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Description of Agonistic Behaviors in Two Species of *Nocomis* (Pisces: Cyprinidae)

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ABSTRACT

Direct observation and review of videotapes of breeding activities in *Nocomis leptocephalus* and *Nocomis micropogon* (Cyprinidae) were used to describe agonistic behavior that occurs between males in each species, and the sequential establishment of spawning territories by male *N. leptocephalus* aside a nest-building male on the upstream slope of a nest. Six agonistic behaviors (non-contact head displacement, non-contact body displacement, chasing, head/body butt displacement, circle swim, and lateral swim/head bobbing) observed between sexually ripe male *Nocomis leptocephalus* were like those occurring between sexually ripe male *Nocomis micropogon*. In *N. leptocephalus*, the nest-building activity (i.e., filling the central trough on the upstream slope of a nest with pebbles followed by the excavation of a spawning pit) after the three-stage process of nest-construction, and small territory size defended around the pit lead to the sequential establishment of spawning territories by squatter males of the species. Whereas reduced aggression prevails among spawning male *N. leptocephalus* over a nest, a nest-building male *N. micropogon* reacts more aggressively towards the satellite male than he does to intruders, indicating that by definition, nest-building male *N. micropogon* treat their respective satellite males as intruders.

Keywords: Aggressive behavior, *Nocomis leptocephalus*, *Nocomis micropogon*, Cyprinidae

INTRODUCTION

Sexually dichromatic and dimorphic tuberculate males of *Nocomis* species construct pebble nests in a three stage process (i.e., excavating a concavity, forming a platform, and building a mound with a single, central trough parallel to the water current) for spawning during spring (Maurakis et al., 1991). A nest-building male *Nocomis micropogon* spawns in the single trough on the upstream slope of his nest (Sabaj, 1992). A nest-building male *Nocomis leptocephalus* fills the central trough with pebbles, then excavates a pit on the upstream slope of the nest where he spawns (Maurakis et al. 1991; Sabaj, 1992). Later other male *N. leptocephalus* excavate spawning pits on the same nest. Whereas nest-building and spawning activities have been described for some species of *Nocomis* (Reighart, 1943; Vives, 1990; Maurakis et al., 1991; Sabaj, 1992), there are few published accounts of agonistic behaviors that occur between sexually ripe males in each species. For example, the circle swim in *Nocomis* species where a male aligns head to tail with another male, resulting in a whorling motion of the two was not described until 1991 by Maurakis et al.

This paper addresses the agonistic behaviors in *N. leptocephalus* and *N. micropogon*, and the events that lead to the establishment of spawning pit territories by male *N. leptocephalus* aside that of the nest-builder on the upstream slope of a nest. Included are analyses of differences in numbers of encounters for each type of agonistic behavior between pairs of spawning males, and pairs of spawning and intruder males in each species.

MATERIALS AND METHODS

Direct observations and videorecordings of *N. leptocephalus* and *N. micropogon* were made at the following sites (state, drainage, collection number, locality, and date):

Nocomis leptocephalus. North Carolina: Little Tennessee, EGM-NC-211, Macon Co., unnamed tributary of Cullasaja River at Jct. of Horse Cove Rd. and Leonard St. in Highlands, 7 June 1988. Virginia: Dan, EGM-VA-202 and EGM-VA-321, Pittsylvania Co., Pumpkin Cr., at St. Rt. 86 bridge at Danville City line, 11 May 1986 and 8 May 1993. James, EGM-VA-225 and EGM-VA-226, Craig Co., Sinking Creek, St. Rt. 42, about 1.6 km S of Co. Rt. 626, 26 and 29 May 1989, respectively. EGM-VA-247, Goochland Co., Genito Creek, Co. Rt. 641, 8 May 1990.

Nocomis micropogon. North Carolina: Littel Tennessee, EGM-NC-216, Jackson Co., Jackson Creek, Co. Rt. 1737, 1.4 km NE of St. Rt. 107 at East LaPorte, 10 June 1988. Virginia: Potomac, EGM-VA-254, EGM-VA-272, EGM-VA-273, EGM-VA-301, and EGM-VA-302, Loudoun Co., Catoctin Creek, Co. Rt. Jct. 663 and 665 at Taylorsville, 25 May 1990, 5 May 1991, 8 May 1991, 22 May 1992, and 23 May 1992, respectively.

