AN ETHOLOGICAL STUDY OF THE SNAKESKIN GOURAMI, <u>TRICHOGASTER PECTORALIS</u>, WITH COMMENTS ON PHYLOGENETIC RELATIONSHIPS AMONG SPECIES OF <u>TRICHOGASTER</u> (PISCES, BELONTIIDAE)

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AN ETHOLOGICAL STUDY OF THE SNAKESKIN GOURAMI, <u>TRICHOGASTER</u> <u>PECTORALIS</u>, WITH COMMENTS ON PHYLOGENETIC RELATIONSHIPS AMONG SPECIES OF <u>TRICHOGASTER</u> (PISCES, BELONTIIDAE)

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PREFACE

The objectives of this study on the snakeskin gourami, Trichogaster pectoralis (Regan), were: 1) to qualitatively and quantitatively describe courtship and reproductive behavior; 2) to elucidate the biological significance of observed behaviors; 3) to determine if a diel activity pattern exists; 4) to describe parental behavior; 5) to make precise comparisons of behavior among T. pectoralis, T. leeri, T. microlepis, and T. trichopterus based on qualitative and quantitative data; 6) to investigate phylogenetic relationships among the four species.

I wish to thank Drs. W. A. Drew, S. A. Marks, and T. C. Dorris who served on the advisory committee. Dr. R. J. Miller served as major advisor and suggested the problem initially. Special thanks and gratitude are expressed to Dr. Miller for his encouragement and assistance during the study and for the many hours of animated discussion on anabantoid behavior and evolution. My sincerest thanks go to my wife, Catherine, for her patient help, understanding, and encouragement at all times throughout the study.

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CHAPTER I

INTRODUCTION

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 are 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 (1968) provided the first primarily quantitative description and analysis of reproductive behavior in anabantoid fishes. Quantitative studies are useful in providing more precise descriptions of behavior and detailed comparisons among species, thus facilitating the probing of phylogenetic relationships (Miller and Hall, 1968). Qualitative studies are more numerous and have been concerned with the behavior, morphology, embryology and physiology of anabantoid fishes (Lissman, 1932; Bennington, 1936; Armirthalingham, 1939; Kulkarni, 1943; Smith, 1937, 1945; Scharrer, Smith, and Palay, 1947; Steinbeck, 1950; Hodges and Behre, 1953; Lindsay, 1954; Hisaoka and Firlit, 1963; Miller, 1964; Hall, 1968; and Hall and Miller, 1968).

Forselius (1957), in a monograph on anabantoid fishes, dealt with their behavior, systematics, distribution, endocrinology, and ecology. From a behavioral standpoint he dealt primarily with _Colisa lalia_ and the hybrid between _C. lalia_ and _C. labiosa_. Sexual and nest discrimination in _Colisa_, _Trichogaster_ and several other anabantoids were described by Picciolo (1964). He found that male *T. pectoralis* was able to discriminate visually between sexes of their own species.

A monograph by Liem (1963) dealt with the osteology, phylogenetic relationships, and systematics of anabantoid fishes as well as some ecological factors involved with the evolution of the group. The osteology of *Ctenops* and *Trichopsis* was investigated by Liem (1965). Regan (1909) was the first to publish a synopsis of the anabantoids and in the process named several new species, among them *Trichopodus* (=*Trichogaster*) *pectoralis*.

The ethology of the anabantoid fish *Macropodus opercularis* has been studied by Ward (1965, 1966, 1967) and Southwick and Ward (1968) as well as Hall (1968) who provided a qualitative description of the courtship and reproductive behavior of *Macropodus*. Temperature controlled meristic variation was described by Lindsay (1954) while Machowicz and Gray (1955) studied branchial circulation in *M. opercularis*. Aggressive behavior and social organization was studied by Miller and Miller (1970).

In a study of *Trichogaster trichopterus* Miller (1964) described social behavior including data on agonistic motor patterns, nest building and reproductive behavior. Frey (1970) studied hierarchial relationships in *T. trichopterus*. Hall (1965) studied the comparative ethology of three anabantoid species and included quantitative data on reproductive and courtship behaviors. Physical and physiological factors influencing spawnings in *T. leeri* and *Macropodus opercularis* were investigated by Hall (1966a) and Hall (1966b) reported on reproductive color changes in *T. leeri*.

Trichogaster pectoralis (Regan), the snakeskin gourami, is the subject of the present investigation. *T. pectoralis* is a member of the subfamily Trichogasterinae of the newly erected family Belontiidae (Liem, 1963). Due to their wide geographical range, encompassing most of southern Asia, India, and parts of Central Africa, the belontiids exhibit much ecological diversity.

T. pectoralis is the largest (over 200 mm) and most economically important member of the genus *Trichogaster*, generally inhabiting ponds, lakes, and sluggish waters of central Thailand and extending into Cambodia and other provinces of Indo-China (Smith, 1945). Unfortunately, *T. pectoralis* is not a popular aquarium species in America due to its large size and the inability of people to get them to spawn (Axelrod, pers. comm.). In Thailand however, this species is extremely popular as a food fish and because it is well adapted to ponds, its cultivation has helped alleviate the food shortage felt in certain southeast Asia countries. Forselius (1957) stated its rating as a food fish was nearly comparable to that of *Tilapia mossambica* Peters. Introduced as a pondfish under the name "sepat siam", *T. pectoralis* was introduced into Malaya from Thailand 20 to 35 years ago (Myers, pers. comm.). In addition to Malaya, *T. pectoralis* has been successfully introduced into Ceylon, India, and many parts of Indonesia (Forselius, 1957).

Unnamed until 1909, *T. pectoralis* was initially described by Regan (1909) as *Trichopodus pectoralis* from specimens from Thailand and Singapore in allusion to the large pectoral fins which are longer than the head length in adults (Smith, 1945).

Trichogaster pectoralis is one of the least known of the anabantoid fishes. Virtually nothing has been published on reproductive or agonistic behavior of this species. Except for a brief field study by Soong (1948) and short, cursory descriptive articles by Beldt (1942), Smith (1945), and Campbell (1948) the literature concerning *T. pectoralis* is meager. Unfortunately, these reports contain numerous inaccuracies rendering them almost worthless. Sexual maturity is reached in nature in approximately four months (Soong, 1948). Spawning may take place at temperatures of 26 to 28°C (Campbell, 1948), and plant fragments were interspersed with the bubbles in the nest. Hatching occurred in 24 to 30 hours.

An attempt was made in this study to describe the courtship and reproductive behavior of *T. pectoralis*, both qualitatively and quantitatively, while investigating its social behavior. In addition, precise comparisons based on qualitative and quantitative data are made for the purpose of proposing phylogenetic relationships among the species of the genus *Trichogaster*: *T. pectoralis*, *T. leeri*, *T. microlepis*, and *T. trichopterus*.

CHAPTER II

MATERIALS AND METHODS

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 because of the difficulty in spawning this species. All other fish stocks were purchased from Gulf Fish Farms, Inc., Palmetto, Florida. Fish were kept in 35 gallon stock tanks when not paired for breeding purposes or other experiments. At least nine pairs of *T. pectoralis* were maintained at all times, but various combinations were used during the study. Size ranged from 50-95 mm in standard length. *T. trichopterus*, *T. leeri*, and *T. microlepis* pairs were maintained throughout the study for comparative purposes. Water temperature was maintained at 75 to 85 F for the duration of the study except in instances where variations were tried in attempts to stimulate spawning. Overhead flourescent lights provided illumination for the laboratory while each tank had an individual light source. A photoperiod of 12 hours (6 AM-6 PM) was maintained throughout the study.

Aquaria ranged from 15 to 35 gallons. 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 (Tetramin) was fed twice daily with feedings of live and frozen Artemia, Daphnia sp., and Chironomus sp. larvae interspersed 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 observation periods per tank over approximately two and one half years. Duration and frequency of periods increased during nest building and spawning activities and during various experimental phases of the study. For several other behaviors, i.e. feeding, etc., observations lasted for the duration of the behavior being performed. During the 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/minute, 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 and duration, as well as temporal patterning of behaviors occurring during encounters between fish can be recorded on the event recorder charts. Recorded data were then transferred to data summary sheets, which facilitated analysis greatly.

An attempt was made in the present study to determine if a diel activity pattern exists in _T. pectoralis_. Heterosexual pairs were established in four aquaria and kept together for a period of two weeks to determine if the pairs were compatible. Tanks were planted with _Vallisneria_ and _Myriophllum_ with gravel bottoms. As indicated previously, a 12-hour photoperiod was used. Pairs were maintained in their respective tanks, without peat moss, and data collected on males only. Data were recorded for 10 minutes on each tank every two hours for a period of 24 hours. Within a period of 40 days the experiment was replicated three times. Durations (seconds) and frequencies were recorded with stopwatches and prepared data sheets for patrolling, inspiration, rest, and total activity, while only frequencies were taken for lateral displays, mouth fights, bites, chases, and tail beats.

Data were subjected to an AOV analysis. Previous studies on diel behavior have used mean values for plotting frequencies or duration without regard to statistical inferences. Because these data often showed clear-cut time effects but not always significant differences among replicates, some graphs are plotted as mean values while others are illustrated as three separate replicates.

CHAPTER III

MOTOR PATTERNS AND TERMINOLOGY

Motor Patterns

Motor patterns for anabantoid fishes of the genus *Trichogaster*, including those for *T. trichopterus*, *T. leeri*, and *T. microlepis* have been described by Forselius (1957), Miller (1964), Hall and Miller (1968), and Wimmer (1970). These descriptions will serve as a basis for discussion of the motor patterns of *T. pectoralis*.

Approach

An approach is 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

The lateral spread display is common during agonistic encounters and anabantoid courtship and reproductive behavior. Median fins and caudal fin are spread maximally at high intensities and only slightly at low intensities. The lateral display may be expressed in the form of an S-shape (sigmoid) at maximum intensity or develop subsequently into tail beating, biting or butting, or chase (Miller, 1964). The displaying fish is usually in a position directly in front of or parallel to the other fish, but can be oriented at any angle to the other fish. The head is directed away from the other fish at all times.

Tail Beating

Tail beating consists of lateral, undulating thrusts of the caudal peduncle and fin and may vary in force and duration. These movements may be performed by one or both fish and occur commonly in courtship and agonistic encounters. Tail beating probably represents greater aggressiveness than the lateral spread display in any given encounter (Miller, 1964). Forselius (1957) termed these "undulating movements."

Opercle Spread

Among the species of the genus *Trichogaster*, this behavior pattern is rare in *T. leeri* and was believed rare in *T. trichopterus* until Frey (1970) reported its occurrence. The inclusion of opercle spreading in the behavioral repertoire of *T. pectoralis* marks the first time it has been reported in this species. Opercle spreading in *T. microlepis* has not been observed (Wimmer, 1970). Unlike its form in some other anabantoids, the opercles and branchiostegals of *T. pectoralis* are spread only minimally. It occurs in an aggressive context while the displaying fish is lateral to and slightly behind the other fish. The head is directed toward the opponent and higher than the caudal fin while the body is positioned into a sigmoid curve with a downward concave horizontal component.

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. Butting is accomplished usually by the female during spawning and appears to reduce 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 grouped under one category, bite-butt.

Fin Tug

Fin tugging occurs when one fish grasps the fin of another with its mouth and holds on for a period of one to several seconds, or actively pulls the fin by undulating tugging movements (Miller, 1964; Frey, 1970). The anal fin is usually the target of attack but the pelvic, pectoral or dorsal fins may also be seized.

Mouth Fighting

Miller (1964) described mouth fighting behavior in *T. trichopterus*, but no documentation of the occurrence of this behavior has appeared in the literature for *T. pectoralis* or other species of *Trichogaster*. Mouth fighting has been recorded for other anabantoids and seems to occur primarily at territorial borders; in many of these boundary encounters, few or no lateral displays occur (Miller, 1964).

A typical mouth fighting sequence occurred when two fish occupied territories in the same tank. Although it was more common between territorial males, it also occurred between males and females and data on 30 male-female interactions were recorded. Mean contact time was 54.3 seconds in male-female mouth fights while males averaged 9.4 thrusts (approaches) per mouth fight and females averaged slightly more, 10.2 thrusts per mouth fight.

Upon meeting, the opponents face each other with pelvic threads projecting anteriorly, dorsal and anal fins folded, and gill covers erect. As the fish begin to lunge both fish tilt slightly. This period is marked by a rapid darkening of coloration during which the fish develops intense vertical reticulations and the gular and cheek regions darken considerably. Iris pigmentation darkens extremely and the coloration is reminiscent of nuptial coloration. In long agonistic encounters both fish lose their typical lateral blotches and caudal ocellus and intensify the vertical reticulations.

A series of lunges by one or both fish seems to initiate these short, violent engagements which are extremely variable. These lunges, termed "pendulum movements" by other authors, occur when boundaries are seemingly threatened by the opponent. Mouth fights do not appear to contain ritualistic elements they sometimes have in other teleost fishes (Miller, 1964), but instead seem rather to be a direct frontal attack and bite occurring simultaneously in both opponents.

When fish fight a grasp of the jaws as in cichlids (Baerends and Baerends-van Roon, 1950) is not seen. The fish that gains the upper hand is the one that succeeds in pushing the upper jaw of the other. Contact is usually brief because no grip is attained, but rather, only lip contact occurs. Miller (1964) has described actual gripping of the jaws in _T. trichopterus_. In over 100 mouth fights observed, a good grip was never achieved and pushing with mouths open maximally and pressing of lips seemed to be the conclusive element of the fight.

Often when one fish would push the other sufficiently to "win" the pushing contest the other would immediately lateral display, usually facing downward. This often brought a bite or butt from the apparent winner. The apparent winner always pushed the loser backward and downward. The longer the mouth fight lasted, the higher the probability that the encounter would develop into an aggressive fight including biting and chasing.

In observations on sexually paired groups the female occupied a small corner of the tank while the male occupied the rest of the tank. In only one case, when the female was slightly larger than the male, was there anything approaching equal-sized territories.

An experiment in which a glass partition separated the tank into two equal parts precipitated the formation of two territories whose boundary was the glass partition. After removal of the partition, the male and female would mouth fight at the exact dividing line where the glass partition had previously been. Neither fish ventured into the territory of the other. The situation lasted two days until the male eventually became dominant and the female had to be removed because she was near death from attacks by the male.

Mouth fights also occur after several agonistic encounters when a male chases a female into a sheltered area, such as a clump of vegetation or overturned pot. She then turns to face her attacker and usually initiates a series of short mouth fights. These are brief and the male usually forces her to flee from her refugium.

During the spawning sequence, mouth fighting is seen in almost every instance when a female takes refuge in a clump of plants or pot and upon the approach of the male, she initiates the mouth fight by lunging toward him. Characteristically, several contacts occur, followed by lateral display by the male after which he returns to the nest.

Chase

Chasing involves the fleeing of one fish with another pursuing. The pursuing fish usually attempts to bite or butt the pursued. Pursued fish usually flee, with fins folded, at moderate to high speeds. Chasing of females by males is common, but size seems to be a determining factor, as large females chase smaller males in non-reproductive situations. Males commonly chase females after spawning bouts are concluded.

Carousel

Carouselling occurs during violent agonistic encounters in which two fish circle each other head to tail while attempting to bite. This behavior usually is rare and occurs well into the fight.

Appeasement

Appeasement postures are most often assumed by females or subordinate males after being attacked. Appeasing fish fold their median fins, the caudal fin usually droops, and the fish tilt laterally or vertically, either upward or downward, exhibiting vital areas to the attacking fish.

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 various behavioral events analyzed in this study.

1. _Bout_. Any social interaction between two or more fish. Synonomous with encounter.
2. _Sexual Bout_. Male-female interactions containing sexual responses by one or both individuals.
3. _Spawning Bout_. Refers to a sexual bout in which clasping and oviposition occur. This corresponds to the "spawning cycle" of Forselius (1957).
4. _Pseudospawning Bout_. This term refers to 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.
5. _Courtship Bout_. A bout containing sexual responses by one or both partners but not attaining the clasp or nuptial embrace.
6. _Clasp Bout_. This type of incipient spawning bout which advances only to the clasp stage. In this bout emission of sex products and swimming inhibition do not occur.
7. _No Clasp Bout_. A sexual bout that does not proceed to the clasp stage.

8. Incipient Spawning Bout. A sexual bout that does not reach the spawning or pseudospawning stage (Forselius, 1957).

9. Spawning Sequence. The complete series of male-female interactions comprising prespawning, spawning, and post-spawning activities; corresponds to "mating cycles" of Forselius (1957). Approximate duration of spawning sequences in *T. pectoralis* is 2 to 5 hours.

10. Prespawning Phase. The prespawning phase is characterized by courtship and/or aggressive bouts that precede the first successful spawning bout.

11. Spawning Phase. This phase includes the period from the first to the last successful spawning bout during the spawning sequence and includes all bouts within this duration.

12. Postspawning Phase. The postspawning phase is 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.

13. Posting. Posting refers to a behavior in which the male positions himself about two inches below the nest with the head usually directed slightly upward at an angle varying from 15 to 30° with the surface.

14. Patrol. Patrolling behavior consists of slow swimming whereby the fish apparently surveys the area without interacting with other fish.

15. Rest. In the experiment concerned with diel activity a very narrow definition of rest was utilized: rest was tallied

when the fish became stationary on the bottom with fins relaxed, exhibiting no movements except slight opercular opening and closing. Thus rest in this study differed from the definition of Wimmer (1970) for rest in *T. microlepis*.

16. *Inspiration*. Inspiration consists of the taking in of oxygen by the fish at the air-water interface. Wimmer (1970) described two "distinctly different" methods of inspiration in *T. microlepis*; however, no such differentiation was made in this study.
17. *Total Activity*. The term total activity was used in the experiment on diel rhythmicity to include all behaviors occurring during a given observation period, except rest. Since rest is defined by its lack of movement, it could not be considered activity.
18. *Miscellaneous Activity*. This category includes behaviors grouped under total activity but not patrolling, inspiration, rest, or any agonistic behaviors. Feeding, snapping at a snail, etc., would be considered miscellaneous activities.
19. *Aggression Only Bouts*. Male-female interactions that do not contain sexual responses by either partner.

