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Breeding Behaviors In *Notropis alborus* (Actinopterygii: Cyprinidae)

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ABSTRACT

Breeding behaviors (establishment of male territories, aggressive behaviors between males, and spawning behaviors) in *Notropis alborus* (whitemouth shiner) were identified with direct field observations and review of videotapes of behaviors recorded in Mines Creek (Roanoke River drainage), Mecklenburg County, Virginia in 1997. Male *N. alborus* established and defended individual territories after a period of combat and jockeying for position over substrate. Five forms of aggressive behavior (non-contact head displacement, non-contact body displacement, chase, lateral head and body butts, and parallel swim) were identified between male *N. alborus*. Spawning occurred over sand and gravel at water temperatures of 27-28 degrees C. Six sequential categories of male and female interactions that led to spawning were identified in *N. alborus*: *Interim* (behavior of a male in his territory); female *Approach* (behavior of a female towards a male in interim); male *Approach* (behavior of an interim male after female's approach); *Alignment* (orientation of male and female over substrate); *Clasp* (flexure of male's caudal peduncle and fin over back of female), and *Dissociation* (behavior of female and male after clasp). Categories of spawning behavior in *N. alborus* also fit descriptions of spawning in *Notropis procne*, and may provide an appropriate framework for describing spawning behaviors in other members of the *N. procne* species-group.

INTRODUCTION

Notropis alborus, whitemouth shiner (Actinopterygii: Cyprinidae), is restricted to small to medium size streams of four Atlantic Slope river drainages (Santee, Pee Dee, Cape Fear, and Roanoke-Chowan) in the Piedmont region of North Carolina and Virginia (Jenkins and Burkhead, 1994). Described by Hubbs and Raney (1947), *N. alborus* exhibits strong affinities to *Notropis heterolepis* and *Notropis rupestris* (Page and Beckham, 1987), and is considered part of the *Notropis procne* species-group (Snelson, 1971; Burr and Mayden, 1981).

Published information on life history aspects of *N. alborus* is exiguous. General habitat descriptions and diet have been documented for the species (Hubbs and Raney, 1947; Snelson, 1971; Gatz, 1979; Jenkins and Burkhead, 1994); however, there is no literature on breeding behaviors of *N. alborus*. Our objectives are to describe breeding behaviors in *N. alborus* and compare them to those in *N. procne* by Raney (1947).

Study Area

Behavioral studies were made in a 900 m stretch of Mines Creek (Roanoke River drainage) in Mecklenburg County, Virginia. This stretch of Mines Creek averaged

TABLE 1. Percentage of size class of substrate material based on weight (g) from spawning substrate (n = 1) and foraging substrate (n = 4), and electivity index values for spawning substrates of *Notropis alborus* in Mines Creek (Roanoke River drainage), Mecklenburg Co., Virginia, 18 July 1997.

	Substrate Size						
Substrate	23mm	11.3mm	6.0mm	2.5mm	0.8mm	<0.8mm	Total wt. (g)
Spawning	27.2	21.2	20.9	11.3	4.9	12.2	161.5
Foraging: $\bar{x}$	22.2	4.1	4.9	5.2	10.4	55.2	380.3
Range	(0-88.7)	(0.9-7.3)	(1.2-8.4)	(1.0-8.7)	(0.1-18.6)	(1.7-80.9)	
Electivity Index Value	0.1	0.68	0.62	0.37	-0.36	-0.64	

4.86 m in width (range=3.0-7.3 m, s.d.=1.17, n=10), and 26.9 cm in depth, (range=10.2-52.0, s.d.=13.4; n=10), and served as a drinking and wallowing area for cattle. Water was classified as white (i.e., not stained with tannic acid), and varied in clarity from completely turbid to clear. Stream substrates consisted of varying amounts of sediment, sand, gravel, rocks, and detritus (Table 1).

