

The reproductive biology of an armoured catfish, *Loricaria uracantha*, from Central America

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Synopsis

The reproductive biology of one of the poorly known armoured catfishes, *Loricaria uracantha*, was studied in Panama. Natural nesting sites consisted of cavities in pieces of wood, open at both ends and positioned above the stream bottom, but artificial cavities of PVC pipe were readily used. Males possess bony bristles on the head and pectoral fins which contact the female prior to oviposition. Males spawned with up to five females in short succession and remained with the eggs until hatching. Following hatching many initiated another spawning cycle. One male was reproductively active for 73 days during which it completed five distinct reproductive cycles. Spawning extended throughout the year.

Introduction

The Loricariidae (armoured catfishes) is the largest (over 400 species) family of Neotropical catfishes. They have a body covering of bony scutes and a ventral suckorial mouth. Benthic species, they often live in streams and use the mouth to cling to objects as well as to feed on algae and detritus. Additional information on the ecology of the family is available in the studies of Pineda (1976) and Power (in preparation). Little is known of the reproductive biology of the Loricariidae. The few reports which exist consist of brief accounts of spawning in aquaria. This report describes the reproductive biology of *Loricaria uracantha* Kner and Steindachner observed in the field in semi-natural circumstances.

Methods

Observations were obtained over a 20-month period in a section of the Rio Frijoles near the Pipeline Road, 9° 9' N, 79° 44' W, 29 km NW of Panama City, in the former Canal Zone. The stream flowed over sand and gravel in the study area and ranged from about 4 to 7 m wide and up to 1 m in depth. The banks adjacent to spawning sites were usually somewhat undercut and lined with terrestrial roots, branches and overhanging vegetation. The water was clear except following heavy rainstorms. The study began with the discovery of a fish guarding eggs in a hollow branch. Despite repeated searching we only encountered five other fish nesting in natural sites. Four of these were utilizing similar hollow branches and the fifth was

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guarding eggs placed in a split in a large log. Other individuals were instead studied as they mated and guarded eggs within sections of PVC pipe suspended in the stream to simulate spawning cavities. Internal diameter of the pipes was about 5 cm and lengths varied from 15 cm to 40 cm. A stone was often jammed in the upstream end of the pipe to reduce the size of the opening while still allowing the passage of a catfish. The pipes were suspended horizontally in the water by means of wires attached to each end and tied to overhanging vegetation. Where the current was strong, a single wire at the upstream end sufficed to hold the pipe in a horizontal position. Most pipes contained a removable section which could be lifted away to allow observation of behavior inside the pipe. A maximum of 12 pipes were available at any one time. The maximum number of pipes used simultaneously was five. Most pipes were distributed over an 18 m distance in a single pool. Nocturnal observations were conducted by means of an infra-red viewer or shielded head lamp. Both night and day observations were accompanied by acoustical monitoring via a hydrophone and amplifier. All references to sound production signify the use of this apparatus. Fish were individually marked by filing a notch into particular body scutes, or by tagging with small colored beads. The census data are the sum of two day and two night time counts of fish in about 150 m² quadrats located over a 3 km section of the stream which included the zone containing the artificial spawning sites. Counts were made by an observer snorkelling upstream. The counts do not indicate absolute density but we believe they are a reliable guide to relative density over time and to the proportion of reproductively active but non-nesting fish. Population (absolute density) estimates were obtained by relating quadrat counts to quadrat depth, bottom area at various depth contours and forest canopy cover. A detailed description of this method will be provided elsewhere by M.P.

Results and discussion

Breeding habitat. The natural spawning sites had two attributes which appeared from subsequent observations to be important: the branches were lodged in

such a way that the cavity was well above (30 cm) the stream bottom; in addition the cavities possessed both a downstream and upstream opening. Eggs were located in the split log in such a way that it also effectively had up- and downstream openings. PVC pipes which touched the substrate or had only one opening were never accepted. Spawning sites on the bottom may be too vulnerable to the massive shifts in the substrate, which occur during the wet season, as well as to discovery by potential egg predators. An upstream opening to the cavity may be necessary for adequate oxygenation of the eggs. The location of pipes seemed to be an important factor governing their acceptability. The most used were those from 15–100 cm of the erosion side of the stream and closer to the surface than the bottom. Generally there was at least 10 cm water under the tube, usually about 30 cm. Water velocity at two tubes containing males and eggs ranged from 0 to 22.3 cm sec⁻¹ (measured with a pygmy current meter). The possibility the species spawns in other than hollow pieces of wood must be considered because such sites are apparently scarce. We found only four or five suitable hollow objects in this and several other streams, and we know of only the six cases noted above of the species spawning in natural sites. The question of the full spectrum of natural spawning sites awaits further field data, however, evidence presented below points to a real scarcity of spawning sites, whether of the type described or others.

