the male tilted his body prior to curving his caudal peduncle over her back. He drove his posterior flank into the female's side between her pectoral and pelvic fins. In this position, the male's body was in a sigmoid configuration. With further contraction (from snout to caudal peduncle) his body formed a semicircle around the female with sufficient force to cause her mouth to gape.

Dissociation: The female, directed vertically, continued to rise into the water column until she broke the surface. The male assumed a position over his spawning furrow.

Disruptive behaviors of a successful spawn were: non-contact head displacement, non-contact body displacement, head/body butt, chase, and parallel swim between male *L. albeolus* as described elsewhere by Maurakis and Woolcott (1993) for *N. leptocephalus*. If tilting by the male occurred prior to the run, the female moved from the furrow. Combat and/or aggressive displays with other species (male *Campostoma anomalum*, *L. cerasinus*, and *Lythrurus ardens*) also disrupted a spawning sequence.

Luxilus cerasinus

Interim: In contrast to the behavior in male *L. albeolus*, male *L. cerasinus* did not form furrows but hovered over their territories (discrete pebble areas) on the upstream slope of a nest of *N. leptocephalus*.

Approach: If a female approached the male from downstream he maintained his position. If she approached from the side he proffered his spawning area by moving laterally away from her. When she was directly over the spawning site he moved back into place.

Alignment: Like Alignment in *L. albeolus*, the male *L. cerasinus* coordinated his swimming with that of the female. After positioning himself against her side over the substrate, he pressed his snout against hers.

The behaviors associated with the Run and the Clasp in *L. cerasinus* were like those described for *L. albeolus*, except that they did not occur in a furrow. Unlike *L. albeolus*, female *L. cerasinus* did not rise towards the surface during Dissociation. Like in *L. albeolus*, the aggressive and combat behaviors in which territorial male *L. cerasinus* engaged conspecific males, and those with *L. ardens* and *Phoxinus oreas*, were disruptive of successful spawning.

DISCUSSION

There are two lineages within *Luxilus* (furrowing species where females rise to surface after clasp, and non-furrowing species where females do not rise to surface after clasp). In addition to *L. albeolus*, furrowing species include *Luxilus cardinalis* (Miller, 1967; Robison and Buchanan, 1988), *Luxilus chrysocephalus* (Hankinson, 1932; Robison and Buchanan, 1988; Smith, 1979), *Luxilus cornutus* (Raney, 1940), *Luxilus pilsbryi* (Pflieger, 1975), and *Luxilus zonatus* (Pflieger, 1975). Like *L. cerasinus*, the species *Luxilus coccogenis* (Outten, 1957) and *Luxilus zonistius* (Johnston and Birkhead, 1988) do not form furrows.

We do not agree with Johnston (1989) who included *Luxilus* species and those of *Campostoma* with pebble nest-building species. The furrowing behavior in some species of *Luxilus* and the pit digging in *Campostoma* species are not forms of pebble nest-building (i.e., construction of mound and pit/ridge nests) as described by Maurakis et al. (1992). Pebble nest-building in cyprinids is a behavior that is an overt movement of pebbles by the use of jaws (keratinized inner mandibular epithelium; McGuire, 1993) in males in species of *Exoglossum*, *Nocomis*, and *Semotilus*. Keratinized inner mandibular epithelium is absent in *L. cerasinus* and *L. cornutus*, nor does it occur in *Campostoma* species which dig pits (McGuire, 1993).

A furrow may create reduced water currents similar to those that facilitated the sinking of gametes into interstices in spawning pits of nests of *Semotilus* species, and those in nests of *N. leptocephalus* as reported by Maurakis et al. (1992). Additionally, the furrow provides a clean protected substrate for spawning and deposition of eggs.

Our observations of the spawning behaviors in *L. albeolus* and *L. cerasinus* support Sabaj (1992), who proposed that his six sequential categories of breeding behaviors for pebble nest-building cyprinids may be applied to the spawning behaviors of other species that spawn over gravel substrates. His categories provided a clear and definitive framework for describing the spawning behaviors in these two lithophilous spawners.

Luxilus albeolus and *L. cerasinus* spawned over the upstream slope of nests when male *N. leptocephalus* were either present or not. As small size eggs and the larger eggs of *N. leptocephalus* were found in the upstream slopes of nests on both dates, it is presumed that *N. leptocephalus* had completed spawning at the unattended nest. Neither *L. albeolus* nor *L. cerasinus* are regarded as obligatory symbionts of *N. leptocephalus*, a questionable mating association described for

Hydrophlox lutipinnis and *N. leptocephalus* by Wallin (1989). Not only have we observed *H. lutipinnis* spawning on nests in the absence of attending male *N. leptocephalus*, but the latter species is present in drainages where *H. lutipinnis* does not occur.

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