MATERIALS AND METHODS

Binoculars (50x lenses) and a videocamera were used to locate, observe and record activities *of N. alborus* from 18 March to 18 July 1997. Small size, clarity, and shallow depth of the stream made it possible to locate, observe, and videorecord activities of fishes from the bank. Observations and videorecordings were made from positions on the stream bank that minimized glare from reflected sunlight. A Nuvicon tri-tube video camera (resolution=350 lines) equipped with a 12X zoom lens (focal length=10.5-126 mm), polarizing filter, and an automatic/manual iris diaphragm was used to videotape activities of *N. alborus* on a videocassette recorder (1/2 inch, VHS tape; tape speed= 9.53 cm/sec) following recommendations by Maurakis and Woolcott (1995) for camera position and angle, lighting, and filming methods. In the laboratory, videotapes were played at normal speed, slow motion, and frame by frame (30 frames/second) to catalogue activities of breeding fishes. Each illustration of a particular behavior was drawn from a single frame of videotape viewed on television, using preserved specimens as models for morphological detail.

Reproductive activities were resolved into categories of behavior reflecting the sequence of female-male interactions that resulted in a successful spawn following methods in Sabaj (1992) and Maurakis and Woolcott (1993). Categories are: interim (behavior of a territorial male between spawns); approach (behavior of female towards interim male); alignment (behaviors affecting orientation of a spawning pair over substrate); run (initiated by female, synchronized movement of aligned pair over substrate); clasp (spawning act, i.e., momentary flexure of male's body about female's body); and dissociation (behaviors of female and male affecting their separation immediately following the clasp). An intruder male is one that enters the territory of an interim male. Territory sizes of interim males were estimated by measuring maxi-

mum extent of substrate defended by an interim male relative to the average size of *N. alborus* ($\bar{x}$ = 46.7 mm, s.d.=9.3, range=31-59 mm, n=26) collected in Mines Creek.

Substrate material of spawning and foraging areas were collected separately with a 1 liter scoop and returned to the laboratory. Samples were air dried, and sifted through five custom built sieves with mesh sizes of 23.0 mm, 11.3 mm, 6.0 mm, 2.5 mm, and 0.8 mm according to methods in Maurakis et al. (1990). Material that sifted through the 0.8 mm mesh was collected in a pan. Mesh sizes were restricted to commercially available prefabricated screen sizes. Weight of substrate material corresponding to each mesh size was used to calculate percentage of material per mesh size.

Preference for specific substrate size for spawning was calculated for each substrate sizes class using an electivity index (Ivlev, 1961). The equation

$$E = \frac{(r_1 - p_1)}{(r_1 - p_1)}$$

(where E=pebble size selection, r = percentage of a particular pebble size in the substrate where spawning occurred, and p = percentage of a particular pebble size in the substrate where foraging took place) was used to determine if selection of pebbles in spawning and foraging areas was non-random. Electivity values range from -1 to +1. Values closer to +1 indicate a greater selection of a particular pebble size. Stream width (m) and depth (cm) were measured with a tape measure and meter stick, respectively.

RESULTS

Breeding behaviors identified in *N. alborus* were: establishment of male territories, aggressive behaviors exhibited by males during interim, aggressive behaviors that disrupted spawning, and sequential spawning behaviors of females and males that led to a successful spawn. Behaviors disruptive of a successful spawn took place primarily during interim, but occurred periodically throughout spawning.

Establishment of male territories - Establishment of territories by individual male *N. alborus* was the first behavior indicative of the onset of spawning. When a single male assumed a position over a particular section of substrate, others darted toward him and displaced him from his position. Behavior of one male displacing another (as if jockeying for position) occurred over several minutes prior to spawning, and periodically after spawning. Eventually, individual territories were established and defended by single interim males. Males that did not establish territories decreased their aggression toward territorial interim males, yet periodically challenged interim males between spawns. Territory area defended by an interim male averaged approximately 50.1 cm^2. An interim male swam in a figure-8 pattern within his territory to fend off intruders (Fig. 1). Average time that an interim male guarded his territory was 6.3 sec (range = 1.5-29.0 sec, s.d. 7.2, n =19).

Aggressive behaviors - Five forms of aggressive behavior (non-contact head displacement, non-contact body displacement, lateral head and body butting, and parallel swim) were identified between breeding male *N. alborus*.

