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Spawning Behavior in *Hemitremia flammea* (Actinopterygii: Cyprinidae)

Eugene G. Maurakis, Science Museum of Virginia,
2500 W. Broad St., Richmond, VA 23220 &
University of Richmond, VA 23173
Ray Katula, North American Native Fishes Association,
308 16th Ave. North, Onalaska WI 54650
William Roston, Roston Family Practice Clinic, Forsyth, MO 65653

ABSTRACT

Spawning behavior in *Hemitremia flammea* (Flame chub) is described from observations made in the field and laboratory. Spawning in the field occurred over clean gravel (size range=18-25 mm) at water temperatures from 12.8-14.4 C. Spawning in the laboratory occurred over clean gravel (11.3 mm) at water temperatures from 18.3-20 C. Males often pursued females and nudged their vents with their snouts. When the female settled to the substrate, a male moved forward and aligned himself alongside her body. Then the female moved slightly forward accompanied by the male and the pair vibrated their caudal peduncles and tails. The spawn ended as the male quickly flexed his caudal peduncle and caudal fin laterally toward the quivering caudal peduncle and caudal fin of the female. The male's flexed caudal area did not cross over but contacted the side of the female's quivering caudal peduncle, which sometimes became arched slightly upwards. Aspects of spawning behavior (males pursuing and nudging vents of females, females selecting sites for spawning, pair alignment, males vibrating caudal fin and peduncle) in *H. flammea* is similar to that described for *Couesius plumbeus* but differs significantly from that of *Semotilus atromaculatus*, a species in the hypothesized sister group of *H. flammea*.

INTRODUCTION

Hemitremia flammea (Flame chub) is restricted to spring habitats primarily in the Tennessee, Duck, and Cumberland river drainages in Tennessee and Alabama, and has been recorded in the upper Coosa River drainage (Mobile Basin) in Alabama (Etnier and Starnes, 1993). Spawning has been reported to occur from late January through May, peaking in March, with tuberculate males available from October through May (Etnier and Starnes, 1993). Etnier and Starnes (1993) observed what they thought to be a spawning aggregation in a shallow seepage area of a pasture in late February, but stated that reproductive behavior and egg deposition sites are unknown. This paper describes spawning behavior in *H. flammea* from field and laboratory observations, and compares it to that found in other lithophilous spawning cyprinids in North America, particularly in *Couesius plumbeus* and *Semotilus atromaculatus*. Recent morphological and molecular studies (Coburn and Cavender, 1992; Simons and Mayden, 1997) support a sister group relationship between *Hemitremia* and species of *Semotilus*, including *S. atromaculatus*.

MATERIALS AND METHODS

Field Studies:

Observations and videorecordings of *H. flammea* were made in a man-made riffle between two spring-fed ponds of Mountain Fork (tributary of Flint River, Tennessee River Drainage) off Winchester Road, about 5 km NE of New Market, Madison Co., Alabama, from 1000-1500 hrs CDT on 10 May 1998 and 2 May 1999; and in laboratory aquaria from January-May, 2000. Underwater videorecordings were made with a Sony VX 1000 digital camera/recorder, equipped with a built-in 100 watt light source, and mounted in a Sting Ray waterproof housing. The camera, manually manipulated or set in a fixed position on the substrate, was positioned about 0.6 m from the substrate where the fish were congregating. Stream width was 10 m, water depth where recordings were made was 45 cm, and maximum visibility was 4.5 m.

Laboratory Studies:

Adult *H. flammea*, collected from Cypress Creek, off Arlic Holt Road, Wayne Co., Tennessee in 1995, were transported to the laboratory. In January, 2000, the fish were transferred to a 40-gal aquarium kept at 7.2 C. Photoperiod was maintained at 6-8 hrs/day in January, and gradually increased with fluorescent lighting to 16 hrs/day from mid-January to late May. A submersible aquarium heater was used to increase water temperature from 7.2-18.3 C from 15 January to 8 March 2000. Groups of 6-8 male and 8-12 female adult *H. flammea*, acclimated to these conditions, were then transferred to a 151 liter aquarium for observation and videotaping. This observational aquarium was fitted with fine grain gravel (mm) and one large (8 x 12 x 15 cm) rock for cover. A single plastic tray (30.5 x 40.6 x 7.6 cm) fitted with gravel (11.3 mm size class) was placed over one part of the substrate to facilitate harvesting of eggs. Bunches of plastic grass were placed at the ends of the aquarium at various times. Routinely, females were removed from the observational aquarium after spawning. Adults were fed dry foods (Tetramin flakes in the morning) and live or frozen foods (glassworms, whiteworms, and blood worms) in the afternoon.

