A QUALITATIVE ANALYSIS OF COURTSHIP AND REPRODUCTIVE BEHAVIOR IN THE ANABANTOID FISH *TRICHOGASTER PECTORALIS* (REGAN) (PISCES, ANABANTOIDEI)

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Courtship and reproductive behavior is described in the anabantoid fish *Trichogaster pectoralis* (Regan). Such behavior was stereotyped and occurred in distinct temporal patterns. Acquisition of nuptial coloration was associated with establishment of a territory, increased aggressiveness, and nest-building activity. A typical spawning sequence began with the approach of the female accompanied by a series of butts delivered at the male. "Rubbing position", a unique motor pattern found in *T. pectoralis*, follows female approach which was then followed in quick succession by circling, clasping, swimming inhibition, and postspawning aggression. Degree of success of individual spawning bouts was associated with duration of the bouts. Spawning sequences in *T. pectoralis*, had the shortest duration of any *Trichogaster* species; however, actual spawning bouts were quite long with short intervals between bouts. Within the genus *T. pectoralis* seems to be the least specialized form.

Perciform fishes of the suborder Anabantoidei are noted for their elaborate, stereotyped courtship and reproductive behavior patterns and for the relative ease with which they can be kept in aquaria. Partly because of these and other factors, the social behavior of anabantoids has recently become the subject of intensive investigation.

Miller and Hall (1) provided the first primarily quantitative description and analysis of anabantoid reproductive behavior. Qualitative studies are more numerous and have been concerned with the behavior of various anabantoid species (2-9).

Forselius (10), in a monograph on anabantoid fishes, dealt with their behavior, systematics, distribution, endocrinology, and ecology. Sexual and nest discrimination in *Colisa, Trichogaster,* and several other anabantoids were described by Picciolo (11). Liem (12) dealt with the osteology, phylogenetic relationships, and systematics of anabantoid fishes as well as some ecological factors influencing the evolution of the group.

Regan (13) was the first to publish a synopsis of the anabantoids and in the process named several new species, among them *Trichopodus* (*Trichogaster*) *pectoralis*. The largest (over 200 mm SL) and most economically important member of the genus, *Trichogaster pectoralis* generally inhabits ponds, lakes, and sluggish waters of central Thailand and extends into Cambodia and other provinces of Indo-China (14). *T. pectoralis* was introduced into Malaya from Thailand 20 to 35 years ago (G. Meyers, pers. comm.) and has been successfully introduced into Ceylon, India, and many parts of Indonesia (10).

Virtually nothing has been published on reproductive or agonistic behavior of this species. Except for a brief field study by Soong (15) and short descriptive articles by Beldt (16), Smith (14), and Campbell (17), the literature concerning *T. pectoralis* is meager. Unfortunately these reports contain numerous inaccuracies rendering them almost worthless. A recent study by Robison and Miller (18) described diel activity patterns of male *T. pectoralis*.

METHODS AND MATERIALS

This study was conducted in the Animal Behavior Laboratory of Oklahoma State University Life Sciences West Building for approximately two and one half years.

T. pectoralis was imported directly from Thailand as wild fish. At least nine heterosexual pairs were maintained at all times, but various pairing combinations were used during the study. Size ranged from 50-95

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mm (SL). Water temperature was maintained at 24 to 29 C for the duration of the study. Fluorescent lights provided illumination for the laboratory while each tank had an individual light source. A photoperiod of 12 hours (6 AM to 6 PM) was maintained throughout the study.

Aquaria ranged from 57 to 132 liters. Each tank was planted with *Vallisneria* sp., *Ceratophyllum* sp., or plastic plants with pieces of clay pots placed on the gravel bottom for shelter. A thermostatically controlled electric aquarium heater and one standard aquarium thermometer was kept in each tank. Commercial flake food was fed twice daily while frozen *Artemia*, live *Daphnia* sp., and *Chironomus* sp. larvae were fed less regularly.

In an effort to spawn *T. pectoralis*, the pH of the water in several tanks was lowered from between 7.6 and 8.2 to as low as 5.7 by addition of peat moss or potassium biphosphate crystals.

Qualitative observations were facilitated by use of prepared data sheets, notebooks, stopwatches, and a tape recorder. Observations were obtained primarily by daily or twice daily 15-minute observations. Data was recorded on water temperature, coloration of male and female, form and structural features of the nest (if present), and general behavior exhibited by the pair.