Non-contact head displacement was performed only by interim males. An interim male turned his head in direction of an approaching intruder. The movement prevented intruders from entering a territory only for duration of the movement. Once head

displacement behavior ended, the same intruder usually swam into the territory of an interim male and initiated chase behavior (Fig. 2).

Non-contact body displacement, performed only by interim males, occurred when an intruder male approached an interim male's territory. The interim male turned his body laterally in direction of an intruder, which prevented entry into the territory only for the duration of the movement (Fig. 3). In one instance, non-contact body displacement failed to prevent entry of an interim male's territory by a larger intruder, which usurped the interim male from his territory.

Chase behavior was initiated by both interim and intruder males; however, chases (n = 32) initiated by intruder males (n = 25) were more frequent than those initiated by interim males (n = 7). Chases increased in intensity and duration over time particularly when combined with lateral head and body butts. During some chases, two male *N. alborus* swam in large circles.

Lateral head and body butting (i.e. physical contact) was the most aggressive behavior observed between interim and intruder males. Lateral head and body butting occurred primarily during chases, but was used when an intruder male entered an interim male's territory. A male initiating the behavior rapidly swam forward and used his head and/or snout to strike the flank or head of the other male (Fig. 4).

All parallel swims (n =10) were initiated by intruder males equal in size to interim males. Two males, facing upstream, aligned in a V-configuration with their caudal fins nearly touching and their heads 2-3 cm apart. Both males swam forward for 1-3sec., maintaining the V-configuration as their caudal fins and peduncles quivered (Fig. 5).

Spawning Behaviors - Spawning occurred over stream bottoms consisting of 6.0 mm and 11.3 mm size classes of substrate material (Table 1) between 27-29^{o}C, in July. Reproductive activities of *N. alborus* were resolved into categories of behavior reflecting the sequence of female-male interactions that led to spawning.

Interim. (male only) An interim male, facing upstream, swam in a figure-8 pattern to guard his territory and engaged in aggressive combat with intruder males (Fig. 1).

Approach (female only). A female approached an interim male by swimming upstream to the territory of a male. Then she swam 20-40 cm upstream of his territory and assumed a stationary position over substrate composed of clean fine gravel and sand (Fig. 6).

Alignment. Once a female postured over clean gravel and sand, an interim male moved forward (Fig. 7) and oriented himself parallel to, and slightly above the postured female (Fig. 8).

Run. Female *N. alborus* do not perform a run.

Clasp. Once aligned in a stationary position, both the female and male vibrated their caudal peduncles and fins simultaneously. The clasp followed as the male angled his caudal peduncle and tail over those of the female. The spawning pair continued to vibrate their bodies for less than a second which dislodged fine sand from the spawning site (Fig. 9).

Dissociation. Dissociation occurred as the male relaxed his clasped caudal peduncle and released the female. The female then swam 15-30 cm upstream, and postured over another spot of clean fine gravel and sand. The interim male followed, and the pair aligned and spawned again. After completing a second spawn, a female dissociated

Table 2. Comparison of environmental parameters and terrritory sizes in *Notropis alborus*, *Notropis procne* (Raney, 1947), and *Notropis stramineus* (Summerfelt and Minckley, 1969)(— = no data available).

Parameter	*N. alborus*	*N. procne*	*N. stramineus*
Spawning temp. (^{o}C)	27.0-28.0	25.5	27.0-37.0
Spawning substrate	Clean gravel (6.0-11.3 mm) and sand	Clean gravel and sand	Deep sand, some fine gravel
Stream depth	~ 10 cm	~ 10 cm	12.5 cm
Interim male territory size (cm^2)	50.1	28.5	—
Stream current (m/sec)	1.7	2.15	—

from her mate and swam downstream. The male either swam downstream in pursuit of the female, or resumed interim activities in his territory.