Descriptions of agonistic behaviors of male *N. leptocephalus* over five nests (60 min/each) and those of male *N. micropogon* over five nests (two nests at 60 min/each, and 3 nests at 30 min/each) follow methods in Maurakis and Woolcott (1995). Individual males were identified by their physical appearance. Types of agonistic behaviors, and numbers of encounters per type of agonistic behavior observed between pairs of males in each species were recorded. In *N. leptocephalus*, males spawning over a nest, in addition to the spawning nest-builder, are designated squatters. In *N. micropogon*, a satellite male is one that deceptively mimics females and pairs simultaneously with true females and parental males (Gross, 1984) accompanies the nest-builder. Males other than these in each species are considered intruders.

Dimensions of spawning pits (*N. leptocephalus*) and troughts (*N. micropogon*) measured according to methods in Maurakis et al. (1992) are used to calculate total territory area defended by a spawning male following Getty's (1981) definition of territory size (2r). Territory area is expressed as percent of total area of available substrate on the upstream slope of a nest.

Number of encounters between pairs of spawning males, and between spawning males and intruders, were totalled in each type of agonistic behavior for each species over each nest, and expressed as number/type/60 min. Total number of encounters per type of agonistic behavior between spawning males was compared to that between spawning and intruder males in each species with a t-test (Steel and Torrie, 1980; SAS, 1985; $p > 0.05$).

TABLE 1. Agonistic behaviors between males in *Nocomis leptocephalus* and *Nocomis micropogon*.

Behavior	Male Activity	
	Spawner	Intruder
Non-contact head displacement	Rotates head toward intruder	Yields position
Non-contact body displacement	Sinusoidal body swing toward intruder	Yields position
Head/body butt displacement	Butts head or body of intruder	Yields position or butts head or body of neighbor
Chase *	Pursuit of intruder beyond nest perimeter	Yields position, flees
Circle swim	Aligns head to tail with intruder, whorls in a circle	Aligns head to tail with neighbor, whorls in a circle
Lateral swim/head bobbing	Aligns parallel with intruder, bobs head dorsoventrally against that of intruder	Aligns parallel with neighbor, bobs head dorsoventrally against that of neighbor

* *N. leptocephalus* ($\bar{x}$ =5.4 sec; range=3-7 sec; n. 7)
N. micropogon ($\bar{x}$ =20.3 sec; range=6-46 sec; n. 9)

RESULTS

Agonistic Behavior.--Six agonistic behaviors (non-contact head displacement, non-contact body displacement, chasing, head/body butt displacement, circle swim, and lateral swim/head bobbing) were identified between pairs of males in each species (Table 1). Chases (averaging 5 sec/chase) by spawning male *N. leptocephalus* rarely extended beyond the perimeter of the nest. In contrast, the nest-builder or satellite male *N. micropogon* chased intruder males several meters (e.g. 15 m; $\bar{x}$ time/chase, 20 sec) from the nest (Table 1).

Average number of spawning male *N. leptocephalus* over nests was 3.4 (2-6); intruder males averaged averaged 4.2 per nest (range, 3-5). Squatters and nest-building males never were usurped by intruder males from their spawning pits. Average area (303 cm^2; range, 154-530 cm^2) defended by a spawning male was 16.7 % of the total average area (1786 cm^2; range, 1608-1963 cm^2) of spawning substrate (Table 2). Average distance between pit perimeters was 7.7 cm (range, 4-11.6 cm)(Table 3).

In *N. micropogon*, an average of 4.2 intruder males (range, 2-7) challenged the nest-builder, and the satellite male (positioned about 1 m downstream of the nest) present at each of five nests. Nest-builder male *N. micropogon* were not usurped from nests by either intruder or satellite males. Only one satellite male *N. micropogon*

TABLE 2. Average area (cm^2) defended by spawning male *Nocomis leptocephalus* and *Nocomis micropogon*.

Species	Nest no.	Defended Area	Total Area upstream slope	% Area Defended
N. leptocephalus	1	300	1608	18.7
	1	201	1608	12.5
	1	243	1608	15.1
	2	530	1963	27.5
	2	380	1963	19.4
	2	314	1963	16.0
	2	154	1963	7.9
		$\bar{x}$ =303	$\bar{x}$ =1786	$\bar{x}$ =16.7
N. micropogon	1	3216	4125	78.0
	2	2124	3094	68.7
	3	3421	4526	75.6
		$\bar{x}$ =2920	$\bar{x}$ =3915	$\bar{x}$ =74.1

TABLE 3. Distance (cm) between pit (P) perimeters in nests of *Nocomis leptocephalus*.