Sexual dimorphism. Like other loricariids, *L. uracantha* shows considerable sexual dimorphism. At least some of this dimorphism is relevant to the reproductive behavior described below. Like other members of the genus (Breder & Rosen 1966), males bear bony facial bristles around the margin of the head and along the dorsal surface of the pectoral fin rays (Fig. 1). These bristles are not permanent structures and can be developed within a 64 day period and lost within 148 days (data from recapture of two marked fish). Possibly related to the role of these bristles is a dimorphism in the mobility of the pectoral fins: the pectoral fins of the male can be extended antero-dorsally much further forward than those of females (Fig. 1). This extension brings the bristle patches of the fin and cheek



Fig 1. Sexual dimorphism in *L. uracantha*, female below, male above. Note bristles on the sides of the male's head and along his pectoral fin rays. The white line indicates the approximate limit to which the female can extend her pectoral fin.

into opposition and conceivably provides males with a grasping organ. Placing a finger or the caudal peduncle of another fish in this area sometimes causes a male to grasp the object rather tightly. Dimorphism in body size has not been previously described in this genus, but, as in many species where male parental care occurs, guarding *L. uracantha* males are significantly larger than females found in tubes (♂ \bar{x} fork length = 105.8 mm, range 89–112 mm, $n = 13$, ♀ \bar{x} fork length = 94.8 mm, range 83–108 mm, $n = 39$, $p < 0.001$, t-test). Sample of non-nesting males and females taken from the population at large also differed significantly in length.

Reproductive behavior. Male were first to occupy spawning sites. Females did not usually appear until about 24 hours after arrival of the male. The male's presence during this time was detectable at a distance by rasping sounds which apparently resulted from scraping motions over the surface upon which the eggs were eventually deposited. Possibly the male was cleaning the substrate in preparation for the eggs. On the one occasion when two males and two females were simply sheltering in a tube with just one opening, no such rasping sounds were detectable.

Females entered pipes both during the day and night. The arrival and entrance of a female was observed only once. This occurred at 2120 h. and was observed by means of the infra-red viewer and at times a shielded headlamp. The female spent about 40 minutes moving over the surface of the pipe and once returned to the stream bottom. Five minutes before the female was sighted and during the time she was on the outside of the pipe, rasping sounds increased in volume and continuity. Whether they were produced by one or both sexes could not be established. Eventually, the female entered the pipe from the upstream opening. The two fish thus lay facing each other in the tube (males always face upstream when inside the pipe). Periodically the male pushed the female backwards making contact with the facial bristles. Other than to resist eviction from the tube, the female was inactive.

Spawning of two pairs was observed. Each sex faced upstream (this indicates females ultimately

must enter from the downstream opening). Often the male was slightly posterior to the female such that her caudal region rested against the cheek bristles. At such times the caudal peduncle or fin was sometimes slapped against the bristles. The pectoral fin of the male frequently was situated in the general vicinity of the female's genital pore. From this position it was sometimes quickly lowered and then raised several times in quick succession, producing a knocking sound and tactile stimulus accentuated perhaps by the pectoral bristles of the male. Rasping sounds possibly generated by the mouth were nearly continuous just prior to spawning and were probably produced by both sexes. Females appeared to mouth the spot where eggs were subsequently deposited. Eggs were released in groups of six or so at 5 to 15 minute intervals during which both sexes rammed and pushed each other in an apparent attempt to situate themselves over the eggs. Brief squeaks and 'smooching' sounds were produced around the period of egg release. The males tended to be fairly immobile prior to and after egg release, sometimes taking up to 5 minutes before moving over and presumably fertilizing the eggs. The two spawnings observed were between 1000 and 1330 hours. Eggs were about 3 mm in diameter and pale yellow on oviposition, becoming darker and more orange with time. Eggs were deposited in a single layer on the bottom upstream half of the pipe. Eggs from subsequent females were added upstream of and around the periphery of previously deposited clutches. Up to three clutches could often be recognized by color and developmental differences. An average clutch size of 83 eggs ($n = 22$) was estimated by counting groups of eggs known or inferred to have come from a single female as a result of the known history of females in a pipe or from egg characteristics. Dissection of three gravid females taken from pipes prior to spawning revealed egg counts ranging from 49 to 69. Judging from marked females and the time they remained in tubes as well as counts of many recently deposited eggs, a female deposited all her eggs in a single prolonged spawning with one male. Females left the pipe within 24 hours of spawning. Males remained with the eggs; irregular dorso-ventral flicking of the paired fins as well as general body movements may

be important in keeping the eggs free of incoming sediments. In two cases where males disappeared the clutches quickly became silt covered and eventually died. At hatching embryos were about 12 mm long (TL) and left the pipe within 24 hours.