DISCUSSION

Descriptions of breeding behaviors in *N. alborus* are the first for any species in the monophyletic *Notropis heterolepis* species-group (*N. alborus*, *Notropis heterolepis*, and *Notropis rupestris*) proposed by Page and Beckham (1987). These three species, which share the presence of a midlateral row of black crescents (Page and Beckham, 1987), are considered by Snelson (1971) and Burr and Mayden (1981) to be part of the larger *Notropis procne* species-group, including *N. alborus, Notropis chihuahua, N. heterolepis, Notropis mekistocholas*, *N. procne*, *N. rupestris*, *Notropis stramineus, and Notropis uranoscopus.* Paucity of information on phylogenetic relationships among members of the *N. procne* species-group is exceeded only by the lack of descriptions of their breeding behaviors. Excepting *N. alborus*, the only detailed descriptions of breeding behaviors for any of the eight species in the *N. procne* species-group is that described for *N. procne* by Raney (1947), and to a lesser degree, that by Summerfelt and Minckley (1969) for *N. stramineus* (Tables 2 and 3). As a result, breeding behaviors in *N. alborus* are compared to those described by Raney (1947) for *N. procne*, and where possible, to those described by Summerfelt and Minckley (1969) for *N. stramineus*.

Water temperatures (27-28^{o}C) when spawning occurred in *N. alborus* were comparable to those (25.5^{o} C and 27-37^{o} C) for *N. procne* and *N. stramineus* reported by Raney (1947) and Summerfelt and Minckley (1969), respectively (Table 2). Summerfelt and Minckley (1969) suggested that spawning at high temperatures during summer may be an adaptation to enhance survival of fry of *N. stramineus* because spring is characterized by drastic water level fluctuations and flood-type conditions. Spawning in *N. alborus* occurred over clean gravel and sand where water depth and velocity were 10 cm and 1.7 cm/sec, respectively, much like the substrates, water depths (~ 10-12.5 cm), and water velocities (2.15 cm/sec) where spawning occurred in *N. procne* and *N. stramineus* reported by Raney (1947) and Summerfelt and Minckley (1969)(Table 2).

TABLE 3. Comparison of breeding behaviors (establishment of territories; aggressive behavior, using categories in Maurakis and Woolcott, 1997; and spawning behavior, using spawning categories in Sabaj, 1992) in *Notropis alborus*, in Mines Creek (Roanoke River drainage), Virginia, and *Notropis procne*, reported by Raney (1947) in Covington River (Rappahanock River drainage), Virginia.

Behavior	*Notropis alborus*	Notropis procne
Establishment of territories	Intermittently, groups of males arrive and jockey for position. Individual males, oriented upstream, establish territories, ($\bar{x}$ =50.1 cm^2. The primary movement involved a back and forth lateral swim ("lazy figure eight").	Same as in *N. alborus* except territory size=28.5 cm^2.
Agonistic Behaviors		
Non-contact head displacement	Performed by interim male upon approach of an intruder male	Same as in N. *alborus*.
Non-contact body displacement	Performed by interim male upon approach of an intruder.	Not observed.
Chase	Primarily initiated by intruder males. Some chases occur in circular paths.	Same as in *N. alborus*.
Lateral head and body butts	Frequently occurs between interim and intruder males usually in concurrence with chases	Not observed.
Parallel swim	Frequently occurs between interim and intruder males of approximate equal size. Initiated by intruder males.	Not observed.
Circle swim (as described by Raney)	Frequently occurs between interim and intruder males of approximately equal size.	Same as in *N. alborus*.
Spawning behaviors		
Interim	Interim male swims in figure-8 pattern within his territory and engages in agonistic behaviors with intruder males.	Same as in *N. alborus*.
Approach	Female moves upstream and lateral or slightly upstream of interim male's territory and assumes stationary position. Male then moves toward female.	Female moves upstream to position slightly below and immediately downstream of interim male's territory, the male blocks her progress by placing his body in her path, without apparent physical contact. Once the female assumes a stationary position, male moves downstream to her location.