Nest 1	P1	P2	P3	Nest 2	P1	P2	P3	P4
P1	0	10	6		0	9	5.5	6
P2		0	8			0	10.6	11.6
P3			0				0	5
P4								0

was usurped by a larger intruder male. Average area (2920 cm^2; range, 2124-3421 cm^2) defended by a nest-builder male *N. micropogon* was 74.1 % of the total average area (3915 cm^2; range, 3094-4526 cm^2) of spawning substrate of a nest (Table 2).

In *N. leptocephalus*, mean number of encounters between spawning males was significantly lower than that between spawning and intruder males for each type of aggressive behavior (Tables 4 and 6). Average number of encounters between spawning male *N. micropogon* was significantly higher than that between spawners and intruders for all aggressive behaviors except lateral swim/head bobbing (Tables 5 and 6).

Sequential establishment of spawning pit territories in *N. leptocephalus*.--An intruder male establishes a spawning pit territory on the upstream slope of a nest via persistent probes and extended combat with a spawning male *N. leptocephalus*. After about 30 minutes, an established (spawning) male yields an area aside or near his spawning pit to the intruder. Aggression towards the new squatter decreases, resulting in a stable relationship that allows a spawner to resume breeding activities, and the squatter to excavate and defend his spawning pit. We observed this sequence

TABLE 4. Numbers of encounters per agonistic behavior in *Nocomis leptocephalus* (S=spawning male: I=intruder male).

Interaction	Nest 1 S-S	1 S-I	2 S-S	2 S-I	3 S-S	3 S-I	4 S-S	4 S-I	5 S-S	5 S-I
Behavior										
Non-contact head displacement	6	37	8	46	16	39	6	26	7	3
Non-contact body displacement	10	60	13	118	19	79	14	35	12	28
Head/body butt displacement	9	19	11	29	16	31	8	20	4	21
Chase	4	11	8	26	4	22	1	31	3	10
Circle swim	2	10	2	7	5	51	0	22	0	16
Lateral swim/ head bobbing	0	3	0	2	1	3	0	8	0	3

of activities (i.e., *probing*, *combating*, *yielding*, *squatting*) leads to the sequential establishment of squatters on the nest, and stable interrelationships among spawning males and as many as five squatters.

In contrast, a nest-builder male *N. micropogon* neither surrenders his spawning trough nor yields any area on a nest to an intruder or satellite male. A satellite male *N. micropogon*, which maintains a position about one meter downstream of a nest, attacks intruder males as they approach a nest.

DISCUSSION

The six types of aggressive behaviors identified between male *N. leptocephalus* occur between male *N. micropogon*. Nest-building behavior that follows after the platform stage, however, is different in the two species, allowing for sequential establishment of multiple males over nests of *N. leptocephalus*, but not over those of *N. micropogon*. Nest-building behavior in male *N. leptocephalus* does not end with construction of a trough, but continues as he fills the trough with pebbles. Next he excavates a spawning pit near the center of the upstream slope of the nest. Compared to the total available substrate on the upstream slope of the nest, average size of the territory around the spawning pit that is defended by the nest-building male *N. leptocephalus* is smaller ($\bar{x}$=21.6 %) than that (74.1 %) in nests of *N. micropogon*. This is conducive to excavation of additional spawning pits by squatting male *N. leptocephalus*. In contrast to the nest-building behavior in *N. leptocephalus*, intruder

TABLE 5. Numbers of encounters per agonistic behavior in *Nocomis micropogon* (S=spawning male; I=intruder male).

	Nest									
	1		2		3		4		5	
Interaction Behavior	S-S	S-I	S-S	S-I	S-S		S-I	S-S	S-I	S-S
Non-contact head displacement	21	1	32	8	24	0	38	12	18	10
Non-contact body displacement	60	11	8	4	60	4	76	14	44	8
Head/body butt displacement	27	30	24	28	22	0	66	6	16	2
Chase	10	10	16	14	13	4	30	16	10	6
Circle swim	2	0	2	0	1	0	6	0	2	0
Lateral swim/ head bobbing	2	0	0	0	0	0	0	0	2	0

TABLE 6. Results of t-tests for average number of encounters per type of agonistic behavior betwen pairs of males of *Nocomis leptocephalus* and *Nocomis micropogon* (S=spawning male; I=intruder male).