Remaining at the spawning site, as Blumer (1979) noted, also permits a male to fertilize additional clutches provided by other females. Eggs of as many as five females were fertilized in a single spawning cycle ($\bar{x} = 2.5$, $n = 13$). The number of females spawning with a male appeared to depend on male body length with large males obtaining more females (a test of the hypothesis that the regression coefficient equalled zero was rejected, $t = 2.225$, $p < 0.05$, $df = 11$).

Acceptance of successive females occurred only during a brief period relative to total incubation time of about 13.5 days at 25° C ($n = 13$). Males nevertheless remained in the pipes until hatching, after which a new cycle of spawning was often initiated. One male thus remained in a pipe for 73 days, during this time it completed five cycles, each cycle consisting of the fertilization of eggs from one to three females. Another male occupied a tube for 52 days and completed three cycles. Four other males completed two cycles apiece. Sometimes subsequent cycles occurred in the males' original pipe; on other occasions the male shifted to a different location.

Of the remaining two-thirds of observed males,

some were never marked and thus could not be recognized subsequently, others spawned in pipes which were dislocated by floods, and all could have spawned previously in natural cavities prior to utilizing our sites. The proportion of males undertaking repeated spawning cycles may thus be higher than that observed.

Breeding season. There appears to be continuous breeding in this species. Spawning pipes were available in varying numbers in all months. Males utilized the pipes every month except April, but recently hatched young were in the river in April. A modest spawning peak may occur in October, near the height of the rainy season. The maximum number of males in a month was five in October (but the average was only 2.5 per month). Gravid females and whiskered males were most abundant in the October quadrat census (Table 1). Spawning throughout the year may result from a shortage of sites and such a shortage is implied by several facts. As noted, only six natural sites containing males and just four or five seemingly suitable sites were located. While it seems probable that other sites of an unknown type are used, the rejection of pipes when one entrance was blocked or the substrate was contacted or a previously accepted tube was moved to a new location suggests the species may have spawning site requirements that restrict the number of suitable sites. The slow 'turnover time' of sites

Table 1. Relative abundance of reproductive and non-reproductive adults (SL > 80 mm) and nesting males. Non-reproductive adults were those which were neither gravid nor whiskered. Numbers in quadrats are the sums of four counts of about 150 one square m quadrats. The population estimate refers to the total number of adults in the pool containing the artificial spawning pipes.

Month	Number of adults in quadrats			Density estimate	Number of ♀♀ in pipes at the same time	
	gravid ♀♀	whiskered ♀♀	nongravid or whiskerless		minimum	maximum
Jan	0	2	173	74	2	3
Feb					2	2
Mar	0	1	132	56	0	2
Apr				55	0	0
May					1	3
June	0	2	86		3	4
July					2	3
Aug	4	10	34	25	1	
Sept					1	1
Oct	10	13	74	32	2	5
Nov						
Dec					2	2

caused by their protracted use by individual males also renders sites effectively scarce. The reappearance of marked fish (four males, three females) in pipes other than the one in which they were first sighted further suggests natural sites are in short supply; were the converse the case, the chance of a fish moving from one artificial site to another artificial one would be low. The estimates of catfish density for the study area and the proportion of fish in reproductive condition (Table 1) further suggests potential occupants were abundant relative to the number of natural and artificial spawning sites.

Comparison with other species in the genus. Parental care appears to be standard in *Loricaria*. In seven of eight species for which information is available, the male guards the eggs. Hordes (1945) reported the female guards in the case of *L. macrops*. The site of egg deposition varies. *L. curvispina* places its eggs over flat rocks in rapids (Dahl 1971). In three species, *L. typus*, *L. vetula* and *L. anus*, the eggs are carried on the enlarged lower lip of the male (Lagler et al. 1962, Breder & Rosen 1966). *L. piracicalae* has its egg adherent to its ventral surface (Breder & Rosen 1966). Aquarium observations indicate similar behavior; *L. filamentosa* will utilize ceramic tubes and narrow crevices (Sterba 1973, p. 454). *L. parva* and *L. macrops* have oviposited over the surface of petrified wood and the aquarium wall respectively (Friswold 1937, Hordes 1945).

It is tempting to speculate that the egg carrying habit evolved as a means of circumventing intra-specific competition for nesting cavities in species such as *L. uracantha*.

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