CHAPTER IV

MAINTENANCE, AGGREGATION, AND FRIGHT

Comfort Movements

The term comfort movements will be used in this study to denote those movements that are used in removing irritants or seem to be stretching movements. Comfort movements were originally described by Baerends and Baerends-van Roon (1950) for cichlid fishes.

Chafing

Chafing involves a movement in which some part of the body of the fish is brought into contact with a stationary object such as a rock, pot, plant, or even the bottom gravel, followed by a rapid push away from the object by means of a lateral undulation of the body. A brief hesitation just prior to initial contact with the object is followed by quick movement of the body against the object. The body part varies, but usually the flanks, belly, or head are involved. The fish completes the chafe by lunging forward in an arching manner or directly ahead.

Fins are folded at the time of movement against the object, but are slightly erected on the glance away from the object. Several chafes may occur in succession on the same or different objects.

Yawning

Yawning occurs when the mouth is stretched forward maximally, causing expansion of the opercular chamber and slight spreading of the opercles. Median fins are erected simultaneously with yawning. Yawning is terminated when the mouth is snapped back to its original position.

Flexing

An exaggerated or extreme lateral flexure of the body is termed flexing. This behavior pattern is also termed "body bend" by some authors. The head is usually directed laterally to form an angle with the body. Duration is short and the body is straightened out almost immediately after initiation of flexing.

Fin Flicking

Fin flicking is tallied when any of the anal, dorsal, pectoral, or pelvic fins is erected and depressed with high frequency. In *T. pectoralis* the dorsal fin is flicked most frequently with pectoral flicking second in frequency. Pectoral flicking or flapping has been considered a separate motor pattern in several studies on cichlids (Baerends and Baerends-van Roon, 1950) and centrarchids (Miller, 1963).

Head Jerking

Head jerking is rare in *T. pectoralis*. This pattern involves rapid lateral movements of the head and anterior body. Wimmer (1970) observed air bubbles expelled in some cases from the mouth and opercles of *T. microlepis* during this behavior, but this was never seen in *T. pectoralis*. Head jerking always occurred in subordinate males and females. In several cases it was accompanied by mouth snapping. Hall and Miller (1968) reported head jerking in *T. leeri*, while Miller (pers. comm.) has observed it in *T. trichopterus*.

Mouth Snapping

Rapid opening and closing of the mouth is termed mouth snapping. A very audible clicking noise usually occurs during the snapping, with release of air from the mouth and opercles.

Coughing

Coughing was rare in *T. pectoralis* but did occur in certain instances as food or gravel was expelled from the buccal cavity. The mouth was opened widely, then rapidly closed in quick movements as the opercles were opened and closed.

In an attempt to learn something of the frequency of occurrence of comfort movements in *T. pectoralis* under laboratory conditions 60 ten minute observations were recorded on several fish housed in aquaria. Figure 1 illustrates the frequency of occurrence of comfort movements. Of all comfort movements recorded, 48.7 per cent were chafes while fin flicking was second in frequency with 23.1 per cent. Flexing accounted for 12.1 per cent, coughing for 7.7 per cent, yawning for 5.1 per cent, mouth snapping for 2.5 per cent, and no head jerking was seen during these observation periods.

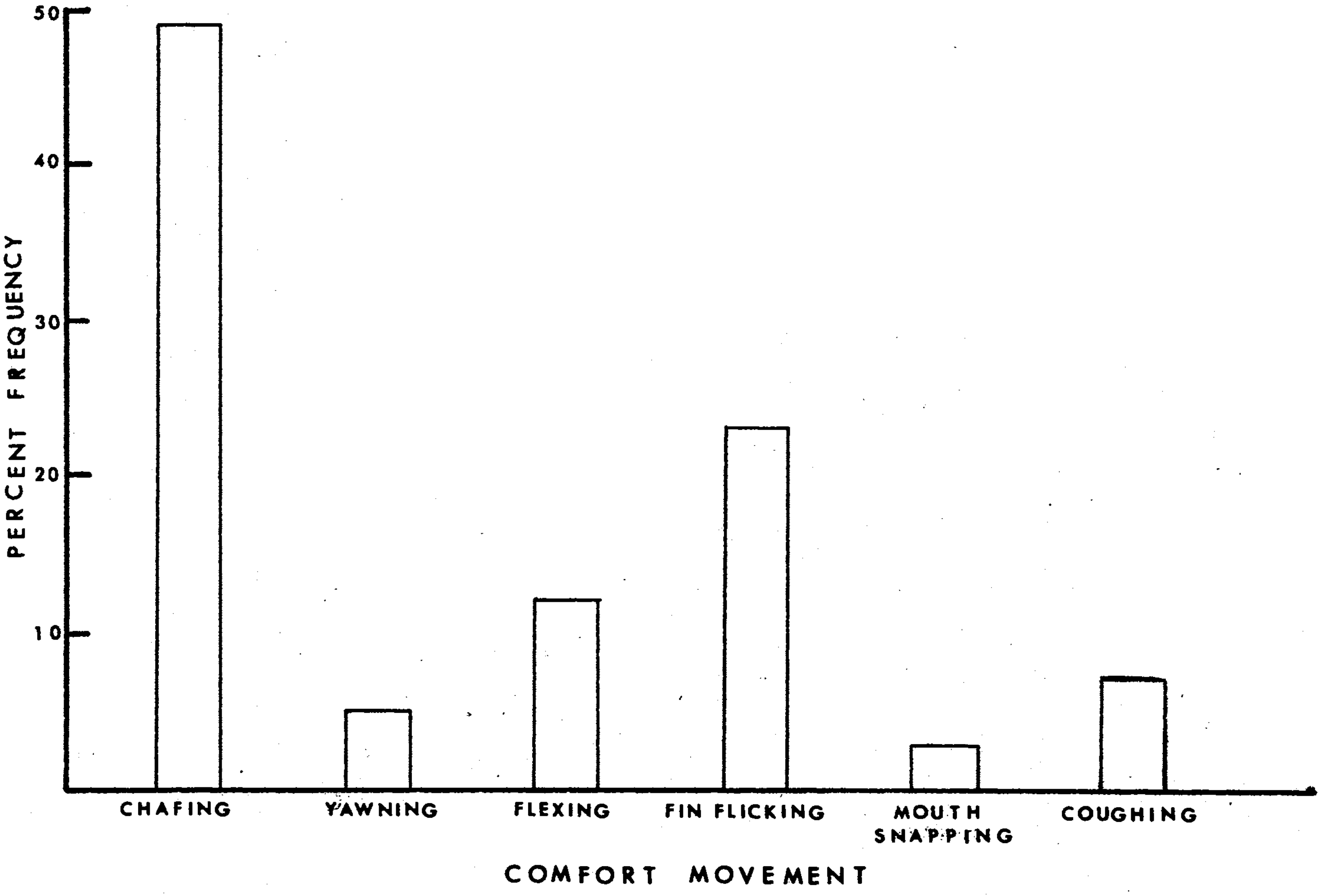


Figure 1. Percent Frequency of Occurrence of Comfort Movements

Feeding Behavior

Despite Liem's (1963) conclusion that species of the genus *Trichogaster* are highly specialized for a herbivorous niche in nature, *T. pectoralis* is omnivorous in aquaria, feeding on a variety of live and commercially prepared foods.

The most common form of ingestion exhibited by *T. pectoralis* is the typical anabantoid method of remaining stationary at the surface while sucking food particles into the buccal cavity. Many times when sucking in food, bubbles are extruded from behind opercle flaps. Some of these bubbles were almost 5 mm in diameter. Depending on the relative position of food particles, fish may move forward or backward slowly, maintaining an angle of about 45° with the surface while feeding. Position of fins and body is notably similar to those of stationary inspiration at the surface. Dried commercial food distributed at the surface was approached and eaten readily; however, sinking foods were also taken. The superior mouth of *T. pectoralis* may reflect a preference for floating foods, and when the two were introduced simultaneously the floating food did seem to be preferred. Many times the sucking action of the mouth caused food particles to sink. This food was eaten by subordinate or smaller fish, or fell to the bottom where it was consumed later.

Bottom feeding involves feeding from the substratum with the head directed downward while the body is at a 45° angle with the substratum. As feeding continues fish move forward and backward over the bottom. In some instances during bottom feeding, forward movement of the body continues as the head remains stationary by pectoral beats. The body moves from an angle of 45° to the substratum to a perpendicular position. Balance in the perpendicular position appears to be maintained by the caudal and pectoral fins with stabilization added by the median fins, which are erected. When feeding on detritus, fish sometimes maintained themselves at angles of 90° and 110° to the substratum. Body movement may proceed to an even more exaggerated posture in which the body shifts into a position in which the body is at an angle of about 130° with the substratum. Sometimes the fish seems to become so involved with feeding that orientation is lost and the fish appears to begin "falling over." They never do "fall over", but instead reorient quickly and continue feeding.

Daphnia appeared to be preferred food over *Chironomus* larvae, frozen or live *Artemia*, and flake food. When presented simultaneously, *Daphnia* was the preferred food. Snails were nipped but never seen to be eaten, even if broken up and placed in the tank. Baby *Poecilia reticulata* were fed but never eaten or even chased.

T. pectoralis feeds on algae quite readily. When feeding on algae the fish take strands of the algae into the mouth and then proceed to back up, moving the head in a sideways motion, pulling out several strands which are then eaten. Large amounts of algae were eaten when placed in tanks.

During feeding, strict maintenance of social hierarchies was not evident. If food was placed over the entire surface, all fish approached and fed. If, however, food was restricted to one surface area, all larger fish approached and fed with smaller, subordinate individuals waiting for sinking food particles. Aggressive actions by the dominant fish toward subordinates were extremely rare in feeding situations. The hierarchy seemed to carry over to feeding but rigid maintenance of it was usually not necessary. In male-female tank situations aggressive behavior by the male toward the female was much more common, but food stimulus was usually enough to keep the female at the surface instead of fleeing. Butts by the male were generally not successful in eliciting flight by the female.

Fright Behavior

Fright behavior in *T. pectoralis* is indicated by three types of behavior much as in *Badis badis* (Barlow, 1962), i.e.: flight (avoiding), movement suppression (concealing), and aggregating. Since *Badis badis* has recently been suggested as belonging to the suborder Anabantoidei based on behavioral and osteological evidence (Barlow, et al., 1968), behavior similarities should not be unexpected. The following is a discussion of each type of fright behavior. A discussion of fright coloration will be given in Chapter VII.

Flight (Avoiding)

In flight behavior the fish swims or darts away from the attacker at high speeds with median fins folded. The fleeing fish usually swims for cover in thick vegetation, overturned pots, or any other protective structure available. However, if cover is absent or too far away the disoriented fish may dart to the substrate where it remains motionless. If vigorously pursued by the attacker the fish usually appeases. If the attack continues the usual tilt of the body laterally or vertically upward or downward indicative of appeasement occurs.

Though most flight behavior is performed in a similar manner there is an element of behavior which occurs that must be considered as avoiding behavior and grouped in this category. Avoiding behavior usually takes the form of one fish swimming far out of the range of another, thus avoiding interaction with the other fish. Another form might be thought of as "flight backwards" as Barlow (1962) termed it. This behavior is quite common in situations when a dominant approaches a subordinate, in many male-female encounters and adult-juvenile encounters, especially when food is involved.

Movement Suppression (Concealing)

Movement suppression is common after agonistic encounters, whether it be male-female, male-male, or female-female encounters, and is most often displayed by subordinate individuals. During movement suppression the fish remains almost totally motionless with median fins erected and pelvic threads thrust forward. The degree of motion in movement suppression seems correlated with the strength of the fear stimulus. If the stimulus is weak (slight noise or movement outside the tank) slight movement of the pectorals and opercular movement continue. However, if the stimulus increases (hitting the tank, bright lights, etc.) pectoral sculling ceases and the only body part moving is the almost imperceptible opening and closing of the opercles. Movement suppression, coupled with the disruptive coloration of *T. pectoralis*, would probably have the greatest protective value in nature in fright situations.

Aggregating

Forselius (1957), in discussing disruptive coloration, pointed out that horizontal bands provide a disruptive coloration occurring more often in schooling fish species which spend most of their time swimming about in open waters of ponds and swamps. He included *T. leeri* and *T. pectoralis* in this category although in this study *T. pectoralis* was essentially a nonaggregating species throughout most of its life. Under certain conditions such as new environment and fright, *T. pectoralis* does exhibit aggregating behavior. Barlow (1962) used aggregating and schooling fairly synonomously, but in this study schooling will be viewed as an extreme form of aggregating tendency, following Breder and Halpern (1946).

Young *T. pectoralis* dart about the tank for several days after hatching searching for food. Most of their time is spent in search of food in relatively solitary fashion. Only under conditions of fright do the young come together in a loosely organized aggregation, dispersing when the fear stimulus is removed. At a later stage, agonistic encounters among juveniles are quite common with two fish approaching each other, laterally displaying, followed by butts and/or bites and chasing of one by the other. Dominance hierarchies are established within five weeks and actual fights after this time are rare, although assertion of dominance is quite a regular occurrence.

Feeding also causes aggregation but this is highly artificial and probably does not occur in nature.

Fright

Fright seems to induce aggregation more readily than any other factor in *T. pectoralis*. Adult fish introduced into new surroundings, such as that of a large tank, sink slowly to the bottom where they remain motionless and stationary sometimes for hours before any movement ensues. Once the initial shock has worn off slightly, fish move in slow, jerky movements, seemingly ready to flee at the slightest movement in the tank. Several days of searching and investigating are required before the fish begin to swim smoothly around their new environment. Until this time all fish surface together, swim together, and feed together. A definite preference was shown for planted areas of the tank. About the third day, individuals were seen beginning to leave the aggregation to feed and investigate for themselves. Occasionally pairs remained together even after the breakup of the aggregation.

Fright has the same effect on adults as in juveniles in that even groups exhibiting rigidly established dominance hierarchies aggregate when frightened. The "protection" of the group seemed to be of primary importance to the aggregation.

Eliminative Behavior

T. pectoralis excretes waste matter in the form of fecal pellets. These pellets are sometimes knocked off by swimming near a rock, plant or other structure in the tank. Extremely long pellets often develop; in some cases they were almost 150 mm long. Fecal pellets were never eaten by other fish, although if falling in the water column they were sometimes engulfed before being expelled in the manner of coughing.

CHAPTER V

BUBBLE NEST DESCRIPTION AND NEST BUILDING BEHAVIOR

The bubble nest of _T. pectoralis_, as in other members of the genus _Trichogaster_ and other anabantoids, serves the following functions: it provides a repository for developing eggs while keeping them at the air-water interface where eggs and young have easy access to atmospheric oxygen for respiration, it provides a discrete area where eggs and fry can be guarded against predation, and it probably serves to localize the male in one area rendering him more conspicuous to females. Miller (1964) first ascribed these three functions of the nest to _T. trichopterus_ and they seem to apply to all members of _Trichogaster_ and most other anabantoids.

Nest Description

The bubble nest of _T. pectoralis_ is a raft-like structure composed of various-sized bubbles and extremely variable in size, depth, and shape, as shown in Table I. Measurements were made on 15 nests during the study with an average size of 96 x 76 x 7 mm. Forselius (1957) suggested a correlation between nest size and size of the male in _Colisa lalia_, however no such correlation was observed for _T. pectoralis_ males. Miller (1964) also observed no correlation in _T. trichopterus_. Bubble size was not measured because of the tremendous variability of bubble size produced among individuals, within the same

TABLE I

BUBBLE NEST DATA FROM *T. PECTORALIS* MALES

Nest Measurements (mm)	Photoperiod	Temperature (^{o}F)	Vegetation
135 x 105 x 7	Not controlled	78	Attached to *Myriophyllum*
80 x 73 x 14	Not controlled	75	Attached to *Vallisneria*
110 x 110 x 4	12 hr.	81	Attached to *Vallisneria*
115 x 95 x 3	24 hr.	78	Some algae
110 x 85 x 4	12 hr.	78	Attached to *Myriophyllum*
150 x 100 x 12	12 hr.	83	Attached to *Myriophyllum*
75 x 50 x 3	24 hr.	84	Attached to *Myriophyllum*
70 x 55 x 3	12 hr.	85	Attached to *Myriophyllum*
70 x 100 x 3	12 hr.	83	Attached to *Elodea*
45 x 30 x 10	12 hr.	84	Attached to *Myriophyllum*
100 x 75 x 13	12 hr.	83	Attached to *Myriophyllum*
100 x 80 x 12	12 hr.	82	Attached to *Myriophyllum*
110 x 83 x 12	12 hr.	82	Attached to *Myriophyllum*
100 x 15 x 3	12 hr.	76	Attached to *Vallisneria*
122 x 88 x 4	12 hr.	84	Attached to *Vallisneria*

$\bar{\bar{X}}$ nest size = 99.47 x 76.27 x 7.73 mm

$\bar{\bar{X}}$ temperature = 81.07^{o}F individual, and at different times. Floating vegetation was used for anchoring the nest, but nests rarely were built in dense vegetation. Most nests were situated in open water surrounded by vegetation, probably to facilitate movement of males beneath the nests, yet still allowing some cover for the male.

Incorporation of plant material into the nest is absent or rare. While *T. microlepis* utilizes a great amount of vegetation in its nest construction and actively searches for plant material, *T. pectoralis* simply uses the growth available as a means of anchoring the floating nest. Bubbles were found attached to vegetation in every nest observed except in several cases where "u-shaped" feeder devices were placed in the tank in the presence of plant material and nests were constructed in the feeders. No active incorporation of vegetation by males was ever seen, however, in one case strands of bottom algae were found in one nest.