	N. leptocephalus $\bar{x}$ no. encounters			*N. micropogon* $\bar{x}$ no. encounters		
Behavior	S vs I	S vs S	$P > \|T\|$ Ho $\bar{x}S$ vs I = $\bar{x}S$ vs S	S vs I	S vs S	$P > \|T\|$ Ho $\bar{x}$ S vs I = $\bar{x}S$ vs S
Non-contact head displacement	12.07	4.04	0.0063	3.1	26.6	0.0020
Non-contact body displacement	19.63	6.86	0.0802	4.1	49.6	0.0140
Head/body butt displacement	7.67	4.24	0.0172	6.6	31.0	0.0686
Chase	6.27	2.06	0.0486	5.0	15.8	0.0221
Circle swim	5.90	0.60	0.0206	0	2.6	0.0406
Lateral swim/ head bobbing	1.27	0.04	0.0404	0	0.8	0.1778

male *N. micropogon* cannot establish a spawning territory aside that of the nest-building male as size of the territory around the single trough defended by a nest-builder *N. micropogon* occupies almost three fourths of the available substrate suitable for spawning. Consequently, space is not available for additional breeding troughs, which are requisite for spawning behavior in the species (Maurakis, et al., 1991).

Reduced aggression exhibited by squatter male *N. leptocephalus* over a spawning nest compares favorably with the description for birds by Fisher (1954), who described the dear enemy phenomen as reduced aggression at mutually exclusive territorial borders. In contrast, a nest-building male *N. micropogon* reacts more aggressively towards the satellite male than he does to intruders, indicating that by definition, nest-building male *N. micropogon* treat their respective satellite males as intruders.

We propose that the occurrence of reduced aggression among spawning male *N. leptocephalus* is an adaptation to maximize spawning in small streams where pebble substrates may be limited. Our evidence conforms to the statements of Lachner (1952) and Lee et al. (1980 et seq.) that the smaller species, *N. leptocephalus* (males average 138 mm SL; Lachner and Jenkins, 1971), typically occurs in smaller streams. Limited availability of suitable habitats in small streams probably forces male *N. leptocephalus* to share the few areas that are available for nest construction, and subsequently for spawning. Larger *N. micropogon* (average male size, 165 mm SL; Lachner and Jenkins, 1971) occur in large to medium sized streams where suitable pebble substrates are common (Lachner, 1952; Lee et al., 1980 et seq.; pers. obs.), and hence no pressure to share space.

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LITERATURE CITED

Fisher, J. 1954. Evolution and Bird Sociality. *In* J. Huxley, A. C.Getty, T. 1981. Competitive collusion: The preemption of competition during the sequential establishment of territories. Am. Nat. 118:426-431.

Gross, M. R. 1984. Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. Zeitschrift fuer Tierpsychologie 60:1-26.

Lachner, E. A. 1952. Studies of the biology of the cyprinid fishes of the chub genus *Nocomis* of northeastern United States. Am. Midl. Nat. 48(2):433-456.

____ and R. E. Jenkins. 1971. Systematics, distribution, and evolution of the chub genus *Nocomis* Girard (Pisces, Cyprinidae) of eastern United States, with descriptions of new species. Smithson. Contrib. Zool. 85: 97 p.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister and J. R. Stauffer, Jr. 1980 et seq. Atlas of North American Freshwater Fishes. N.C. St. Mus. Nat. Hist., Raleigh, N.C.

Maurakis, E. G. and W. S. Woolcott. 1995. Methods of videotaping fishes from above the surface of the water. Southeast. Fish.Counc. Proceedings 31:4-6.

_____, _____, and M. H. Sabaj. 1992. Water currents in spawning areas of pebble nests of *Nocomis leptocephalus* (Pisces: Cyprinidae). Southeast. Fish. Counc. Proceedings 25:1-3.

_____, _____, and _____. 1991. Reproductive-behavioral phylogenetics of *Nocomis* species-groups. Am. Midl. Nat. 126:103-110.

Reighard, J. 1943. The breeding habits of the river chub, *Nocomis micropogon* (Cope). Pap. Mich. Acad. Sci Arts Lett., 24:397-423.

Sabaj, M. H. 1992. Spawning clasps and gamete deposition in pebble nest-building minnows (Pisces: Cyprinidae). M.S. thesis, Univ. Richmond. 85 p.

SAS Institute, Inc. 1985. SAS User's Guide: Statistics, version 5. SAS Inst., Inc., Cary, N.C.

Steel, R. G. D. and J. H. Torrie. 1980. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc. New York, N.Y.

Vives, S. P. 1990. Nesting ecology and behavior of hornyhead chub *Nocomis biguttatus*, a keystone species in Allequash Creek, Wisconsin. Am. Midl. Nat. 124:46-56.