Quantitative data on courtship and reproductive behavior, bubble blowing, and agonistic behavior were obtained by use of an Esterline-Angus Event Recorder (Model A620X) wired to two 10-key keyboards using a paper speed of 7.62 cm/min., and prepared data and summary sheets. Identifiable units of behavior were determined in a six month test prior to initiation of the present study. Frequency, duration, and temporal patterning of behaviors occurring during encounters between fish were recorded and then transferred to data summary sheets which facilitated analysis.

RESULTS AND DISCUSSION

Terminology

In *Trichogaster pectoralis*, as in other species of *Trichogaster*, courtship and reproductive behavior tends to occur in discrete bouts of varying duration and complexity. The following terms are used to represent behavioral events analyzed in this study:

Bout. Any social interaction between two or more fish. Synonomous with encounter.
Sexual Bout. Male-female interactions containing sexual responses by one or both individuals.
Spawning Bout. A sexual bout in which clasping and oviposition occur. Corresponds to the "spawning cycle" of Forselius (10).
Pseudospawning Bout. A sexual bout which is identical to a spawning bout except release of gametes does not occur by either fish, although swimming inhibition may be exhibited by either male and/or female.
Spawning Sequence. The complete series of male-female interactions comprising prespawning, spawning, and postspawning activities; corresponds to "mating cycles" of Forselius (10). Approximate duration of spawning sequence in *T. pectoralis* is 2 to 5 hours.
Courtship. Those activities that seem to attract and/or stimulate the spawning partner, thus facilitating successful spawning (6). Most courtship activities are initiated by females.
Prespawning Phase. Phase characterized by courtship and/or aggressive bouts that precede the first successful spawning bout.
Spawning Phase. Period from the first to the last successful spawning bout during the spawning sequence and includes all bouts within this duration.
Postspawning Phase. That period of time following the last successful spawning bout. This phase is terminated when the female remains in seclusion for long intervals and the male displays extreme aggressive behavior toward her while guarding the nest.

Motor Patterns

Motor patterns for anabantoid fishes of the genus *Trichogaster* have been described by Forselius (10), Miller (6), Hall and Miller (8), Wimmer (9), and Robison (19). These descriptions will serve as a basis for discussion of the motor patterns of *T. pectoralis*.
Approach. Any behavior in which one fish swims directly toward a second fish. Pelvic threads are usually thrust forward with median fins slightly erected.
Lateral Spread Display. At high intensities median and caudal fins are spread maximally, although only slightly spread at low

intensities. At maximum intensity the lateral display is often expressed in the form of an S-shape (sigmoid) or develops subsequently into tail beating, biting, butting, or chasing (6). The displaying fish is generally directly in front of or parallel to the other fish, but can be oriented at any angle. The head is always directed away from the other fish.

Tail Beating. Tail beating consists of lateral, undulating thrusts of the caudal peduncle and fin and often varies in force and duration. One or both fish may perform these movements during courtship and agonistic encounters. Tail beating seems to represent greater aggressiveness than the lateral display in any given encounter (6).

Opercle Spread. Robison (19) first reported opercle spreading in *T. pectoralis.* Opercles and branchiostegals are spread only minimally. Opercle spreading occurs in an aggressive context while the displaying fish is lateral to and slightly behind the opponent. The head is higher than the caudal fin and directed toward the opponent while the body forms a sigmoid curve and tilts downward slightly.

Biting and Butting. Biting seems to be the most effective aggressive behavior in *T. pectoralis.* When biting, the mouth is open, and is closed upon contact with the other fish. Biting may result in loss of scales, and/or tearing or shredding of fins, particularly in the region of the anal fin and caudal peduncle of the opponent. Butting by the female occurs during spawning and appears to reduce male aggression. Butting consists of thrusting or nudging the opponent with the mouth closed and without clear attempts to bite. Due to the difficulty involved in discriminating between bites and butts, both were group under one category, bite-butt.

Mouth Fighting. Mouth fighting behavior was first described for *T. pectoralis* by Robison (19). It seems to occur primarily at territorial borders where few lateral displays occur.

During the spawning sequence, mouth fighting occurs mainly when a female takes refuge in a clump of plants or pot. When the male approaches, she initiates the mouth fight by lunging toward him. Characteristically, several contacts occur, followed by male lateral display, after which he returns to the nest.