Behaviors recorded on 10 hrs. of videotape (2 hrs in the field and 8 hrs in the laboratory) were reviewed at normal speed, in slow motion, and frame by frame to identify specific behaviors of female and male *H. flammea* following methods in Maurakis and Woolcott (1995). Reproductive activities of male and female *H. flammea* were resolved into six chronological categories that reflected the sequence of male-female interactions characteristic of a successful spawn, following Sabaj (1992; 2000) 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* (initiated by a female, synchronized movement of aligned pair over substrate), *clasp* (spawning act, i.e., momentary flexure of male's body about that of female at end of her *run*), and *dissociation* (behaviors of male and female affecting their separation immediately following the clasp). Behaviors other than those associated with the spawning sequence were considered disruptive of a successful spawn.Accounts of spawning behavior in *H. flammea* are summarized from observations and review of videotapes made in the field and laboratory.

RESULTS

Field Studies:

Spawning occurred over clean gravel (diameter 18-25 mm) in moderate current at the head of a riffle joining two spring-fed ponds at temperatures between 12.8-14.4 C. Male *Campostoma oligolepis* (largescale stoneroller) occasionally moved over the substrate where male *H. flammea* were posturing, but were not observed spawning, digging, or foraging in this area.

Laboratory Studies:

Spawning occurred over substrates composed of primarily of 11.3 mm size gravel between 18.3 C (8 March 2000) and 20 C (9 June 2000).

Spawning Behaviors:

Interim: In the field, about 200 male *H. flammea*, swimming against the current, hovered over approximately 1 m^2 of substrate. Within this 1 m^2 area, males frequently formed two to three well-defined groups, each group maintaining position over a discrete area of substrate where they jockeyed for position. No one male consistently dominated other males. Within these sub-areas, males also foraged as they dislodged gravel with their snouts. They also dipped their heads or snouts into substrate and then expelled sand from their mouths. Aggressive behaviors observed between males were lateral head butts, body swings, chases, and short parallel swims. In the laboratory, male behavior during interim was like that observed in the field, *albeit* numbers of males in the aquarium were lower.

Approach: From a downstream position, a female swam forward against the current to the substrate regardless of the position of the majority of males. The female slowed her forward movement as she lowered her body into a downstream slope of a depression formed by natural arrangements of gravel in the substrate and rested on the substrate. Usually a female was followed by a single male, although at times a couple of other males were in close proximity.

Alignment: One to four males chased a female as she moved from one area of substrate to another, frequently nudging her genital area with their snouts. Males maneuvered themselves about the female and attempted to direct her to the substrate regardless of where other males congregated. Successful alignment occurred when a male moved forward from a downstream position and aligned himself head to tail with the female. At times, two males aligned with a female, one on each side of her body. Other times, as many as six males maneuvered themselves alongside and on top of the female and each other. The maneuvering of several males about a female often resulted in the female swimming away.

Run: After a male aligned himself aside a female, the female moved slightly forward with three to four quick tail beats and was accompanied by the male who also moved forward with quick tail beats. At the end of the short run, the pair began to vibrate their caudal peduncles and caudal fins as the female followed the contour of the substrate. At times, a couple of males, one on each side of the female, accompanied the female during her run.

Clasp: The male ended his vibrations with a quick flexing of his caudal peduncle and tail laterally toward the quivering caudal peduncle and caudal fin of the female.

The male's flexed caudal area did not cross over but contacted the side of the female's quivering caudal peduncle, which sometimes became arched slightly upwards.

Dissociation: After the clasp, the female moved off of the substrate. She either returned to the substrate to spawn again, or moved away from the spawning area. At times the female was appressed to the substrate by several males just after being clasped. She flexed her caudal fin against the substrate, springboarding herself upwards. As the female rose vertically into the water column, she often was accompanied by a male. Near the water's surface, but without breaking it, the female regained horizontal and swam away. After clasping, a male either followed the female to the same (or a different) spawning area where they spawned again, or joined other males congregating over the substrate and engaged them in aggressive behaviors.

During and after the spawning act, as many as 30 male *H. flammea* converged upon the spawning pair, most of which writhed and burrowed head first (caudal fins oriented upward) into the substrate where spawning occurred, presumably to eat eggs. Burrowing episodes, involving as many as 30 males and lasting up to 30 seconds each, also occurred when a single male butted gravel with his snout, presumably in search of food.