Nest Building

In anabantoid fishes, air inspired at the surface is transformed into small bubbles in the oral cavity, coated with mucus secreted from unicellular glands in the oral cavity, and then expelled to form a bubble nest in several different ways. Four principal types of motor patterns were found to exist in *T. pectoralis* bubble blowing. These were: surface blowing, sub-nest blowing, jetting, and opercular emission of a few large bubbles. Relative frequency of each motor patterns used in nest building is shown in Figure 2.

Surface inspiration with surface release is infrequent, occurring only 8.5 per cent of the time and was found to occur primarily in the

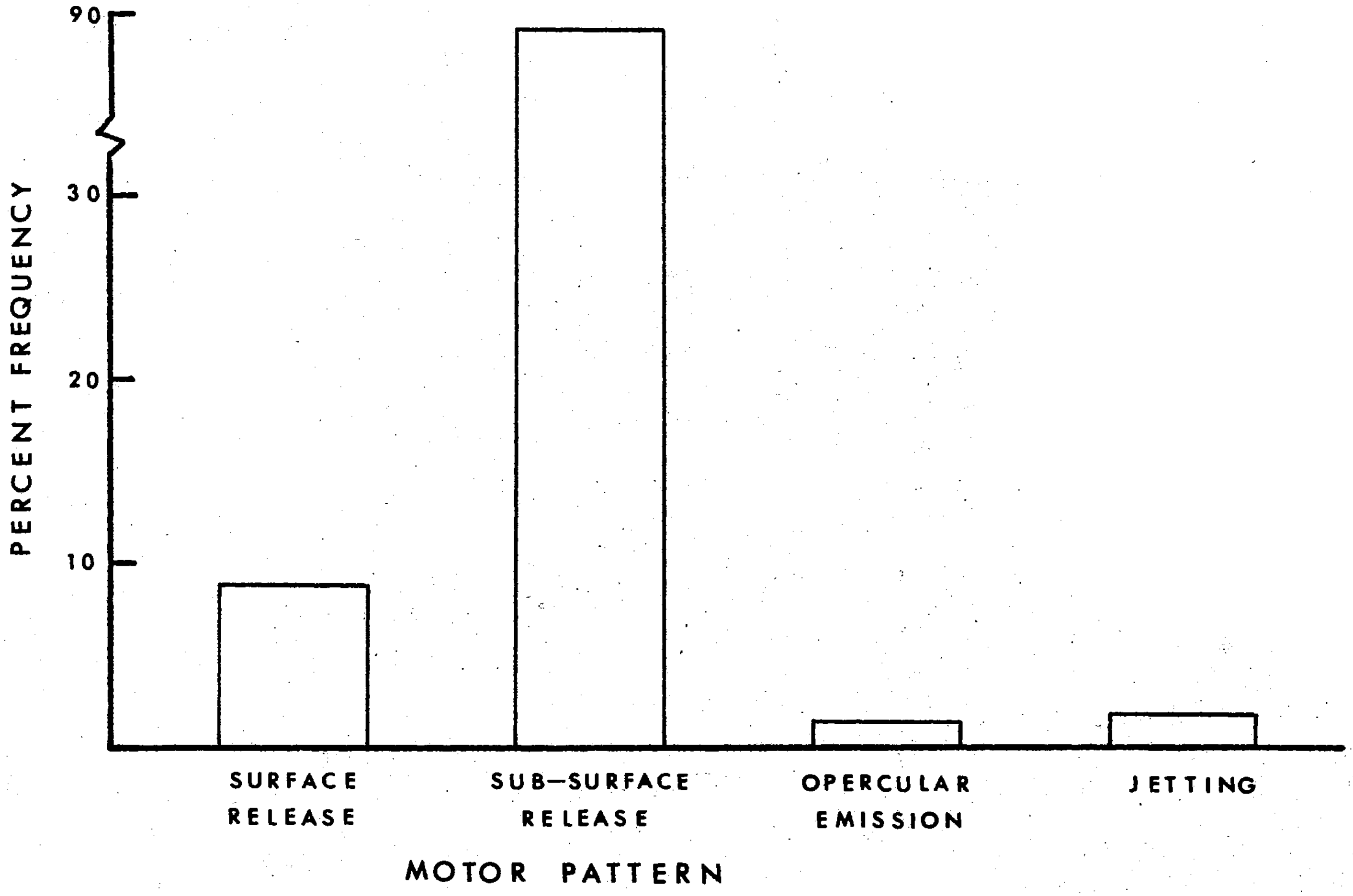


Figure 2. Percent Frequency of Motor Patterns Used in Nest Building

early stages of nest building (in the prespawning phase) although on several occasions it was recorded during the postspawning phase. This pattern consists of inspiration of air at the surface and then the expelling of short bursts of bubbles which form in shallow collections.

That surface inspiration with sub-nest release is of major importance in nest building in _T. pectoralis_ is easily seen from Figure 2. Sub-nest or sub-surface blowing accounts for 88.1 per cent of all bubble blowing in this species. Sub-surface blowing is typical of prespawning males and entails the gulping or snapping of air at the surface with movement to an area below the nest where clouds of small bubbles are released. This results in a deepening of the nest. Surface inspiration with sub-nest release may continue for several minutes without interruption as the male inspires, drops below the nest, expells bubbles, and then surfaces to repeat the process again and again.

Jetting, defined by Hall (1965) as emission of bursts of air and water through the nest, is rare (2.0 per cent) and was observed during the postspawning phase only. Jetting involves gulping of air from the surface movement to a spot below the nest and squirting air and water through the nest. Hall (1965) suggested jetting may provide a frothy nest for eggs and fry.

Opercular air emission is the most infrequently used method of bubble blowing (only 1.4 per cent) and consisted of emission of a few large bubbles from the opercles of prespawning and spawning males. When under the nest opercular emission probably aids in establishment of a deeper nest, although its significance as a factor in nest building is questionable due to its rarity and its occurrence far from the nest in some instances.

Nest Care During Spawning

During the spawning sequence there is much individual variation in nest care shown by T. pectoralis males. However, there do seem to be notable changes in behavior in periods before, during, and after spawning. Figure 3 presents data collected for frequency of air snapping trips and air snaps per trip from three spawning sequences and reflect changes occurring as the spawning sequence unfolds.

Generally, air snapping trips flucuate during the early part of nest building and tend to reach a peak prior to initiation of the spawning phase of the spawning sequence. A maximum of 34 air snapping trips was recorded prior to spawning.

A sharp increase in air snapping trips occurs just prior to the initiation of the spawning phase. During the spawning phase males are busy courting and spawning with females and except for rather hurried collections of eggs do not make many trips to the surface. With actual spawning concluded, a rise in air snapping trips occurs due to increased nest building activity. Males constantly search for and retrieve eggs for placement into the bubble nest, and continue to arrange and add to the nest.

A gradually decreasing trend in air snapping trips occurs next as the eggs are collected and compacted into a small thickened portion of the nest, which relieves the male of much additional bubble blowing. Consequently, more attention is directed toward protection of eggs from potential predators. By approximately 12 hours following the

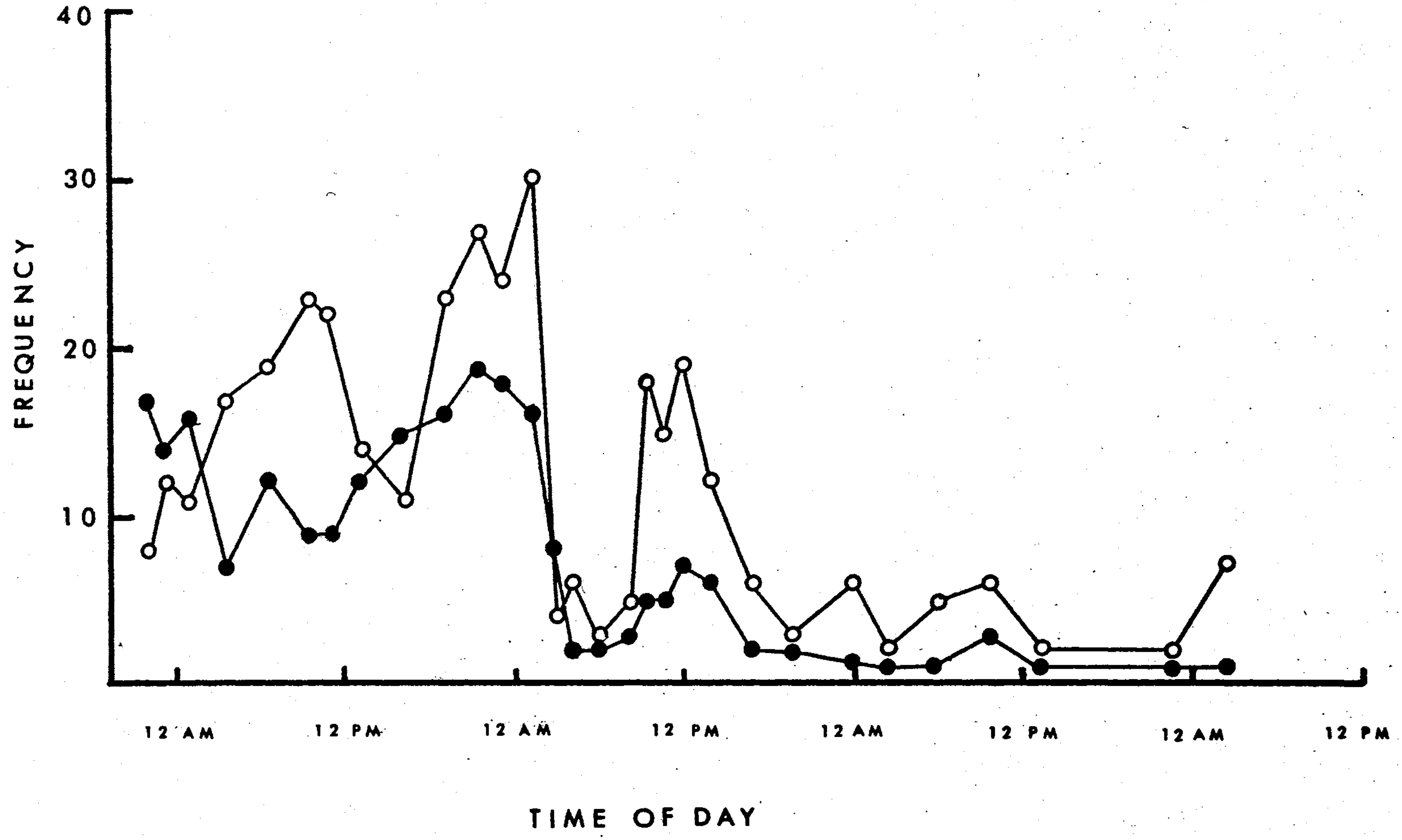


Figure 3. Average Frequency of Air Snapping Trips and Air Snaps Per Trip (open circles=air snapping trips, closed circles=air trips per snap)

spawning phase termination, few air snapping trips are made by guarding males.

Changes in air snapping occurring during the various phases of the spawning sequence are easily demonstrated: in three spawning sequences the mean frequencies for air snapping trips recorded for prespawning males were 17.4, 17.6, and 16.3. For males in the spawning phase the means were 5.5, 10.8, and 5.6. The relatively high value (10.8) was due to the inclusion of a frequency of 30 air snapping trips just after the beginning of the spawning phase. Mean frequencies of air snapping trips for the period after spawning was 5.2, 7.7, and 9.6.

When the three spawning sequences were averaged, the mean frequency of air snapping trips prior to spawning was 17.1, during spawning 7.2, and after spawning 7.4.

Air snaps per trip to the surface generally followed much the same pattern as air snapping trips, i.e., a maximum frequency occurred prior to the beginning of the spawning phase, followed by a decrease during the spawning phase, and another increase after the spawning phase. They then decreased gradually until they reached a relatively constant level.

Mean frequencies for the three spawning sequencies were tabulated for air snaps per trip. Frequencies during the period prior to spawning were 23.7, 13.9, and 14.8; during spawning, 6.8, 4.2, and 4.3; and after spawning, 16.0, 2.4, and 4.6. These data demonstrate the high variability of air snaps per trip among males, as well as the cyclic changes occurring during the sequence.

High initial frequencies prior to the actual spawning phase can be attributed to increased male nest building activity as he works on the nest. This activity is slowed considerably during spawning due to courtship and reproductive activities of the male, but then increases as he collects eggs and places them into the bubble nest.

CHAPTER VI

DESCRIPTIVE ANALYSIS OF COURTSHIP AND REPRODUCTIVE BEHAVIOR

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 pairs of *T. pectoralis* in aquaria.

Courtship and Prespawning Behavior

Courtship as used herein will refer to those activities that seem to attract and/or stimulate the spawning partner thus facilitating successful spawning (Miller, 1964). Most courtship activities are initiated and carried out by the male in *T. pectoralis*.

Acquisition of nuptial coloration in *T. pectoralis* usually is associated with establishment of a territory, increased aggressiveness, and nest building activity. In *T. pectoralis* territoriality and nest building during spawning appear to occur only in the male. Darkened nuptial coloration in addition to territorial behavior may function to render the male more conspicuous beneath the nest to the female. The female during this period remains hidden in the far corner of the tank away from the nest, usually at the bottom or in heavy plant growth if provided, surfacing rarely. Surfacing often elicits male attack. If the female is physiologically 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 after some movement by the female such as surfacing or feeding. During this period the male is primarily concerned with blowing bubbles, arranging them, and defending his new territory against intruders.

The nest is fairly well established before the male approaches more frequently to court the female. These initial approaches are rapid and direct and accompanied by partial to full median fin erection, terminating in lateral display, tail beating, or attack. Lateral display by the male may develop into a sigmoid posture followed by tail beating in some cases. 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 (1964) occur to give 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 non-reproductively motivated females may be severely beaten and killed if not removed due to restricted space preventing escape. During the study 17 females were killed by males.

Leading to the nest, described by Miller (1964) and prominent in *T. trichopetrus* 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. Her presence under the nest seems to inhibit male aggression. Return of the male to the nest area probably functions to locate the nest for the female. 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 (1964) suggested that behavior preceding spawning is 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 certain instances the smooth merging of courtship activities into spawning activities negates a sharp distinction.

Female approach is characterized by a rapid, direct movement up to the male under the nest and 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. Female butting is prominent in *T.*

pectoralis and precedes each spawning bout. A comparison of female butting between T. pectoralis and T. leeri is presented in Table II. As the female approaches, the male may give a lateral display. Female approach and butting probably functions in inhibiting male aggression by serving as a signal releasing behavior (LD) 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 (Hall and Miller, 1968). Picciolo (1964) reported that shape of fins, plumpness of the abdomen and general body form appear to be important sex recognition characters in Trichogaster species, although on several occasions plump female T. pectoralis were killed or severely injured by males. Examination of dead females showed the presence of many mature ova.

TABLE II

COMPARISON OF FEMALE BUTTING DURING SPAWNING BOUTS IN T. PECTORALIS AND T. LEERI

	T. leeri	T. pectoralis
Total Bouts	98	19
Total Butting Sessions	160	138
Total Number of Butts	2090	717
Avg. Number Butts/Session	13.06	5.19
Avg. Number Butts/Bout	21.32	37.74
Avg. Number Sessions/Bout	1.63	7.26

Occasionally female approach is halted by male approach followed by male aggression, and return of the female to the far corner or bottom of the tank. Strongly motivated females which remained under the nest while being repeatedly butted could eventually bring about a halt to male aggression. Fluttering (Hall and Miller, 1968) was observed for _T. pectoralis_ females while far away from the nest.

Female approach seems to be facilitated if the male orients so that the female does not have to approach head-on.

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 herein termed "rubbing position." Miller (1964) described a unique motor pattern for _T. trichopterus_ he 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. Males 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 (1968) also showed that during spawning bouts in _T. trichopterus_ the female continued to butt the male until rubbing position was achieved and clasping occurred. Rubbing position, ending in curving, lasts for 4 to 103 seconds, with an average duration of 30.2 seconds. Rubbing has an average duration of 70 seconds in _T. trichopterus_ (Miller, 1964). 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 (Miller, 1964).

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*. Rubbing position thus seems to be intermediate between no rubbing and 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 for 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. 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 (1968) 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 (1964) 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 peduncle 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 folded over that of the female with his head directed downward.

Just prior to egg release, quivering of the female's fins and body becomes most pronounced. Male ejaculation occurs several seconds after the roll is completed and occurs prior to egg release. No "terminal squeeze" (Hall and Miller, 1968) 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. A number of eggs (8-70) are released at the termination of each spawning bout.

Both male and female 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 (1957) 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 (Hall, 1966a), *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 might no longer be a need for the female to remain in a state of swimming inhibition longer than males. In most instances, the female regains her orientation first, then swims slowly from the nest area 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.

No qualitative differences could be discerned between spawning and pseudospawning bouts, except the presence or absence of gametes at the termination of the bout itself. Miller (1964) has theorized that pseudospawning and spawning are identical in motivation, the only difference being that no ripe eggs are present in a suitable position in the female reproductive tract in pseudospawning. Pseudospawnings tend to occur in the early stages of the spawning phase or near the termination of this phase. Miller (1964) suggested the reason for this was in the early stages of the spawning phase ripe eggs are probably not yet present in the ovary while near the end of the phase the lumen may have been emptied.

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 larvae and wriggling larvae are retrieved when they fall out of or stray from the nest area and are transported back to the nest into which they are placed by the male.