TABLE 3. continued		
Behavior	*Notropis alborus*	*Notropis procne*
Alignment	Male aligns himself parallel t o and slightly above female.	Still oriented upstream, male aligns with female.
Run	No run performed by female.	Same as in *N. alborus*.
Clasp	Once aligned, male flexes his caudal peduncle and tail across those of female. Both vibrate vigorously for a second.	Once male aligns with female, he places his pectoral fin underneath female's head and breast and throws his caudal peduncle across posterior portion of her body. Both vibrate vigorously for a second.
Dissociation	After an initial spawn, female moves upstream 15-20 cm where spawning sequence repeats. After the second spawn, female moves downstream and resumes foraging. Male either resumes interim behavior or moves downstream in pursuit of female.	After spawning, female moves downstream and resumes foraging. Male returns to his territory.

Establishment of territories by male *N. alborus* was comparable to that described for *N. procne* by Raney (1947). In both species several males intermittently jockeyed for position over a particular portion of substrate where attrition of males proceeded until single males remained and guarded individual territories. Within a territory, the "lazy figure-8" swimming behavior described by Raney (1947) for male *N. procne* was like that observed in male *N. alborus* (Table 3; Fig. 1).

Categories of aggressive behaviors described by Maurakis et al. (1997) provided a useful framework to organize and describe aggressive behaviors exhibited by breeding male *N. alborus*. Two (i.e., chase and non-contact head displacement) of the five aggressive behaviors (i.e., chase, parallel swim, non-contact head displacement, non-contact body displacement, and lateral head and body butts) between breeding male *N. alborus* were reported for male *N. procne* by Raney (1947). The most noticeable difference in aggressive behaviors between the two species is that of physical contact (i.e., lateral head and body butt) and the occurrence of parallel swims between male *N. alborus*, behaviors not reported between male *N. procne* by Raney (1947). Circle swim (where two males align head to tail and whorl several seconds in a tight circle) described for species of *Nocomis* by Maurakis et al.(1997) was not observed in *N. alborus*. However, during chases, two male *N. alborus* frequently swam in large circles, comparable to the description by Raney (1947) where two male *N. procne* chased each other in a circular path for several seconds.

Spawning activities of male and female *N. alborus* were like those described for *N. procne* by Raney (1947) with two exceptions. During the clasp, a male *N. procne* places his pectoral fin underneath a female's head and breast, a maneuver not observed

in *N. alborus*. Secondly, location of spawning (relative to a male's territory) varied between the two species. In *N. procne*, spawning occurred slightly downstream from the center of a male's territory; in *N. alborus*, it occurred slightly upstream or lateral to the center of a territory.

Spawning behavioral categories (i.e., *Interim*, male only; *Approach*, female only; *Alignment*; *Run*; *Clasp*; and *Dissociation*) of Sabaj (1992) served as a template for identifying and describing spawning activities and interactions of male and female *N. alborus*. However, in two instances, spawning behaviors in *N. alborus* differed trenchantly from those in species (e.g. *Exoglossum maxillingua*, *Nocomis leptocephalus*, and *Semotilus atromaculatus*) for which Sabaj (1992) created the categories. Female *N. alborus* do not perform a *run* as described for *E. maxillingua*, *S. atromaculatus*, and *N. leptocephalus* by Sabaj (1992), and for *Luxilus albeolus* and *Luxilus cerasinus* reported by Maurakis and Woolcott (1995). Secondly, an interim male *N. alborus*, after being approached by a female (Fig. 6), approaches the female postured over suitable substrate slightly upstream or lateral to the territory defended by the male (Fig. 7). Thus, the sequence of female and male behaviors that led to a successful spawn in *N. alborus* are defined: *Interim* (male only); *Approach* (by female), *Approach* (by interim male); *Alignment*; *Clasp*, and *Dissociation*. This set of categories of sequential spawning behaviors in female and male *N. alborus*, also fitting the descriptions for spawning in *N. procne* by Raney (1947), could be a more appropriate framework than that of Sabaj (1992) for describing spawning behaviors of other species (e.g. *N. heterolepis* and *N. rupestris*) in the larger *N. procne* species-group.

