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Heterogeneric Spawning Between *Campostoma a. anomalum* and *Nocomis l. leptocephalus* (Actinopterygii: Cyprinidae)

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ABSTRACT

Analysis of videotapes indicated that a male *Campostoma a. anomalum* clasped individual female *N. l. leptocephalus* in the spawning pit of a gravel nest of a male *N. l. leptocephalus*. Chronology of behaviors of male *C. anomalum* and female *N. leptocephalus* that resulted in three heterogeneric spawns were resolved into six sequential categories of activities: interim, approach,alignment, run, clasp, and dissociation. The heterogeneric clasp by the male *C. anomalum* is similar to that in male *Rhinichthys a. atratulus*, but unlike that of male *N. leptocephalus*.

INTRODUCTION

Hybridization between species of pebble nest-building minnows and their nest associates (species that congregate and may spawn over a nest but do not contribute to its construction) has been attributed to either chance cross fertilization or mismating (Jenkins and Burkhead, 1994). However, Maurakis and Woolcott (1992) provided empirical evidence that intergeneric hybrid crosses may result from intimate contact between species where male *Nocomis l. leptocephalus* clasped female *Campostoma a. anomalum* in spawning pits of nests of *N. leptocephalus*. The following describes our observations of a male *C. anomalum* clasping female *N. leptocephalus*, independently of male *N. leptocephalus*, in the spawning pit of a spawning male *N. leptocephalus*.

MATERIALS AND METHODS

Breeding behaviors of fishes were observed and videotaped over nests of *N. leptocephalus* in Pumpkin Creek, Dan-Roanoke River drainage, St. Rt. 86, 1 km N of St. Rt. 205, Pittsylvania Co., Virginia, 15 May 1987. Cameras and techniques used to videotape activities of fishes follow those in Maurakis and Woolcott (1995); water temperature=16.5^{o}C. Activities recorded on film were reviewed at normal speed, in slow motion, and frame by frame to identify specific behaviors of fishes. Reproductive activities of male *C. anomalum* and those of male and female *N. leptocephalus* were resolved into six chronological categories that reflected the sequence of male-female interactions following Sabaj (1992) and Maurakis and Woolcott (1993): Interim (behavior of male between spawns), Approach (behavior of female directed towards interim male), Alignment (behavior affecting orientation of a spawning pair over substrate), Run (upstream swim, initiated by female aligned by male), Clasp (spawning

act, i.e., momentary flexure of male's body about that of female at end of her run), and Dissociation (pair separation immediately following the clasp).

RESULTS

The chronology of behaviors that led to three heterogeneric spawns of individual female *N. leptocephalus* by a male *C. anomalum* in the spawning pit of a breeding male *N. leptocephalus* (one of five male *N. leptocephalus* spawning on the upstream slope of a nest) follows:

Interim: The male *C. anomalum* maintained a position about 5-7 cm aside and downstream of a male *N. leptocephalus* positioned over his spawning pit (the head of the male *C. anomalum* was level with the pelvic fin of the male *N. leptocephalus*).

Approach: A female *N. leptocephalus* swam forward to the downstream edge of the spawning pit, and then to the gravel substrate at the center of the pit, about 2 cm below the ventrolateral portion of the body of the male *N. leptocephalus*.

Alignment: The male *C. anomalum* moved laterally and slightly upstream into the pit to a position alongside and head to head with the female *N. leptocephalus*. The male *N. leptocephalus* continued interim behavior, hovering over the pit just above and to the side of the heterogeneric spawning pair.

Run: A female initiated the spawning run. With her body pressed to the substrate, she moved 2-3 cm upstream while quivering her caudal peduncle and fin. Almost simultaneously, the male *C. anomalum* moved forward with his body pressed against the female *N. leptocephalus*. At the end of a run, a female abruptly pitched her head 30 degrees upward with the ventral surface of caudal peduncle pressed to the upstream slope of the spawning pit. As a female's snout approached 30 degrees from the substrate, she rolled the anterior portion of her body away from the male *N. leptocephalus* and toward the male *C. anomalum*. During conspecific spawning clasps, a female *N. leptocephalus* typically rolls the anterior portion of her body away from her partner placing her dorsum in contact with his anterior flank (Sabaj, 1992). Thus, female *N. leptocephalus* in this study appar performed their spawning runs in response to the nearby male *N. leptocephalus* but subsequently was clasped by the male *C. anomalum* when the male *N. leptocephalus* failed to react. During heterogeneric spawning clasps, the male *N. leptocephalus* continued interim hovering behavior over his pit.

Clasp: Turning his head toward a female *N. leptocephalus*, and quivering his caudal peduncle and fin, the male *C. anomalum* tilted his upper body toward a female, as he placed his caudal peduncle and fin over her back. The clasp of the male *C. anomalum* pinned the ventral surface of the body of a female *N. leptocephalus* to the substrate, as the two continued to quiver before dissociating. The male *N. leptocephalus* continued to hover over the pit.

Dissociation: After clasping, the male *C. anomalum* drifted to his previous position aside the male *N. leptocephalus*, and the female *N. leptocephalus* drifted downstream of the spawning pit. At dissociation, the male *N. leptocephalus* aligned with and clasped another female *N. leptocephalus* on the opposite side of the dissociating male *C. anomalum* and female *N. leptocephalus*. Shortly thereafter, the male *N. leptocephalus* aligned with and clasped one of the females that had spawned with the male *C. anomalum*.

DISCUSSION

Hybrids of *C. anomalum* and *N. leptocephalus* have been reported by Raney (1947) and are sometimes common (e.g. Grady and Cashner, 1988). Based on our observations, intraspecific spawning behaviors of *N. leptocephalus* stimulate nearby male *C. anomalum* to converge and participate in what Jenkins and Burkhead (1994) describe as a "mating frenzy." Mating frenzy promotes conditions for mismating, which is one of two mechanisms (besides chance cross fertilization) that Jenkins and Burkhead (1994) recognized as leading to hybridization between nest-building and nest associate species. Under certain circumstances, this stimulus may be sufficiently strong to override species recognition. The five male *N. leptocephalus*, sometimes spawning in rapid succession with one female after another, were accompanied by as many as 40 individuals per nest associate species (*C. anomalum*, *Clinostomus funduloides*, *Luxilus albeolus*, *Luxilus cerasinus*, *Lythrurus ardens*, *Phoxinus oreas*, *Rhinichthys atratulus*) that were congregating and spawning (i.e. *L. cerasinus*) over the nest.

The heterogeneric spawning clasps performed by male *C. anomalum* in our study raises the question, do male *C. anomalum* clasp conspecific females in the same manner? The heterogeneric spawning clasp by the male *C. anomalum* is a distinct action. The clasp is like that reported for male *Rhinichthys atratulus*, but unlike the semicircle clasp reported for male *N. leptocephalus* (Sabaj, 1992; Sabaj et al., in review; Maurakis and Woolcott, 1989; Traver, 1929). In a study of the reproductive behavior of *Campostoma anomalum pullum*, Miller (1962) stated that his motion picture analysis did not reveal a male clasp, but that the details of spawning behavior were almost impossible to see. Miller (1962) described the spawning act as the male pressing against a female. Miller (1962) also indicated that at larger pits where more males were present, a female would dart down beside the resident male causing an instantaneous convergence into the pit by all nearby peripheral males. He presumed the spawning act to occur at this time, while males were twisting and writhing to get next to the female. We have observed and videotaped this same convergence, but interpreted it as disruptive of a successful spawn because females quickly fled the pit before a male became aligned.

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