Forselius (1957) listed two successive actions during the male's collection of fry and eggs: (1) approach released by visual stimuli from the egg or fry as it falls, which is then (2) engulfed and tested chemically and/or tactually in the mouth. He further asserts that depending on the chemical and 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 and subsequently returned to the tank, away from the nest area along with food particles. In every case the eggs were collected and returned to the nest while food was sometimes eaten. There is a long-standing belief among some aquarists that anabantoids will not eat during care of the nest, eggs, or fry, and it is this inhibition of feeding motivation that is responsible for the male not eating the eggs or fry. This idea was repeatedly proven incorrect as live *Daphnia* were provided to the pair just hours after the spawning sequence and were greedily eaten, as were commercial dried foods.

Miller (1964) in *T. trichopterus* found nesting activity *per se* was greatest immediately before and after spawning, but longer after spawning when eggs and young were present in the nest. From Table III it can be seen that duration per occurrence under the nest is approximately the same in spawning and prespawning phases, 32.6 seconds and 31.8 seconds respectively, increasing to 36.8 seconds during the postspawning phase. 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 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 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.

TABLE III

AVERAGE DURATION SPENT UNDER NEST DURING THREE SPAWNING PHASES

	Prespawning	Spawning	Postspawning
Total Duration Under Nest (sec.)	2773	1881	7039
Times Under Nest	85	59	191
Average Duration Per Time 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

Some Quantitative Aspects of Spawning

Five spawnings were observed during the two year study; however, quantification of complete spawning sequences is available for only three. General quantitative data are shown in Table IV while bout category analysis is shown in Table V.

Spawning sequences in T. pectoralis averaged 140.67 minutes. This is a bit surprising as the duration is quite short for anabantoid spawning sequence durations. All spawning occurred between 10:00 A.M.

TABLE IV

GENERAL QUANTITATIVE DATA ON COURTSHIP AND REPRODUCTIVE BEHAVIOR IN T. PECTORALIS*

	T. pectoralis
Total Number of Bouts	211
a. Male Initiated	145
b. Percent of Total Initiated by Male	68.72
c. Female Initiated	66
d. Percent of Total Initiated by Female	31.28
Total Duration of All Bouts (Seconds)	8443
Average Bout Duration (Seconds)	40.01
Total Duration of Spawning Sequences	
a. Minutes	423
b. Seconds	25363
c. Average Duration Per Complete Spawning Sequence (Minutes)	140.67
Average Number of Spawning Bouts/Spawning Sequence	6.3
Average Sexual Bout Duration (Seconds)	67.89
Average Psuedospawning Bouts/Spawning Sequence	3.3
Average Clasp Bouts/Spawning Sequence	3.0
Total Interval Duration Following Bouts (Seconds)	16920
Average Interval Duration Following Bouts	
a. Minutes	1.13
b. Seconds	73.74

*Based on 3 complete spawning sequences in *T. pectoralis*

TABLE V

BOUT CATEGORY ANALYSIS OF SEXUAL BOUTS IN *TRICHOGASTER PECTORALIS*

1. Total Number of Bouts	211
a. Average number of bouts per spawning sequence	70.33
2. Total Number of Spawning Bouts	19
a. Male initiated	2
b. Female initiated	17
c. (male and female) percent of total bouts	9.00
3. Average Duration of Spawning Bouts (Seconds)	263.60
4. Total Number of Pseudospawning Bouts	10
a. Male Initiated	2
b. Female Initiated	8
c. (male and female) percent of total bouts	4.74
5. Average Duration of Pseudo-spawning Bouts (Seconds)	251.33
a. Male initiated	231.67
b. Female initiated	259.72
6. Total Number of Clasp Only Bouts	9
a. Male initiated	1
b. Female initiated	8
c. (male and female) percent of total bouts	4.21
7. Average Duration of Clasp Only Bouts (Seconds)	279.75
a. Male initiated	263.00
b. Female initiated	293.33
8. Total Number of Courtship Only Bouts	51
a. Male initiated	28
b. Female initiated	23
c. (male and female) percent of total bouts	24.12

TABLE V (continued)

9. Average Duration of Courtship Only Bouts (Seconds)	29.06
a. Male initiated	12.45
b. Female initiated	59.50
10. Total Number of Aggression Only Bouts	55
a. Male initiated	49
b. Female initiated	6
c. (male and female) percent of total bouts	26.06
11. Average Duration of Aggression Only Bouts	5.92
a. Male initiated	3.06
b. Female initiated	8.78

and 5:30 P.M. The longest spawning sequence was 2 hours and 57 minutes.

Males initiate almost 69 per cent of all bouts during the spawning sequence, compared to about 31 per cent initiated by females. Average sexual bout duration was 68.89 seconds. Rubbing position, unique in T. pectoralis, prolonged sexual bout duration just as rubbing in T. trichopterus prolongs sexual bout duration (Hall, 1965). Average interval duration following bouts was 73.74 seconds. This short interval helps explain the shorter spawning sequences in T. pectoralis as the bouts themselves are quite long.

The average number of bouts per spawning sequence was 70.33. Of this figure 9 per cent were spawning bouts. An average of 6.3 spawning bouts were recorded per spawning sequence. The importance of female receptivity and physiological readiness to spawn is obvious as 88.8 per cent of all spawning bouts were initiated by the female. As with T. leeri (Miller and Hall, 1968) female initiated bouts tend to contain more of the activities associated with the terminal act of spawning and are therefore considered more successful.

Average duration of the spawning bouts was 263.60 seconds, longest of any species of Trichogaster.

Pseudospawning bouts during the spawning sequence were rare, comprising less than 5 per cent of all bouts. Average duration of pseudospawning bouts was 259.72 seconds.

Females initiated 88.89 per cent of the clasp only bouts which comprise only 4.2 per cent of all bouts and have an average duration of 243.33 seconds.

Table VI shows the average clasp duration in spawning, pseudospawning, and clasp only bouts. Clasp duration in spawning bouts averages 60.8 seconds versus 68.5 seconds in pseudospawning bouts. A pronounced decrease is seen between clasp duration in these bout types and in clasp only bouts in which clasp duration averages 19.3 seconds. This would be expected because of the incomplete nature of clasp only bouts.

TABLE VI

AVERAGE DURATION AND AVERAGE CLASP DURATION IN SPAWNING, PSEUDOSPAWNING AND CLASP ONLY BOUTS IN _T. PECTORALIS_

	Avg. Duration (Sec.)	Avg. Duration of Clasp (Sec.)
Spawning Bouts	263.6	60.8
Pseudospawning Bouts	251.3	68.5
Clasp Only Bouts	279.8	19.5

In _T. pectoralis_, courtship only bouts comprise 24.12 per cent of all bouts during a spawning sequence, and are initiated about equally by male and female, although the male initiates slightly more. Male initiated bouts are much shorter (12.45 seconds) than are female initiated bouts (59.50 seconds). Hall (1965) ascribed these shorter male initiated bouts to the fact that males exhibit rapid return to nest care, bubble blowing, and defense of territory if the female does respond appropriately.

Aggression only bouts are initiated mainly by the male and comprise 26.06 per cent of all bouts, a major portion of the spawning sequence. These bouts are usually brief when male-initiated (3.06 seconds) but are of longer duration if female-initiated (8.78 seconds). Aggression only bouts consist of butting or biting, chasing, mouth fighting, tail beating, or other agonistic behaviors.

Postspawning Agonistic Behavior

Table VII shows male-female postspawning agonistic behavior while the male is continuing to guard the nest. Male approach, having threat value, constitutes the most frequent agonistic behavior. Any movement by the female elicits approach by the male and usually subsequent attack by him. Biting is usually quite severe in postspawning encounters and females were often removed to prevent their death. Male chases are quite common, often triggered by female surfacing, while lateral displays were rare.

Females approach males rarely, except in situations where mouth fighting is involved and in such cases the male has entered the female's shelter area and usually initiated the encounter. Each movement forward (pendulum movement) was regarded as an approach in such instances. Female biting is rare and no chasing of a male by a female was ever seen. Appeasement by females is quite common in male-female postspawning encounters, but in some instances even appeasement is not sufficient to reduce male aggression. In nature, of course, females could conveniently escape such male aggression because of the proximity of dense vegetation coupled with the fact that males do not wander far from the nest area during postspawning phase.

TABLE VII

AGONISTIC ACTIVITY OF MALE AND FEMALE <u>T. PECTORALIS</u> DURING POSTSPAWNING PHASE

Sex			Approach	Chase	Butt/Bite	Lateral Display	Appeasement
Male	S-1	A*	30	11	78	0	-
		B	55	3	8	2	-
		C	2	2	3	0	-
		D	5	0	0	0	-
		E	26**	0	0	0	-
	S-2	A	1	1	12	1	-
		B	6	3	21	0	-
		C	4	0	0	0	-
		D	3	2	1	2	-
		E	13	5	6	1	-
	S-3	A	3	0	0	0	-
		B	27	2	3	2	-
		C	5	1	1	0	-
		D	0	0	0	0	-
		E	2	1	0	1	-
Female	S-1	A	0	0	1	4	7
		B	0	0	1	0	1
		C	0	0	0	0	0
		D	3	0	0	3	0
		E	17**	0	0	3	0
	S-2	A	0	0	0	0	1
		B	0	0	0	8	5
		C	1	0	0	0	0
		D	0	0	0	0	0
		E	3	0	0	3	1
	S-3	A	0	0	0	0	0
		B	11	0	0	4	1
		C	0	0	0	3	0
		D	0	0	0	0	0
		E	0	0	0	0	0

*A,B,C, etc., represent 15 min. observation periods; S-1, etc. are spawning sequences.

**Mouth fights.

CHAPTER VII

COLOR CHANGES IN T. PECTORALIS

Reproductive Color Changes

Reproductive color changes in teleost fishes are well-documented in the literature, having been described for *Trichogaster trichopterus*, (Miller, 1964), *T. leeri* (Hall, 1966b), *Badis badis* (Barlow, 1962) and several cichlid species by Baerends and Baerends-van Roon (1950) among a host of others. Forselius (1957) surveyed color changes in several additional anabantoid species. Reproductive color changes resembles agonistic color changes in these species, except that the former are usually more intense. Functional implications of many of these color changes are unknown (Hall, 1965).

Picciolo (1964) reported that visual cues are important factors in sex and species discrimination in *T. leeri*, *T. trichopterus*, and *T. pectoralis*. He noted that males exhibited aggressive behavior towards males and courtship behavior towards females in 80 to 100 per cent of the tests, except for *T. pectoralis* in which the values were 70 per cent aggressive behavior towards male stimulus animals and 53 per cent courtship behavior towards female stimulus animals. Unfortunately, he had only five individuals on which to base his statements about *T. pectoralis*.

That visual cues are not the only important stimuli for sex recognition is indicated in a study by Mainardi and Rossi (1968) on chemical communication in Colisa lalia. They found that when pairs were in chemical communication with each other, all of a group of 13 males assumed typical courtship coloration and built bubble nests. When 13 pairs had only visual communication with each other, males neither assumed courtship coloration nor built bubble nests. Chemical stimulation from the female thus seems to be a strong stimulus for the development of reproductive coloration in male C. lalia. However, many observations have been made in which reproductive coloration and bubble nest building have occurred in the absence of visual and/or chemical contact. Such was not the case in T. pectoralis, as males never assumed nuptial coloration or built nests in the absence of females. Even when females were placed within sight of the male no bubble nests were ever built, although darkening did occur.

Forselius (1957) indicated that species discrimination might be based on female recognition of conspecific male coloration in his studies on members of the genus Colisa. The same situation probably occurs in the genus Trichogaster where males of the four species exhibit great dissimilarities in nuptial coloration ranging from very slight changes in T. microlepis to pronounced changes in T. leeri. Unlike Colisa females, however, Trichogaster females do not show great intrageneric similarity, but instead are quite different in coloration.

No description is as yet available on reproductive color changes of T. pectoralis. While not as strikingly colorful as certain other Trichogaster species, T. pectoralis nevertheless undergoes marked changes in coloration during the reproductive cycle and these changes are useful indicators of the motivational states of the participants.

The following is a description of the reproductive color changes which occur in male and female _T. pectoralis_ at the onset of spawning. Figure 4 illustrates color patterns in _T. pectoralis_ under various conditions. Numbers below correspond to numbers in Figure 4.

Male Nuptial Coloration

1. Eye Color

At the time of spawning the eye of the male becomes uniformly dark black. The non-breeding male possesses a light eye traversed by a dark semi-vertical band (Figure 5). The band persists in the spawning male but it is much more intense in the breeding than non-breeding male. Eye color is a good indicator of social rank in non-breeding males and females, with subordinate fish having the darker eyes.

2. Cheek Color

The lower portion of the operculum below the eye becomes extremely dark from the posterior edge of the operculum anteriad nearly to the lower lip. A small light area exists between the lower lip and the cheek coloration.

3. Lip Color

There is a decided increase in dark pigmentation on the edges of the lower and upper lips. Immediately anteriad of the eye is a continuation of the lateral band through the eye and onto the snout

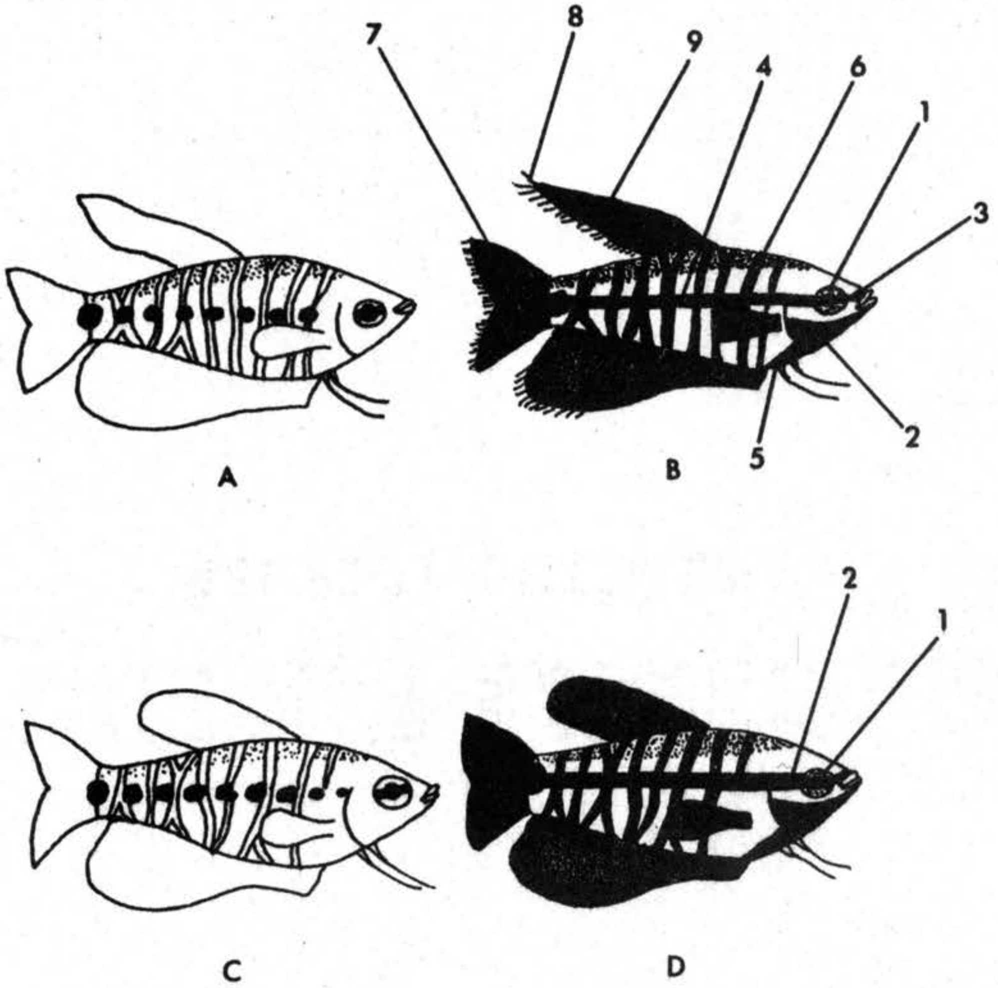


Figure 4. Structural, Body Marking and Color Changes in T. pectoralis (A=non-breeding male, B=breeding male, C=non-breeding female, D=breeding female)

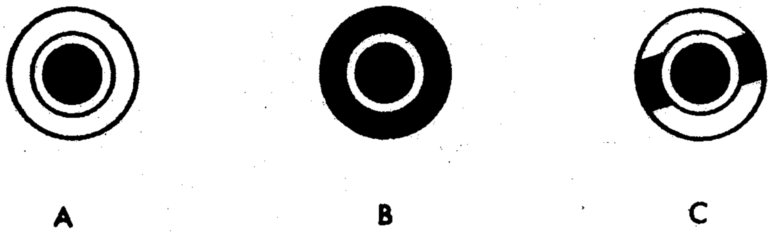


Figure 5. Eye Color Patterns (A=fright, B=agonistic and reproductive, C=normal) in *T. pectoralis*

and upper lip. No such coloration exists in non-breeding males or females.

4. Lateral Band

In the non-breeding male the lateral band consists of many separate black blotches of pigment running horizontally from the caudal peduncle onto the operculum to an area behind the eye. In breeding males, these blotches intensify and join to form a solid darkened lateral band running from the caudal ocellus (which can not be differentiated) to the rear of the eye.

5. Gular Coloration

Breeding males acquire a deep purplish-black color on the gular and upper breast regions. This is a continuation of the cheek darkening. Intensity varies, but this area is usually quite dark and remains so throughout the spawning phase and care of fry in the post-spawning phase.

6. Vertical Reticulations

In the non-breeding male and female there are faint vertical reticulations termed "snakeskin" markings on the lateral surfaces of the body, hence the name snakeskin gourami. These black, vertical anastomosing lines increase in intensity during the reproductive cycle and are distinctly seen running the entire length of the body except for the head region and caudal fin.