DISCUSSION

Spawning behaviors in *H. flammea* are somewhat similar to those described for *Couesius plumbeus* (Lake chub) by Brown (1969) and Brown et al. (1970). In both species, males and females congregate in shallow areas of streams to spawn (lake chubs also spawn along rock shores and shoals of lakes). *Hemitremia flammea* has been observed to spawn in 0.3 m of water over road gravel that had washed in from a nearby gravel drive on 5 May 1993 at a water temperature of 15 C (R. Mayden and B. Kuhajda, pers. comm.). Mayden and Kuhajda (pers. comm.) also noted when a female approached the spawning area, she was followed by 2-5 males, but spawning occurred with 1-3 males. After spawning, several individuals crowded in to eat eggs. Whereas we only observed flame chubs spawning on gravel, Brown et al. (1970) observed lake chubs spawning over a variety of substrates (i.e., on gravel, among or beneath rocks, beneath large boulders and on silt and leaves). Nest-building has not been observed and there is no evidence of parental care in either species.

In both species, males pursue females and use their snouts to nudge the female's vent region. Brown et al. (1970) noticed in aquaria that male lake chubs actively pursued, nudged and swam aside ripe females but were less interested in spent females. Hunter and Hasler (1965) demonstrated that milt and ovarian fluid of *Lepomis cyanellus* (green sunfish) attracted *Lythrurus umbratilis* (Redfin shiner) to sunfish nests and stimulated the shiners to spawn. Brown (1969) used this information to speculate that the female's ovarian fluid may elicit the male's nudging behaviors in lake chubs.

Brown et al. (1970) noted for *C. plumbeus* held in aquaria that the spawning act lasted about a second and described it accordingly: "A male would...force himself against [the female] and, as he vibrated vigorously and she appeared to struggle, the nonadhesive eggs would freely disperse." As we described in flame chubs, the female initiated a short run with a few quick tail beats after which she vibrated her caudal peduncle and tail over the substrate. The closely aligned male similarly vibrated his body as he accompanied her run and completed the act by laterally flexing his caudal peduncle and tail toward the quivering female. Although Brown et al. (1970) did not specify a run and quivering in female *C. plumbeus*, their description suggests that the spawning act in both species are quite similar. Furthermore, in both species the site of gamete deposition appears to be ultimately determined by the female as she moves toward the substrate with one or a few male swimming alongside.

Spawning behavior in *H. flammea* is significantly different from that reported for *Semotilus atromaculatus*, a species in the proposed sister-group of *H. flammea* (Coburn and Cavender, 1992; Simmons and Mayden, 1997). None of the spawning behaviors exhibited by male and female *H. flammea* during interim, approach, alignment, run and clasp, or dissociation were consistent with those described by Sabaj (1992) and Maurakis et al. (1993) for *S. atromaculatus* and *S. thoreauianus*. During interim behavior in *S. atromaculatus*, a single male uses his mouth to construct a pit-ridge nest and remains stationed in the pit unless engaged in spawning on the pit/ridge interface or aggressive behaviors with other males away from the nest (Sabaj, 1992), behaviors not observed in *H. flammea*. During the approach, a female *S. atromaculatus* always moves toward a male in his nest. The male *Semotilus* effectively determines the spawning site by constructing the nest. In contrast, female *H. flammea* may move to substrates away from congregating males for spawning. Female *H. flammea* do not retroflex as do female *S. atromaculatus* reported by Sabaj (1992) and Maurakis et al. (1993). Male *H. flammea* do not perform a spawning clasp like that described for *S. atromaculatus* by Sabaj (1992) where a male completely encircles an uplifted female.

Differences in spawning behaviors between *H. flammea* and *Semotilus* species do not conflict with the *Semotilus-Hemitremia* sister-group of Coburn and Cavender (1992) and Simmons and Mayden (1997). Pit-ridge nest building probably represents an autapomorphy that evolved within the *Semotilus* ancestral lineage after separation from the ancestral stock common to *Hemitremia* and *Semotilus*. For example, Johnston and Page (1992) indicated that the primitive *Phoxinus* and *Margariscus* and derived *Couesius, Dionda, Hybognathus* are broadcast spawners (i.e., species that scatter eggs and sperm with no previous preparation of substrate). By this definition, *H. flammea* can be considered a broadcast spawning species. However, delineation of chronological categories of spawning behavior of Sabaj et al. (2000) for closely related species (*Phoxinus, Margariscus, Couesius, Dionda,* and *Hybognathus*) will allow the use of behavioral characters to refine resolution among species relationships proposed by Coburn and Cavender (1992) and Simmons and Mayden (1997).

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