Chase. Chase involves the fleeing of one fish with another pursuing. The pursuing fish usually attempts to bite or butt the pursued which flees with fins folded. Males commonly chase females after spawning bouts are concluded.

Appeasement. Appeasement postures are frequently assumed by females or subordinate males after being attacked. Median fins are folded while the caudal fin droops and the fish tilt laterally or vertically, either upward or downward, exhibiting vital areas to the attacking fish.

DESCRIPTIVE ANALYSIS

Courtship and reproductive behavior in *T. pectoralis* is stereotyped and occurs in distinct temporal patterns. The description below is based on five series of observations on spawning pairs of *T. pectoralis* in aquaria.

Courtship and Prespawning Behavior

Acquisition of nuptial coloration usually is associated with establishment of a territory, increased aggressiveness, and nest building activity in males. Darkened nuptial coloration in addition to territorial behavior may function to render the male beneath the nest more conspicuous to the female. During this period the female remains hidden in the far corner of the tank away from the nest, usually at the bottom or in heavy plant growth if present, surfacing rarely. Surfacing often elicits male attack. If the female is ready to spawn she too will acquire nuptial coloration during the period of male nest building. Males seldom approach females during nest building and usually do so only after some movement by the female such as surfacing or feeding. During this period the male is primarily occupied with blowing bubbles, arranging them, and defending his territory against intruders.

The nest is fairly well established before the male approaches the female. These initial approaches are rapid and direct and accompanied by median fin erection, terminating in lateral display, tail beating, or attack. Lateral display develops, in some cases, into a sigmoid posture followed by tail beating. During male attack the female will appease, usually tilting the head upward or downward. Following the display or attack, the male returns rapidly to a position beneath the bubble nest. Mouth

fighting may occur if the female is well hidden in plant growth or in an overturned pot, providing her some protection so that she may face the male intruder. She may initiate the mouth fight by lunges toward the male. "Pendulum movements" as described by Miller (6) occur giving the impression of a female-male territorial border dispute. These mouth fights are short in duration and after several mouth contacts the male returns rapidly to the nest.

Non-reproductively motivated females hide in the far corner of the tank and remain motionless. Male aggression is greatly increased at this time and since the restricted space prevents escape, nonreproductively motivated females may be severely bitten and killed if not removed. During this study 17 females were killed by males.

Leading to the nest (6) which is prominent in *T. trichopterus* courtship, is absent in male *T. pectoralis*. Instead, the male approaches the female, lateral displays, then returns to the nest. After several seconds the female may swiftly approach the nest area, terminating her approach with a series of rapid butts directed at the dorsolateral region of the male. The importance of female receptivity and physiological readiness to spawn at this time is obvious as 88.8 percent of all spawning bouts were initiated by the female. As with *T. leeri* (1) female initiated bouts tend to contain more of the activities associated with the terminal act of spawning and may therefore be considered more successful.

Return of the male to the nest area probably functions to locate the nest for the female. Her presence under the nest seems to inhibit male aggression. In nature she would probably stay far away from the nest and well hidden in dense vegetation; therefore the nest would not be easily visible to her.

Spawning Phase

Differentiation between courtship and actual spawning activities is difficult. Miller (6) suggested that behavior preceding spawning was loosely organized and of a preliminary nature serving either to stimulate the partner or to aid in synchronizing movements of the pair. Activities under the nest were clearly associated with the spawning act and had a rigidly fixed sequence. In some instances the smooth merging of courtship activities into spawning activities prevented a sharp distinction.

Independent female approach involves a rapid, direct movement up to the male under the nest and is terminated by a series of 1-15 butts by the female on the dorsolateral region of the male just anterior to the base of the dorsal fin. Such butting is prominent in *T. pectoralis* and precedes each spawning bout. As the female approaches, the male may give a lateral display. Female approach seems to be facilitated if the male orients so that the female does not have to approach head-on. Female approach and butting probably functions in inhibiting male aggression by serving as a signal releasing behavior (lateral display) which leads to clasp and spawning. Morphological features, coloration, and the manner of approach may serve to identify females and concomitantly inhibit or decrease male aggression (8). Picciolo (11) reported that fin shape, plumpness of the abdomen and general body form appear to be important sex recognition characters in *Trichogaster* species, although on several occasions during the present study, plump female *T. pectoralis* were killed or severely injured by males. Examination of these dead females revealed the presence of many mature ova.