7. Caudal Ocellus

A basi-caudal ocellus is present on the caudal peduncle in all *T. pectoralis*, except in the fear pattern (Figure 6). The ocellus darkens and enlarges slightly in breeding males and females. Smith (1945) in his key to the species of *Trichogaster* states "no round black spot.... on the caudal peduncle." This is inexplicable as *T. pectoralis* has a caudal ocellus as large or larger than *T. trichopterus*. This observation perhaps may have been due to the poor condition of Smith's specimens.

8. Dorsal, Anal, and Caudal Extensions

Filamentous extensions of the soft rays of the dorsal and anal fins are characteristic of spawning *T. pectoralis* as they are for spawning *T. leeri* males (Hall, 1965); however, no one has described caudal fin extensions. These are short extensions of the caudal rays easily seen in breeding males. The extensions usually disappear at or near the end of the spawning cycle, although in males that have never spawned, the extensions remain for many weeks. Although the functional significance is unknown, the growth of these extensions is presumedly related to increased mitotic rate resulting from increased gonadal hormone level (Bullough, 1961). If this is true, it indicates the long durations male *T. pectoralis* are able to remain in reproductive readiness in aquaria.

9. Fin Color

All fins darken greatly in breeding males and females. The anal fin is perhaps the most striking, as the upper portion is a velvety blue, edged ventrally with an amber hue. All other fins are dark blackish. In non-breeding individuals, all fins are clear, except for several whitish-blue spots on the median fins.

Female Nuptial Coloration

Non-breeding female T. pectoralis are marked similarly to non-breeding males.

1. Eye Color.

Uniform darkening of the eye and orbit accompanies onset of breeding condition. The eye of the female is extremely dark, more so than the male.

2. Lateral Band

During spawning the separate blotches of black pigment which loosely form a horizontal band in non-breeding fish intensify to form a solid lateral band extending from the caudal ocellus to the eye and forward onto the snout.

Non-reproductive Color Changes

Fright Coloration

Extreme blanching results when a fish is placed into a new situation, startled, or otherwise disturbed. Figure 6 illustrates the resultant condition. All fin color is lost, along with the lateral blotches and caudal ocellus. Vertical reticulations are more prominent, probably because of the fading of other colors. The eye

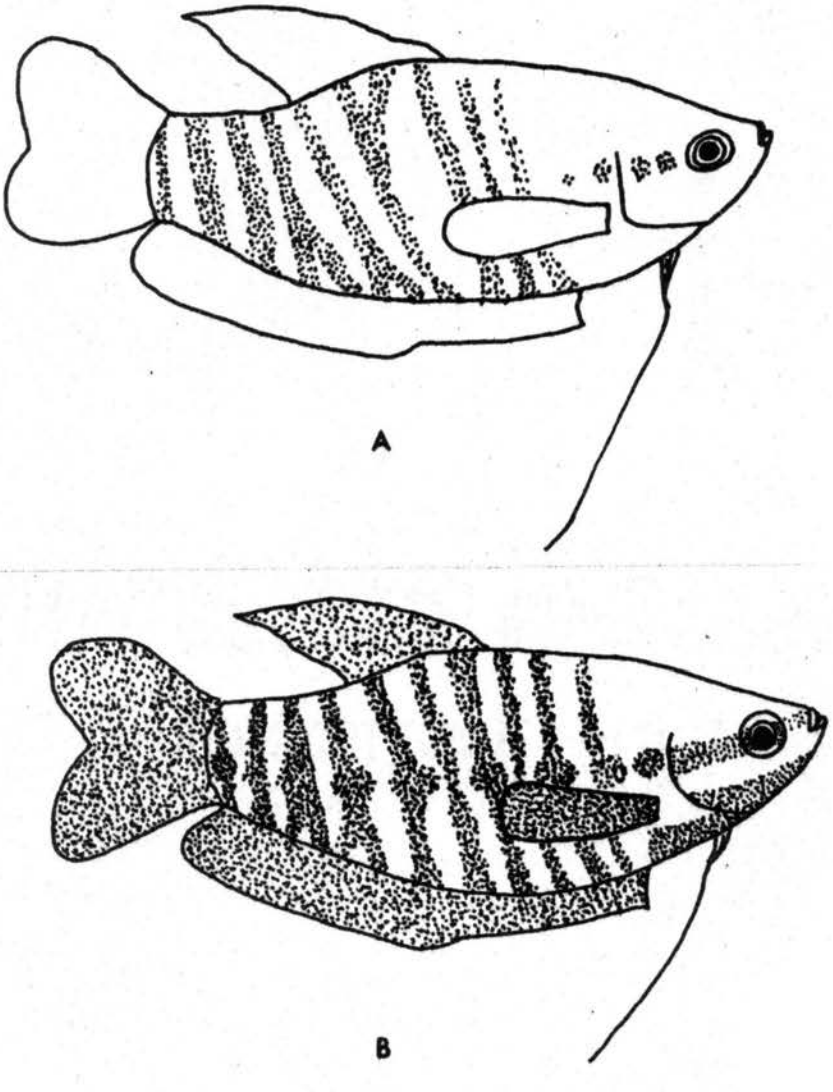


Figure 6. Fear and Agonistic Color Patterns Exhibited by T. pectoralis (A=fear, B=agonistic coloration)

is a key indicator of the motivational state of the fish. In fright the eye blanches entirely, except for the dark pupil (Figure 5).

Agonistic Color Changes

Although agonistic and reproductive color changes are probably mediated by the same neural mechanisms, certain discrete color changes occur during boundary fighting and dominance encounters in *T. pectoralis* which differ from reproductive patterns to a slight degree.

During male-male encounters in which intense fighting occurs, males darken as they do in the reproductive cycle. Darkening of fins and eyes, intensification of vertical reticulations, and gular and cheek darkening remain as long as the bout lasts and sometimes persist much longer if the two males occupy adjacent territories. In highly aggressive males which have fought for a considerable time, the lateral blotches which occur in the non-reproductive state fade completely leaving only the most faint indications of its former presence. As the body darkens, a concomitant loss of the caudal ocellus occurs while vertical reticulations intensify. This is quite different from reproductive coloration in which the lateral blotches fuse forming a solid dark lateral band. The same changes occur in females in similar situations. This type of darkening is not limited to *T. pectoralis*. *T. trichopterus*, usually silvery with a dark spot on the side and a basi-caudal spot, undergoes similar color changes in aggressive situations in which the dark lateral spot and caudal ocellus disappear, being replaced by dark blue vertical reticulations, which cause it to look a great deal like *T. pectoralis*. These color changes in aggressive encounters in *T. trichopterus* perhaps may be indicative of close phylogenetic relationship between T. pectoralis and T. trichopterus.

With the darkening of body structures and areas, a condition exists in fighting T. pectoralis which is almost exactly like the color changes in fish that are frightened (loss of lateral band and caudal ocellus). This suggests that the neural mechanisms which mediate fear may play some role in agonistic behavior and that even the most aggressive individuals exhibit some fear of the opponent. When encounters are settled, coloration of subordinates quickly return to the non-reproductive condition.

CHAPTER VIII

DYNAMICS OF PARENTAL BEHAVIOR AND DEVELOPMENT OF THE YOUNG

Parental behavior is defined herein as the behavior used in the care and protection of the eggs, larvae, and fry by the male, commencing with the collection of the eggs after the initial spawn and continuing until the fry are free swimming several days later. Nests are deserted by males after a variable length of time, usually about eight days. Females take no active part in parental care, instead remain far from the nest and the male protector. No instance of female predation of eggs was recorded.

Search, Approach, and Collection of Eggs

Upon completion of the clasp both male and female enter a period of swimming inhibition in which the pair, still enjoined, sink slowly toward the bottom. The male maintains his head in an upward position during this period within 1-2 centimeters of the body of the female. Number of eggs released prior to swimming inhibition varies from 10-80. The eggs are yellowish and buoyant, thus floating to the surface after oviposition, unless influenced by the current caused by the moving fins of one or both parents.

Before complete recovery from swimming inhibition, the male makes futile attempts to bite the female, often while still trying to right himself. The female usually recovers first and swims away rather swiftly. The male may attempt to chase the fleeing female, but usually remains near the nest gathering eggs. Sometimes egg collection is begun prior to full recovery from swimming inhibition.

Collection of eggs is a rather simple process and occurs when the male opens his mouth maximally, drawing in eggs and water into the buccal cavity. This type of collection usually occurs at the surface and looks much like feeding. In retrieval of mid-water eggs the male approaches each egg and engulfs it as in feeding on sinking food particles, then places the eggs into the nest. A mucous coating formed in the mouth serves as a foam covering of the nest. On several occasions as many as 12 eggs were collected by the male, who then approached the female in the far corner, lateral displayed, and butted her before returning and placing the eggs in the nest. Eggs which drifted away from the nest were subsequently searched for and found, then placed in the nest.

Placement of Eggs in the Nest and Subsequent Nest Care

Placement of the retrieved eggs occurs when the male swims beneath the nest and thrusts his snout and mouth into the bottom part, releasing eggs into the lower portion of the nest. He then either surfaces for air, submerges to spray bubbles from a position below the nest, or continues egg collection. In _T. pectoralis_ this placement area is usually in a thickened portion of the bubble nest. Some eggs were observed up to two centimeters above the surface of the air-water interface in this thickened area of the nest.

Jetting is rare in T. pectoralis. In several cases air is snapped after the eggs have been retrieved and air bubbles are released into the nest with the eggs.

Once in the nest the eggs are enclosed in foam bubbles which have a rather short existence and have to be constantly replaced. Occasionally a few eggs float freely in the nest and are subsequently disturbed by the fanning action of the pectoral fins of the male or dislodged when the male is frightened. If eggs do become dislodged the male gathers them and returns them to the bubble nest.

The incubation period for T. pectoralis is 18-28 hours. The most rapid maturation occurred within 18 hours at a surface temperature of $82^{\circ}F$, the slowest occurred within 28 hours at $80^{\circ}F$.

After hatching, the larvae are in the wriggling stage and movement for any distance is impossible due to the lack of differentiated fins, presence of yolk sac and hydrostatic organ. Larvae can be seen sinking slowly, then spurting back towards the nest or surface. These jerky movements attract the attention of the male and he takes the larvae into his mouth, and places them in the nest. By the third day a mass of grayish-black tails can be seen hanging from the nest with their tails forming a 90° angle with the surface.

An interesting behavior quite common in T. pectoralis males was snail biting. This behavior was not common in males except during the postspawning phase when eggs were in the nest. Any snail that was in the vicinity of the nest was attacked and vigorously bitten, causing the snail to fall to the bottom. As the snail sank, males often bit or attempted to bite the falling snail 1-6 times on the way down. In some cases males did not bother the snail once it began to fall. This behavior probably has considerable significance in nature as a means of protecting eggs against predation by snails and other macroinvertebrates that might crawl through the vegetation in an effort to feed on the floating eggs.

During the first week the nest deteriorates rapidly unless constantly replenished by bubbles, and the young at this time are becoming free swimming, although excursions of any distance are still impossible. Instead, a jerky motion, followed by a slow sinking followed by another spurt forward characterize their travel. Many young are seen at the end of the first week lying among the vegetation or attached to the sides of the tank. By this time (8-9 days) the nest is usually gone.

After the free swimming period, there are no definite schools, but aggregations do form and swim around the surrounding area. As Forselius (1957) has noted in some anabantoid species, "the school breaks up and the young males begin to live more or less completely on their own." Since sexual differentiation is impossible in _T. pectoralis_ fry, no comment can be made verifying his observation although individuals do leave the loose grouping and begin to search for food, etc., on their own, coming together thereafter only when frightened.

Activities Directed Toward Larvae, Young, and Conspecifics

Males remained on guard beneath the nest orienting toward any movement inside or outside the tank. When orienting toward a movement all median fins were erected, with pelvics thrust outward in the direction of the disturbance. Males exhibited extreme aggression, attacking any object placed near the bubble nest. In one instance a thermometer was being lowered next to the nest for determination of surface temperature when the male approached and bit it, almost knocking it from the hand of the observer. This same response occurred when trying to retrieve eggs for observation. In an effort to determine how far the male would go to defend the nest, two fingers were inserted in a small opening at one corner space of the glass cover, a distance of about eight centimeters from the nest periphery. The fingers were waved menacingly over the nest. During this time the male has oriented toward the fingers. The male approached the fingers with fins spread, pelvics outstretched, and suddenly leaped out of the water through the open space and onto the floor. He was promptly returned to the tank where he assumed his guard duties after regaining orientation in the tank without any apparent harm. The next morning the entire bubble nest and contents had been moved further toward the rear of the tank.

An intruder fish, _Poecilia reticulata_, was introduced into the tank to determine if interspecific aggression was exhibited by _T. pectoralis_. The new addition was quickly and decisively chased from the nest area. The chase of the new addition was repeated several times.

Male _T. pectoralis_ guarded the bubble nest even when the nest was shifted to a different location in the tank. Strict territoriality is maintained by the male up to six to eight days after spawning. In this period conspecifics and other species are prevented from approaching the nest area. In two cases the female was removed two days after spawning to prevent her death from attacks by the aggressive male. Her anal fin, caudal fin, and the area above the anal to the caudal was severely mauled. During this time the female is almost totally restricted in movement and is attacked even when surfacing.

Females were never seen to eat eggs as Wimmer (1970) recorded for T. microlepis and Miller (1964) for T. trichopterus; however, strong attacks by the male may be more inhibitory in T. pectoralis. Unlike T. microlepis males, T. pectoralis males have no difficulty removing any and all intruders from the nest area at top speed.

Chronological Appearance of Coloration

Young T. pectoralis are strikingly different in appearance and coloration from adults. The following represents the chronological appearance of coloration in young T. pectoralis (Figure 7).

4-7 mm

Upon hatching, larvae exhibit a characteristic silver-gray body coloration with the beating heart and dark eyes their most readily distinguishable features. A small patch of melanophores is present on the caudal peduncle forming a clearly visible dark ocellus. Body myomeres are eaily seen, and the mouth is well defined. Fins lack differentiation and yolk sac is still present.

8-12 mm

This second stage is most significantly marked by the appearance of the future lateral band eminating from the caudal ocellus and extending anteriad to about the region of the posterior edge of the dorsal fin. The eye, while still a strong feature, no longer completely dominates the appearance of the fish because of the growth

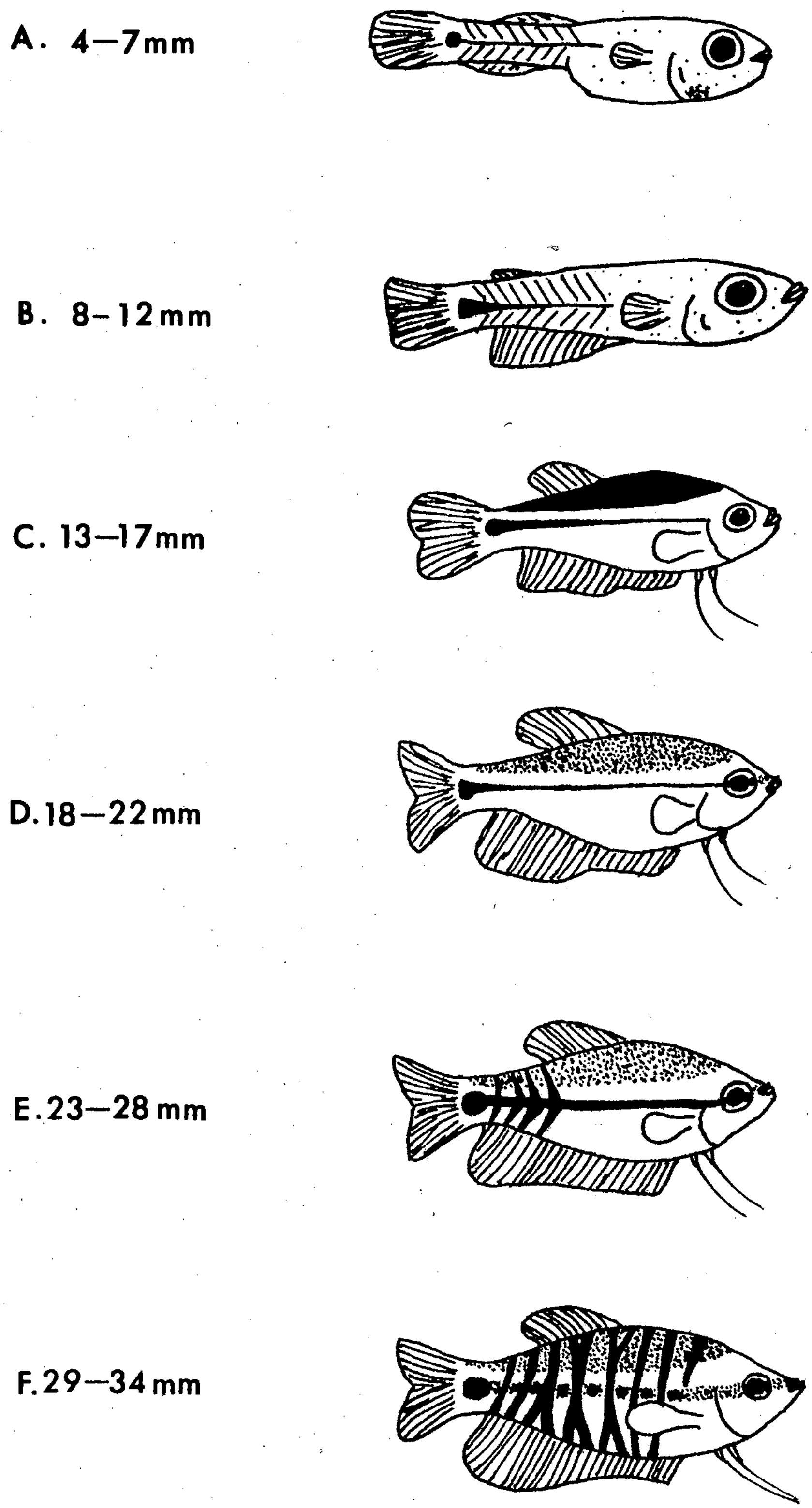


Figure 7. Chronological Appearance of Coloration in Young T. pectoralis

of the rest of the body. Myomeres can still be seen but pelvic threads are as yet inconspicuous. The belly is silvery while fins are colorless.