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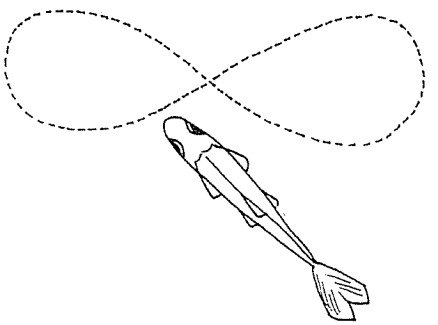

FIGURE 1. Male *Notropis alborus* in interim.

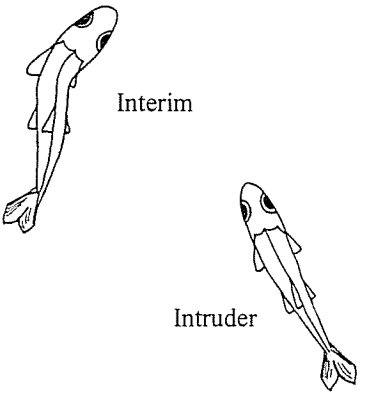

FIGURE 2. Non-contact head displacement by male *Notropis alborus*.

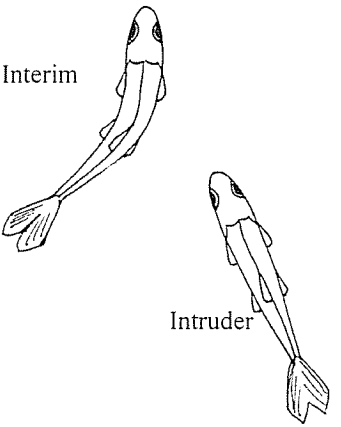

FIGURE 3. Non-contact body displacement by male *Notropis alborus*.

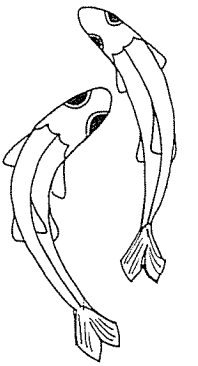

FIGURE 4. Lateral body butt by male *Notropis alborus*.

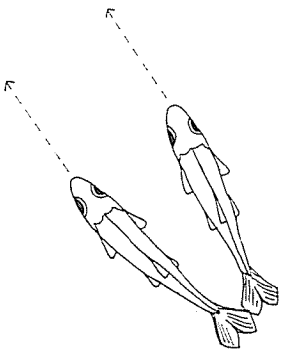

FIGURE 5. Parallel swim between two male *Notropis alborus*.

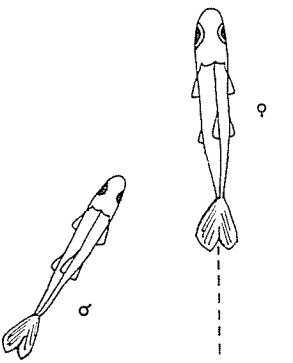

FIGURE 6. Female *Notropis alborus* approach of a conspecific male in interim territory.

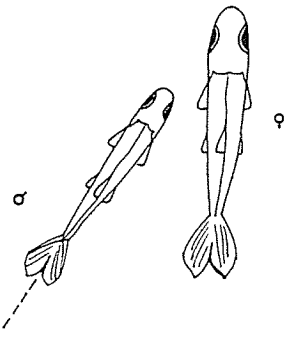

FIGURE 7. Male *Notropis alborus* approach of a conspecific female postured for spawning.

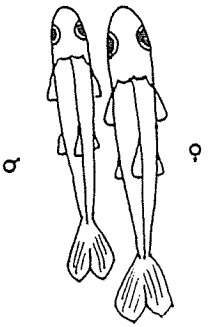

FIGURE 8. Alignment of male and female *Notropis alborus* prior to clasp.

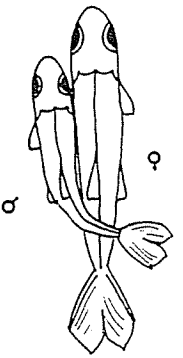

FIGURE 9. Male *Notropis alborus* clasp of a conspecific female

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