Occasionally female approach is halted by male approach followed by male aggression, and return of the female to an area of hiding. Strongly motivated females can eventually bring about a halt to male aggression by remaining under the nest while being repeatedly butted. Fluttering (8) was observed for *T. pectoralis* females while far away from the nest.

Following approach and butting by the female the male assumes a position beneath the female partially or completely folding his dorsal fin. This position is called "rubbing position" (19). Miller (6) described a unique motor pattern for *T. trichopterus* called "rubbing." Rubbing position is almost identical to "rubbing" in orientation and posture of the two participants, except that there are no back and forth rhythmical movements by the male beneath the belly of the female in *T. pectoralis*. The male remains stationary, directly beneath the female with head pointed slightly upward.

The female butt may be a stimulus releasing rubbing position because butting must occur before the male assumes this position. She is able to keep the male in this position by butting if the male attempts to back up. A male sometimes attempted this and if he was able to back up sufficiently to get her snout above his, he would turn and bite her. If the female butted the male several times as he began to move backwards, he would move forward, returning to rubbing position. Miller and Hall (1) also showed that during spawning bouts in *T. leeri* the female continued to butt the male until curving position was achieved and clasping occurred. Rubbing position, ending in curving, lasts 4 to 103 seconds, with an average duration of 30.2 seconds. Rubbing has an average duration of 70 seconds in *T. trichopterus* (6). Rubbing position may function as a tactile stimulus in keeping the pair in close proximity in a position favorable for curving and clasping. Rubbing position probably functions in the same manner as rubbing, i.e., it enables the partners to remain together for additional time and provides additional mutual stimulation while facilitating subsequent position changes culminating in clasping and spawning.

It seems logical to consider rubbing as being a more complex behavior derived from rubbing position. Due to the absence of rubbing or rubbing position in all other species of *Trichogaster* it would seem to have systematic value perhaps indicating close relationship between *T. trichopterus* and *T. pectoralis* (20). Rubbing position thus seems to be intermediate between rubbing and no rubbing behavior.

Subsequent to assuming rubbing position the male begins to curve his body into a semicircle and swim in a rather tight circle. The ideal position of the female at this time is perpendicular to the center of the body of the male. A unique characteristic is that in almost every spawning bout during circling the male circled toward the surface where he snapped air, making an audible snapping noise (the female remained in the perpendicular position as he snapped air). He then continued to circle while the female moved into the semicircle, maintaining her snout on or near his dorsum just anterior to the dorsal fin. Circling duration varies from 2 to 17 seconds during the spawning sequence, with an average duration of 6.4 seconds. This average is somewhat misleading, as well-synchronized pairs circle only 2-4 seconds before clasping is initiated. Because of the high frequency of disruptions at this stage during the spawning sequence, circling is an extremely important stage. Longer circling duration increases the chance that the female will lose orientation to the male, which results in incomplete bouts and male aggression toward the female as is true in *T. leeri* (1). A highly motivated female may cause the male to return to rubbing position after circling breaks off by again butting him.

After the male has curved his body and has begun to swim in a circle the female swims into the curve placing her snout immediately anterior to the origin of the dorsal fin of the male. As the female mounts, the male clasps her by bringing his head and caudal fin together around her body in a u-shaped posture. Improper orientation of the female at this point is a common cause of bout disruption or termination. With the initiation of the clasp the female flexes her body into a rigid sigmoid posture. The exact function of this posture has not been determined, but Hall and Miller (8) hypothesized that it may facilitate egg release or be of value in rolling the clasped pair. Another possible alternative was in helping the male attain a firmer clasp. As Miller (6) observed for *T. trichopterus*, proper maintenance of the clasp position is essential for successful spawning in *T. pectoralis*. Proper maintenance of the clasp is largely accomplished by caudal fin movements of the pair.

After attainment of a firm clasp, both fish usually begin quivering. In conjunction with movements of the caudal penduncle and caudal fin of both sexes (mainly the male), the roll is initiated. As a result of these movements the pair actually turn or "roll" over ending up with the ventral surface of the female directed upward and the body of the male folding over that of the female with his head directed downwards.