13-17 mm

The lateral band extends completely to the operculum. Pigment occurs on the lips. The dorsum takes on a dark,olive-brown coloration while the belly remains silver as does the area directly above the dark lateral band and ventral to the dorsum. Pelvic threads are now visible, though still short. Reddish gills show through the operculum. The pupil of the eye is black, though no stripe through the eye is yet noticeable. Fins remain colorless.

18-22 mm

The dark dorsolateral area lightens somewhat, but this area still remains darker than the rest of the body. The caudal ocellus becomes more difficult to see as the lateral band darkens and extends forward onto the opercle and snout. Pelvic threads are easily seen.

23-28 mm

Vertical reticulations appear at this size. They first occur on the caudal peduncle and extend dorsally and ventrally. Reticulations extend anteriad on the lateral area of the body from the caudal ocellus, which at this time is difficult to distinguish from the lateral band, to a position at the rear of the dorsal fin.

29-34 mm

Vertical anastomosing reticulations occur the entire length of the body. The caudal ocellus is not distinguishable from the lateral band which extends onto the opercle through the eye and onto the snout. The anal fin takes on a mottled appearance with whitish spots scarcely recognizable.

35 mm and over

Fish of this size possess a lateral band composed of patches of dark pigment. The caudal ocellus has become nothing more than another black blotch of dark pigment. Vertical reticulations remain, as does the olive dorsum. Slight dark pigment can be seen on the opercle, through the eye and onto the snout. This coloration may be thought of as "adult coloration."

It should be remembered that these are arbitrary divisions decided upon by the observer. Size ranges for these pattern changes may vary somewhat depending on conditions under which the fish are kept and raised. One important aspect is the fact that this development of coloration depends greatly on development of the fish itself and not on its age *per se*. In experiments to deliberately keep certain individuals stunted, some fish retained the pattern of an earlier stage when actually a year old. This points out the difficulty of basing many of the color phases on age when size seems to be of primary importance. This should be considered in descriptions of animals such as "10-15 days old."

CHAPTER IX

DIEL ACTIVITY PATTERNS IN *T. PECTORALIS*

Many biological phenomena recur at regular intervals in both plants and animals and are referred to as biological rhythms (Darnell and Meierotto, 1965). The most frequently occurring biological rhythm is the diel or circadian rhythm (Harker, 1958; Darnell and Meierotto, 1965). Diel rhythms of fishes have been studied by relatively few investigators (Deacon and Wilson, 1967) and most of these studies have dealt with activity periods for particular species (Spencer, 1939; Carlander and Cleary, 1949; Hasler and Villemonte, 1953; Hobson, 1965; Darnell and Meierotto, 1965; and Deacon and Wilson, 1967). Generally, studies on fishes have been conducted in the wild using traps of some type and extrapolating activity patterns from per cent of captured populations. There have been relatively few attempts to bring animals into the laboratory under conditions where qualitative and quantitative data on their behavior could be acquired. Under such conditions fishes have been shown to exhibit periodicity in movement (Spencer, 1929, 1939), feeding (Childers and Shoemaker, 1953), and oxygen consumption (Clausen, 1936; Spoor, 1946).

Since field studies were not feasible in this study, the following laboratory study was conducted. Fish were conditioned six months on a 12 hour electronically controlled photoperiod. The only light during the darkened hours was a small covered lamp facing downward which supplied light to a Daphnia tank. This would probably be equivalent to moonlight in their natural habitat. Hobson (1968) concluded that total darkness was an atypical situation in studies on marine fishes and this assumption is probably true in most aquatic habitats.

Diel activity patterns have recently come under investigation in anabantoid fishes. Hopkins (pers. comm.) reports a diurnal and nocturnal activity rhythm in aquaria for T. trichopterus. Wimmer (1970) found a diel rhythm in T. microlepis. The data reported below represent observations on the activity patterns shown by T. pectoralis. Frequencies and durations of various behaviors were described in Chapter II.

If there were no significant differences among replicates, the data was averaged and a single mean value was plotted for each observation time. Significant differences among observation times ($p<.05$) indicated that there was a time effect whereby the fish were not performing the behavior equally at all observation times but exhibited definite differences in frequency or duration of the behavior at different observation times. If there were no significant differences among observation times, this indicated that the behaviors were being performed approximately the same in frequency or duration at all observation times.

Frequency of patrolling behavior showed significant differences among replicates ($p<.05$) and observation times indicating a definite time effect. Patrolling frequencies were thus presented for each replicate. Patrolling frequency (Figure 8) exhibits much variation between replicates in the early morning hours (0600) varying from

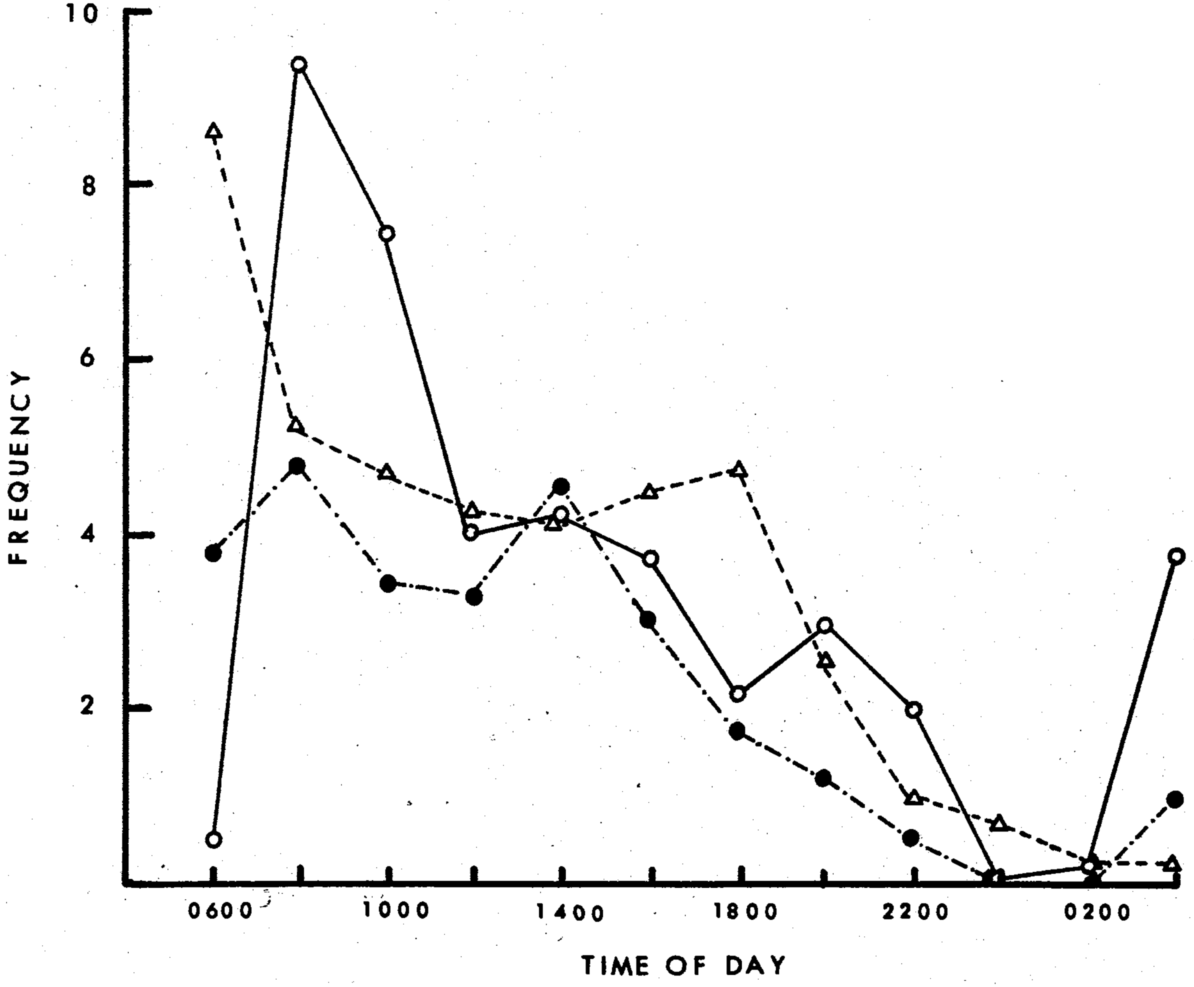


Figure 8. Average Frequency of Patrolling Behavior (open circles=replicate one, triangles=replicate two, closed circles=replicate three)

0.5 patrols/10 min. to 8.8 patrols/10 min. A range of from 4.8 patrols/10 min. to 9.5 patrols/10 min. occurred at 0800. A definite decrease in patrolling activity is noted from 0800 to 1000 continuing until 1200 followed by a slight increase from 1200 to 1400. After 1400 a general decreasing trend in patrolling frequency is seen until darkness at 1800. Patrolling is sporadic after lights out (1800) but usually decreases until 2400. During the period of 2400 to 0200 almost no patrolling activity was recorded, however patrolling increases from 0200 to 0400 as the fish is about to be exposed to "daylight" at 0600. This general increase at 0400 seems to indicate the fish anticipates the approach of light at 0600.

AOV analysis of patrolling duration indicated a significant time effect ($p<.05$) over the 24 hour period analyzed but no significant differences among replicates occurred, indicating that the pattern of these replicates was generally the same. Mean values could therefore be calculated for patrolling duration and are shown in Figure 9. A definite increase in patrolling duration from 187.3 seconds to 270.9 seconds occurred from 0600 to an 0800 peak, followed by a rather sharp decrease at 1000 and continuing until 1200. From 1200 until 1400 an increase from 175.2 seconds to an afternoon peak of 205.4 seconds is reached. A reduction of patrolling duration followed this slight increase until 1800 (darkness) and continued until a low of 0.6 seconds was recorded at 0200. This period of decreased patrolling duration is accompanied by a decrease in patrolling frequency (Figure 8). After 0200, duration of patrolling increased until lights turn on.

Frequency of inspirations subjected to AOV analysis revealed no significant differences among replicates; however, there was a definite

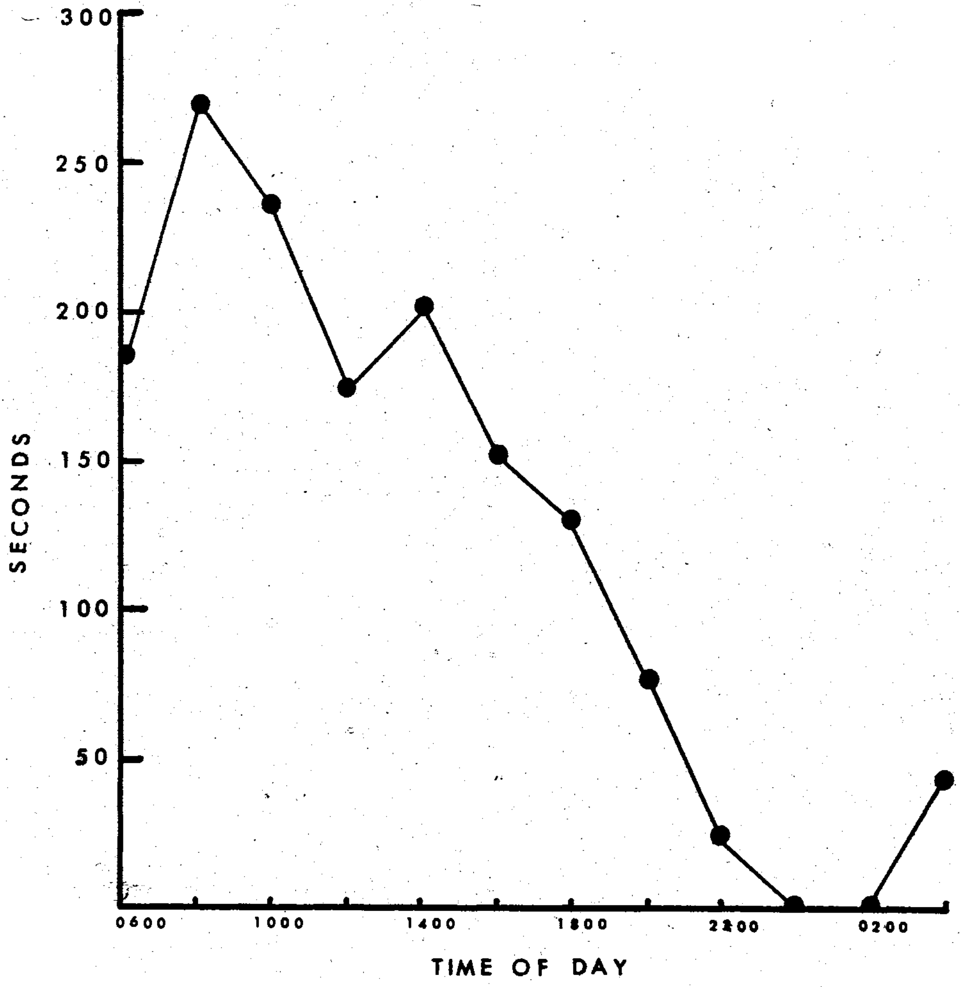


Figure 9. Average Duration of Patrolling Behavior

significant difference ($p<.05$) among observation times. Mean values for the replicates are plotted in Figure 10. An increase in inspiration frequency from 4.5 inspirations/10 min. to 9.3 inspirations/10 min. occurred from 0600 to 0800, followed by a general decrease from 0800 that continued until 1800, stabilized until 2000, increased slightly from 2000 to 2200, then decreased and remained relatively constant until 0400. The data suggest a morning peak in inspiration frequency of 9.3 inspirations/10 min. followed by relatively lowered inspiration frequencies throughout the remainder of the 24 hour cycle.

Durations of inspiration are shown in Figure 11. A significant difference was noted ($p<.05$) among observations and replicates ($p<.05$) necessitating plotting of values for each replicate. Generally high variability occurred in inspiration duration from 0600 until 1200, afterwhich a general increasing trend became evident from 1200 until 1400 followed by a general decrease to 1600. This decreasing trend continued until 2000 where fluctuations again occurred to cause difficulty in interpretation.

Due to the infrequency of rest behavior, it was not analyzed statistically (Figures 12 and 13). Because of the narrow definition employed for rest behavior, i.e. no movement by the fish, true rest was rarely seen and as expected occurred primarily after 1800 increasing generally until about 0400. Rest duration presented much the same pattern having highest values after 1800 but exhibiting high variability.

Analysis of total activity probably is a better overall indicator of daily activity pattern of *T. pectoralis* than any single parameter. Individual replicate variation clouded the importance of this activity

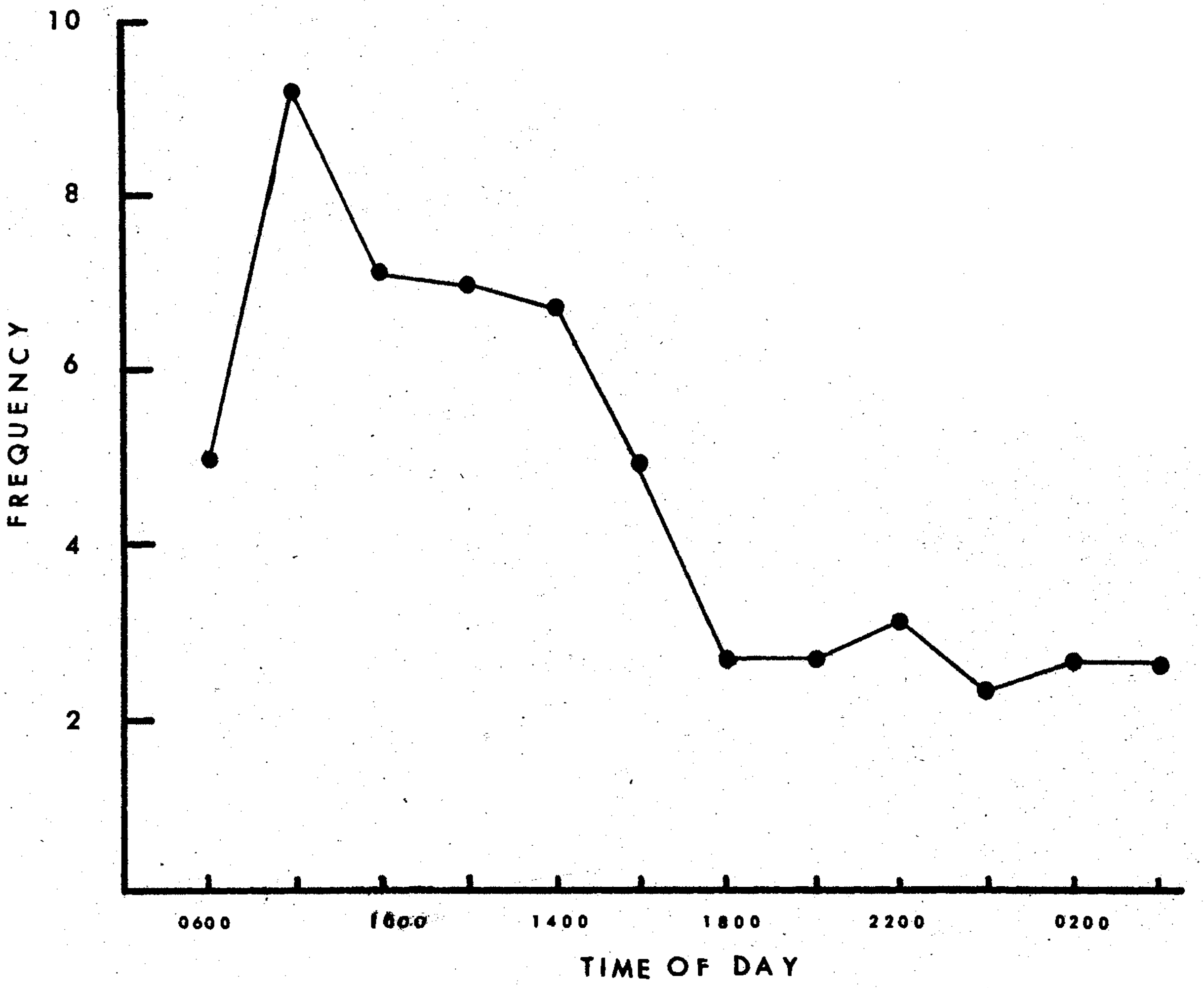


Figure 10. Average Frequency of Inspiration

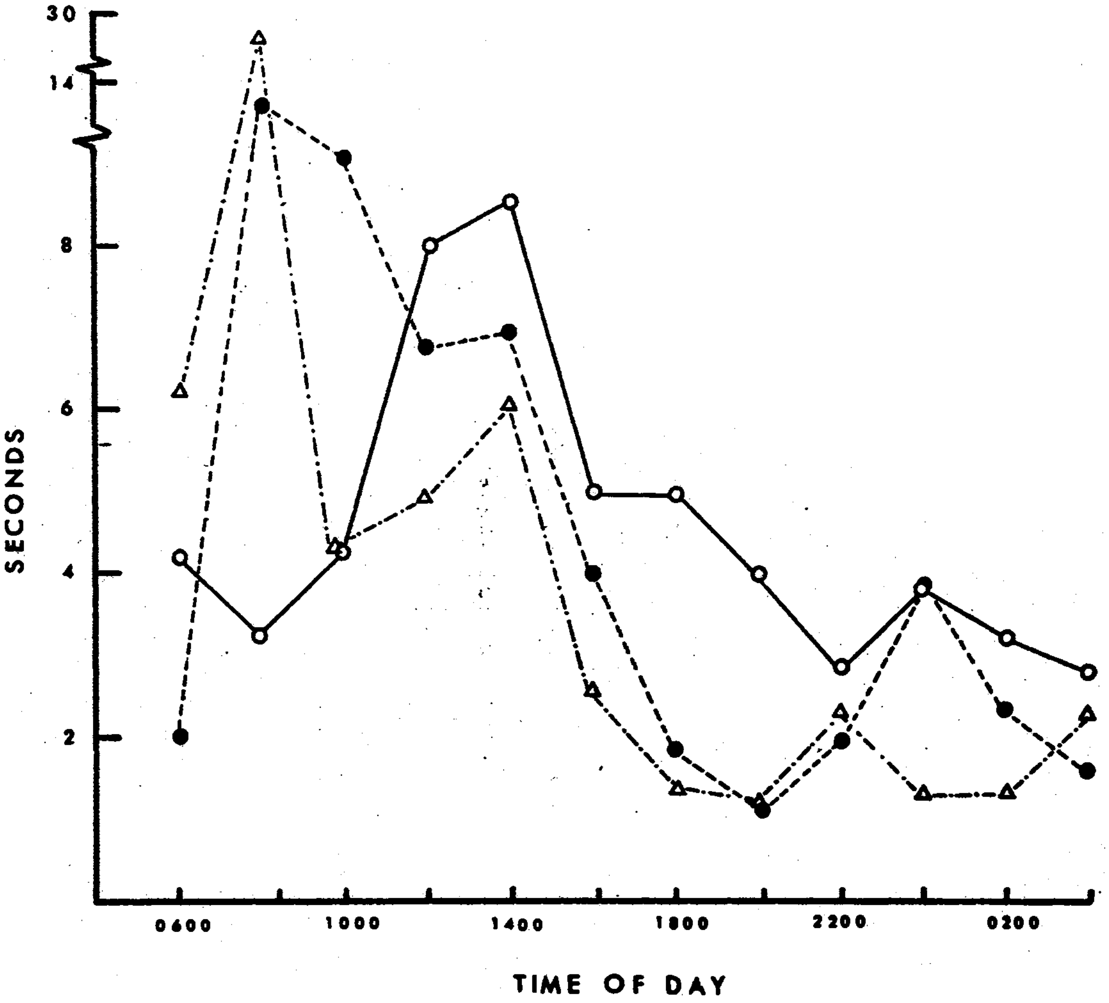


Figure 11. Average Duration of Inspiration (closed circles= replicate one, open circles=replicate two, triangles=replicate three)

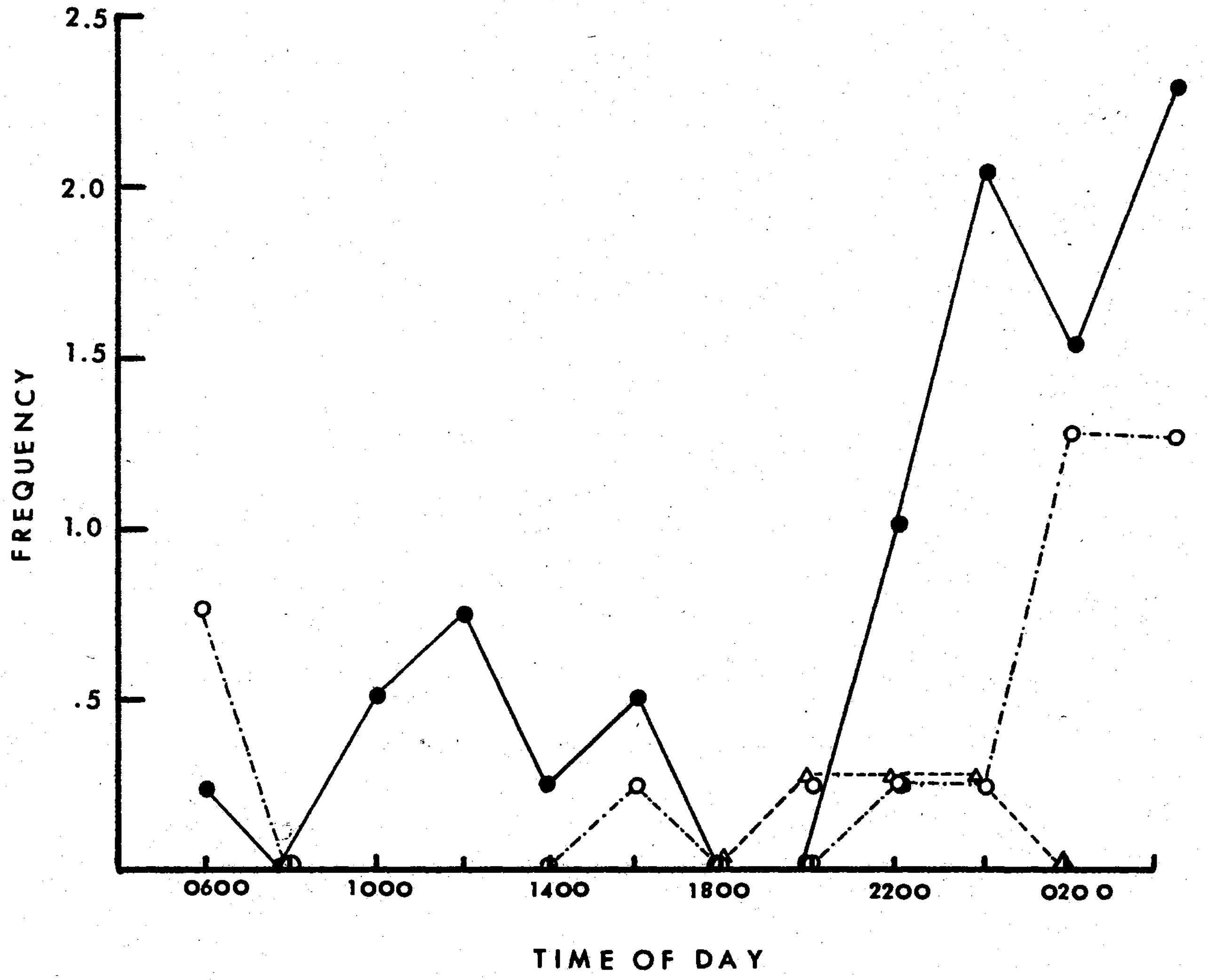


Figure 12. Average Frequency of Rest Behavior (open circles=replicate one, closed circles=replicate two, triangles=replicate three)

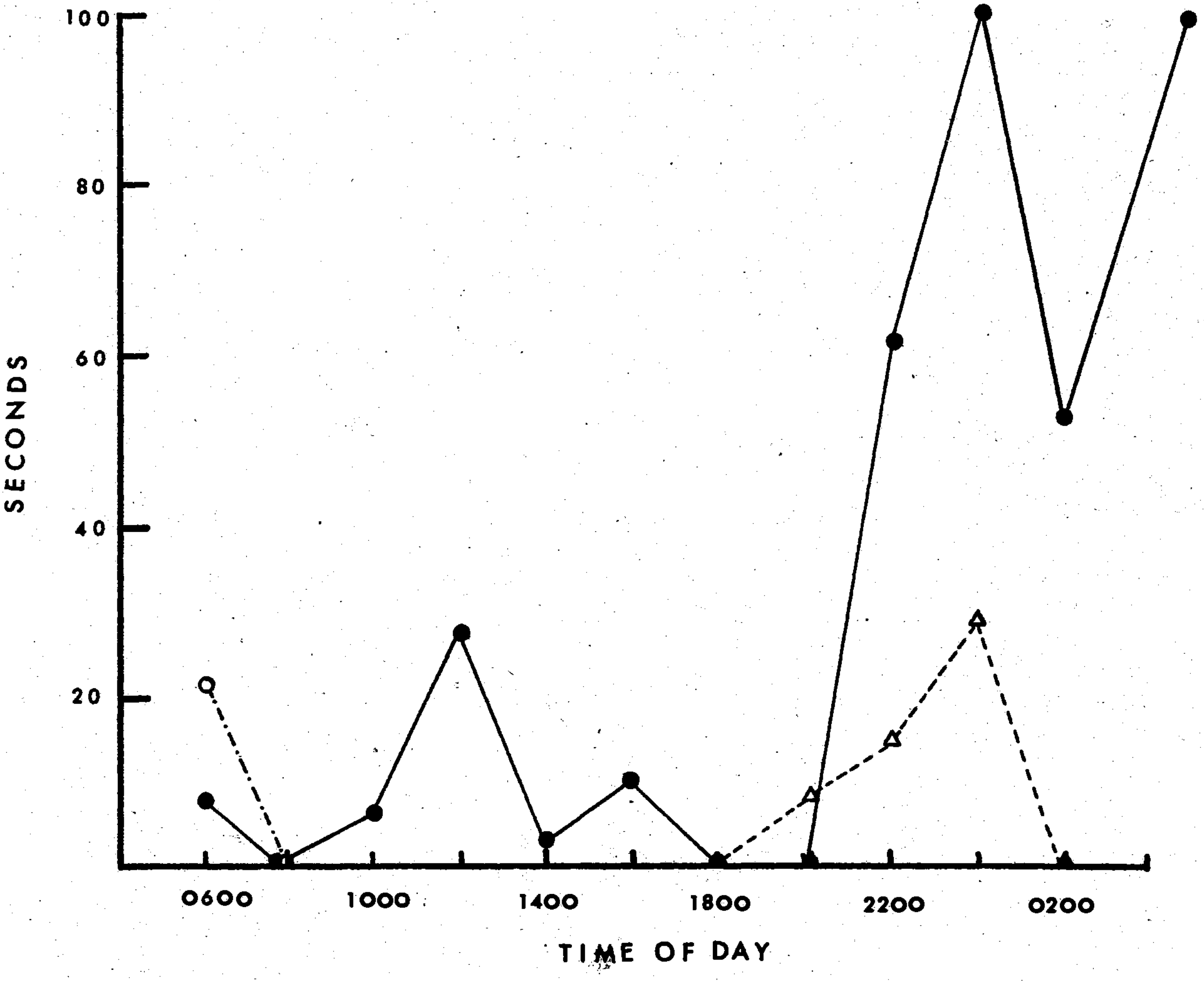


Figure 13. Average Duration of Rest Behavior (open circles= replicate one, closed circles=replicate two, triangles=replicate three)

as an indicator of biological rhythm. AOV analysis of the frequency of total activity revealed significant differences ($p<.05$) among replicates while also revealing significant differences ($p<.05$) among observation times, thus a definite replicate and time effect (Figure 14). Variability of total activity frequency in the morning hours from 0600 to 1000 among replicates made interpretation difficult, however from 1400 until 1800 a definite decrease in frequency of activity occurred. The decrease continued after the lights were turned out (1800) until about 2400, after which a slight increasing trend in total activity occurred until 0400 was observed.

Duration of total activity represents another useful indicator of the fish's activity during the 24 hour period. Analysis of duration of total activity indicated no significant differences among replicates, but significant differences did exist among observation times ($p<.05$). Mean values are plotted in Figure 15. From a mean of 369.8 seconds total activity duration at 0600, duration increases to a peak of 457.4 seconds at 1000 followed by a decrease to 368.7 seconds at 1200, then another increase at 1400 to 404.8 seconds. This second peak at 1400 is followed by a rapid decrease to 294.6 seconds at 1600 and further decreases throughout the lights out until 0200. From 0200 to 0400 total activity duration increases from a daily low of 30.8 seconds to 158.5 seconds.

Hourly percentages of total activity of _T. pectoralis_ were based on 12 males and are presented in Figure 16. Again a general increase in activity from 0600 to 0800 and a peak at 1000 are seen. After 1000 a nearly continuous decrease occurs until 2400. After 2400 a gradual increase in total activity occurs until 0400.

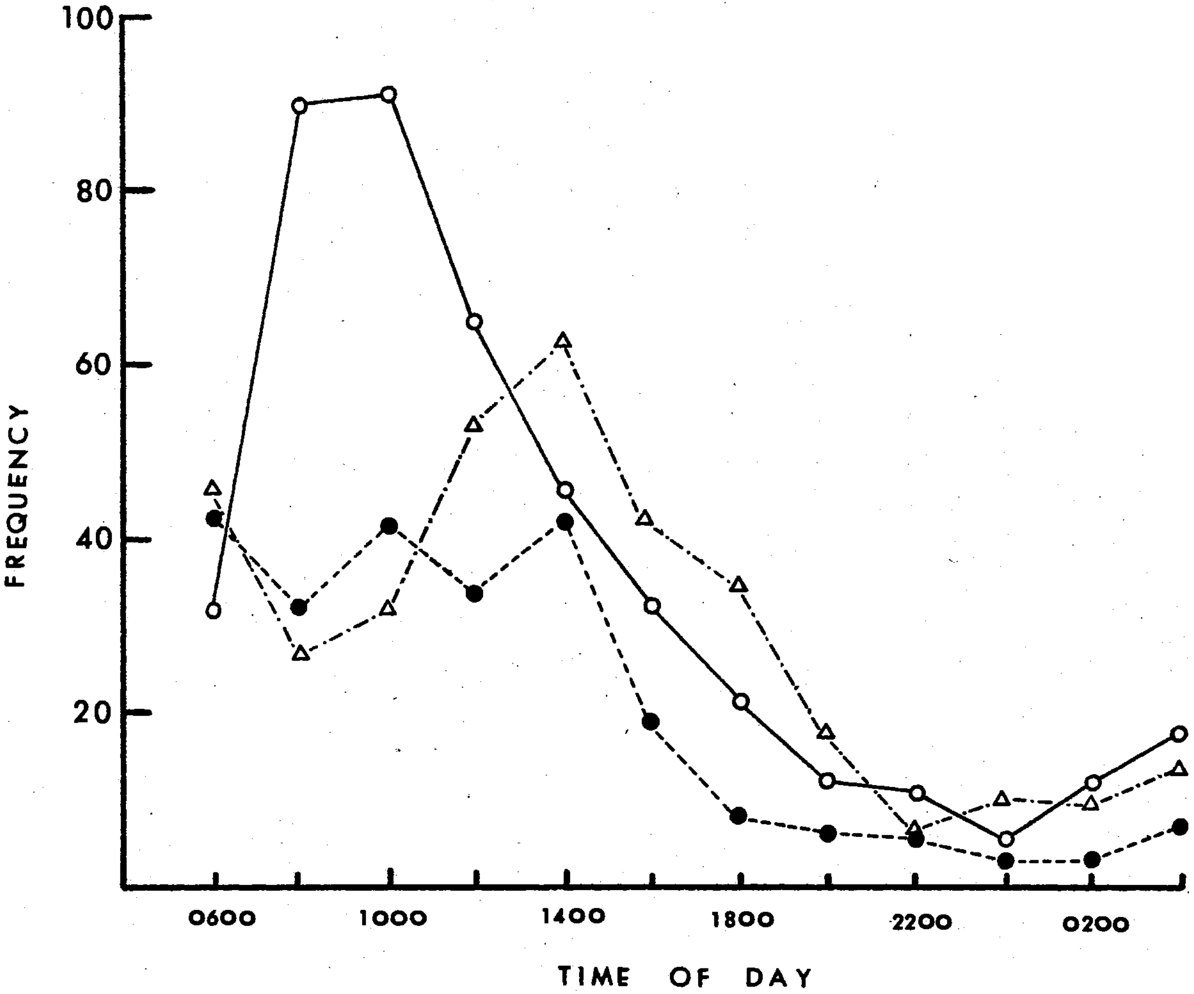


Figure 14. Average Frequency of Total Activity (open circles= replicate one, triangles=replicate two, closed circles=replicate three)