Just prior to egg release, quivering of the female's fins and body becomes pronounced. Male ejaculation occurs several seconds after the roll is completed and occurs prior to egg release. No "terminal

squeeze" (8) as occurs in *T. leeri* is seen in *T. pectoralis*, although ejaculation is accompanied by intense muscular contractions and quivering of the body. At the time of egg release the female is usually oriented with her genital pore in close proximity to that of the male and pointed toward the bottom of the nest. Between 8 and 70 eggs are released during each spawning bout.

Both fish then enter a 2-12 second period of swimming inhibition in which the pair sinks slowly toward the bottom as the male loosens the clasp. They remain motionless and tend to lose orientation to each other. Forselius (10) reported that in anabantoids the male generally recovers first from swimming inhibition. Such is not the case in the genus *Trichogaster*. As in *T. leeri* and *T. trichopterus* females (21), *T. pectoralis* females usually recover 1-2 seconds earlier than males. Longer swimming inhibition in females might function as a means of allowing the attention of the male to be directed toward recovery of eggs. Because of the extreme aggressiveness of male *T. pectoralis* in this phase and the fact that their eggs float (as do eggs of all species of *Trichogaster*), there may no longer be a need for the female to remain in a state of swimming inhibition longer than the males. In most instances, the female regains her orientation first, then swims slowly from the nest toward the far corner. Swimming inhibition may be brought to an abrupt halt with male aggression and female fleeing, however. The fleeing female elicits male chasing and biting directed at her anal and caudal fins. Female appeasement postures are commonly observed in these situations although their value in inhibiting male aggression is slight. Subsequent female movement such as surfacing may elicit male aggression.

Postspawning Phase

During the postspawning phase of the spawning sequence the male searches for eggs, places them into the nest, repairs and rearranges the nest, and protects the eggs from predators. Free-swimming and wriggling larvae are retrieved when that fall out of or stray from the nest area and are transported back to the nest by the male.

Forselius (10) listed two successive actions during the male's collection of fry and eggs: (a) approach released by visual stimuli from the egg or fry as it falls, which is then (b) engulfed and tested chemically and/or tactually in the mouth. He further asserts that depending on the chemical and/or tactile stimuli provided by the object caught and on the motivation of the male at the moment, the object is either eaten, falls to the bottom, or is brought to the nest. Several times during the study eggs were manually removed from the nest by the use of an eye dropper. The eggs were subsequently returned to the tank together with food particles in an area away from the nest. In every case the eggs were collected and returned to the nest while the food was sometimes eaten.

Miller (6) in *T. trichopterus* found nesting activity *per se* was greatest immediately before and after spawning, but the most total time was spent after spawning when eggs and young were present in the nest. Duration per occurrence under the nest in *T. pectoralis* is approximately the same in spawning phases and prespawning phases, 32.6 seconds and 31.8 seconds, respectively, increasing to 36.8 seconds during the postspawning phase (Table I). Thus in all phases the male spends approximately the same amount of time under the nest per trip under the nest, although for differing reasons in each phase, i.e. nest building in

TABLE 1. *Average duration spent under nest during three spawning phases.*

	Prespawning	Spawning	Postspawning
Total Duration Under Nest (sec.)	2773	1881	7039
Occurrences Under Nest	85	59	191
Average Duration Per Occurrence Under Nest	32.6	31.8	36.8
Duration (sec.) of Recorded Activity	10920	6420	10380
Average Duration (sec.) Under Nest Per Minute of Activity Recorded	15.2	17.5	40.7

prespawning phase, actual spawning activities in the spawning phase, etc. When the data are analyzed with regard to the duration under the nest per minute recorded, a quite different picture emerges. From a low of 15.2 seconds per minute in prespawning phase, the time per minute under nest rose to 17.5 seconds per minute in the spawning phase, followed by a large increase to 40.7 seconds during the postspawning phase. The reason for the large increase was the occurrence of posting behavior in which the male remains almost motionless beneath the nest protecting the eggs.

Spawning sequences in *T. pectoralis* last approximately 140 minutes. During a spawning sequence, there are approximately 70 bouts, of which 6-7 are spawning bouts. Spawning bouts average 263 seconds, longest of all *Trichogaster* species. Spawning efficiency is low as only 9% of all bouts initiated culminate in spawning.

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