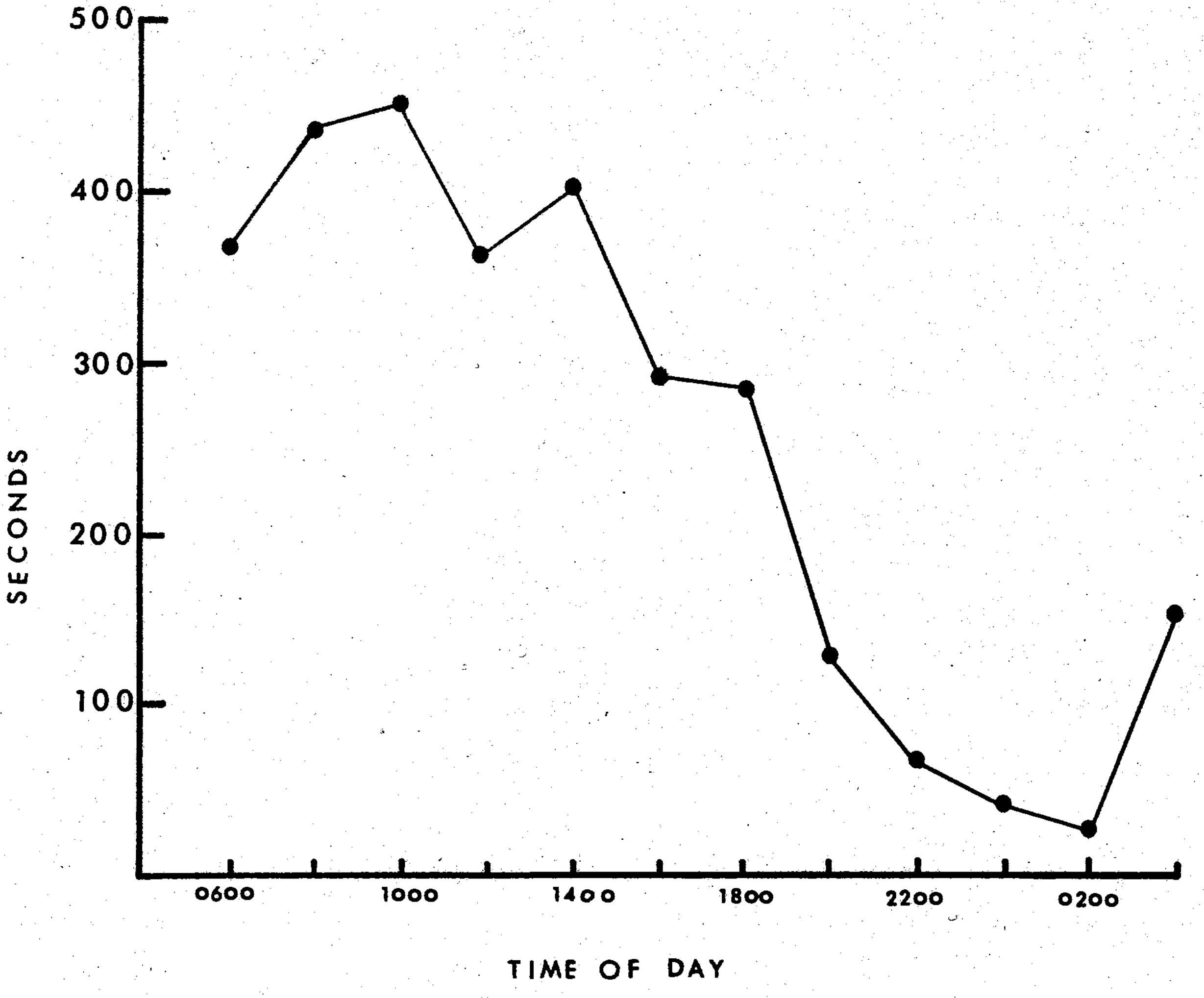


Figure 15. Average Duration of Total Activity

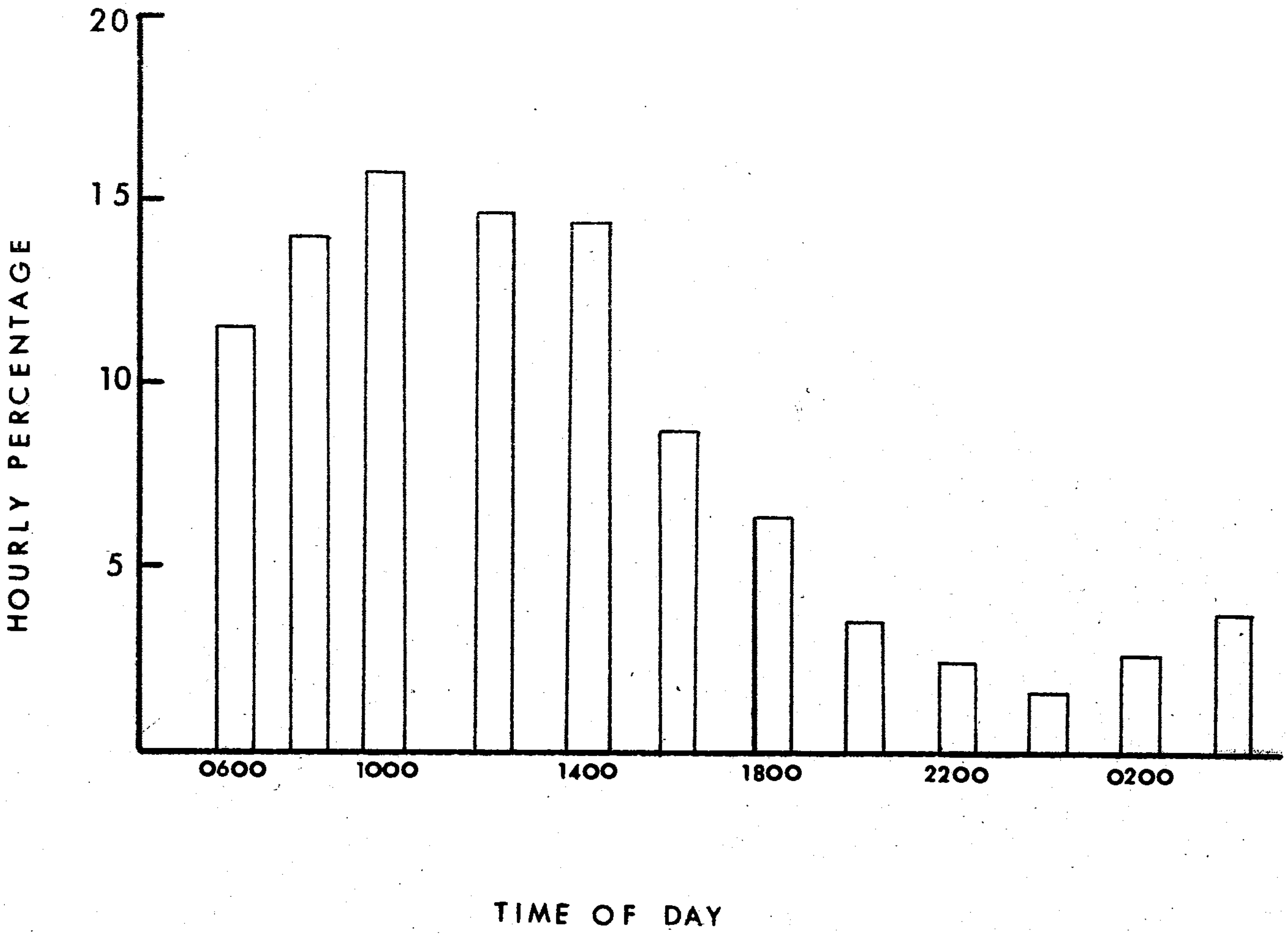


Figure 16. Hourly Percentages of Total Activity

Relative Frequency of Behaviors

To provide an indication of the relative frequency of behaviors shown by _T. pectoralis_ during a 24 hour period, the relative frequency of each behavior expressed as a percentage of total activity recorded during the experiment was calculated and is shown in Figure 17. A total of 4223 behaviors were recorded.

The most frequent single behavior was biting. Bites represented 28.91 per cent of all behaviors recorded indicating it is the most prevalent behavior in heterosexually paired situations. Another agonistic behavior, approach, accounted for 19.42 per cent of total activity. Approach is very common in aquaria and seems to be used as a threat behavior. A grouping entitled miscellaneous activity, defined in Chapter III, constituted 17.95 per cent of the total activity and includes such behaviors as feeding, chafing, yawning, and other comfort movements. Inspiration accounted for 15.91 per cent of all recorded activity.

These four behaviors or groups of behavior represent a combined percentage of 82.19 per cent of behaviors recorded during the experiment. The remaining behaviors are represented in percentage frequency by patrolling (10.35 per cent), chase (3.34 per cent), lateral display (2.25 per cent), mouth fight (1.54 per cent) while tail beating (0.33 per cent) was most infrequent.

Agonistic Behavior

Of 4223 behaviors recorded during the study, 2356 were agonistic behaviors. Percentage frequency of each behavior is shown in Figure 18.

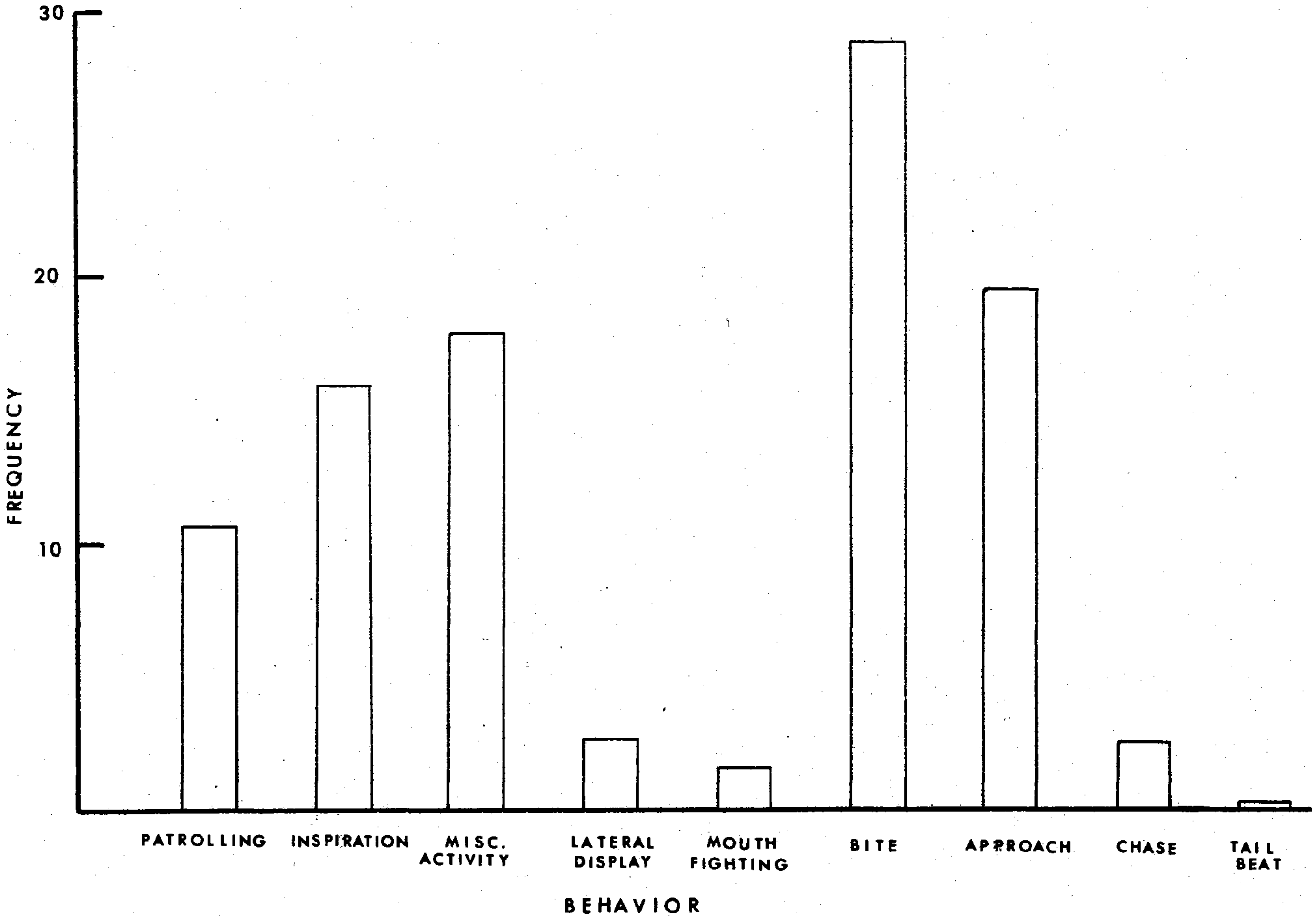


Figure 17. Percent Frequency of Individual Behaviors Expressed as a Percentage of Total Activity

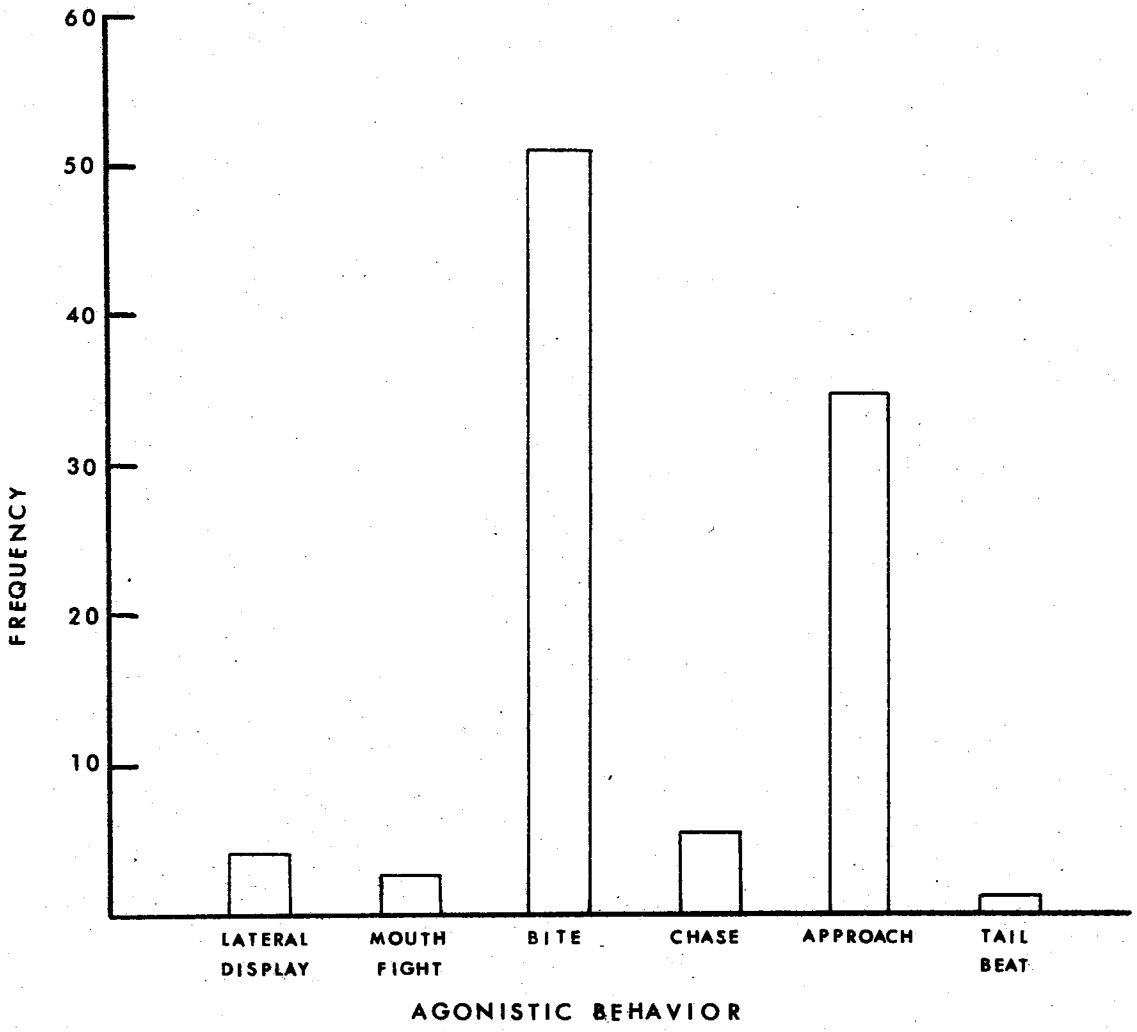


Figure 18. Percent Frequency of Agonistic Behaviors Expressed as a Percentage of Total Activity

Biting and approach represented 86.63 per cent of all agonistic behaviors. Bites alone accounted for 51.83 per cent of agonistic behaviors thus representing over half of all agonistic behaviors recorded while approach constituted 34.80 per cent of agonistic behaviors. After approach, in order of magnitude, came chase (5.98 per cent), lateral display (4.03 per cent), mouth fight (2.76 per cent), and tail beats (0.59 per cent).

Diel Rhythm of Agonistic Behavior

AOV analysis of all agonistic behaviors except tail beating (which was not analyzed because of too few observations), revealed no significant differences among replicates; therefore, replicates were lumped and means plotted in Figures 19 through 23. All agonistic behaviors exhibited significant differences among observation times ($p < .05$) showing a definite time effect.

Mouth fights (Figure 19) exhibited a slight peak at 0800, followed by fluctuations throughout the 24 hour period.

Lateral display (Figure 20) frequency of 0.75/10 min. was recorded at 0600 followed by a slight decrease at 0800 then fluctuations at 1000 and 1200. A peak of 2.4 lateral displays/10 min. occurred at 1400. A notable decrease in lateral displays took place after 1400 until 1600. From 1600 until 1800 a slight increase occurred, after which no lateral displays were ever seen in darkness.

Peaks of biting occurred at 1000 (22.8 bites/10 min.) and at 1400 (21.3 bites/10 min.) followed by a decline to an ultimate low point of 0.08 bites/10 min. at 2400 (Figure 21). Some biting occurred throughout the 24 hour period even in darkness.

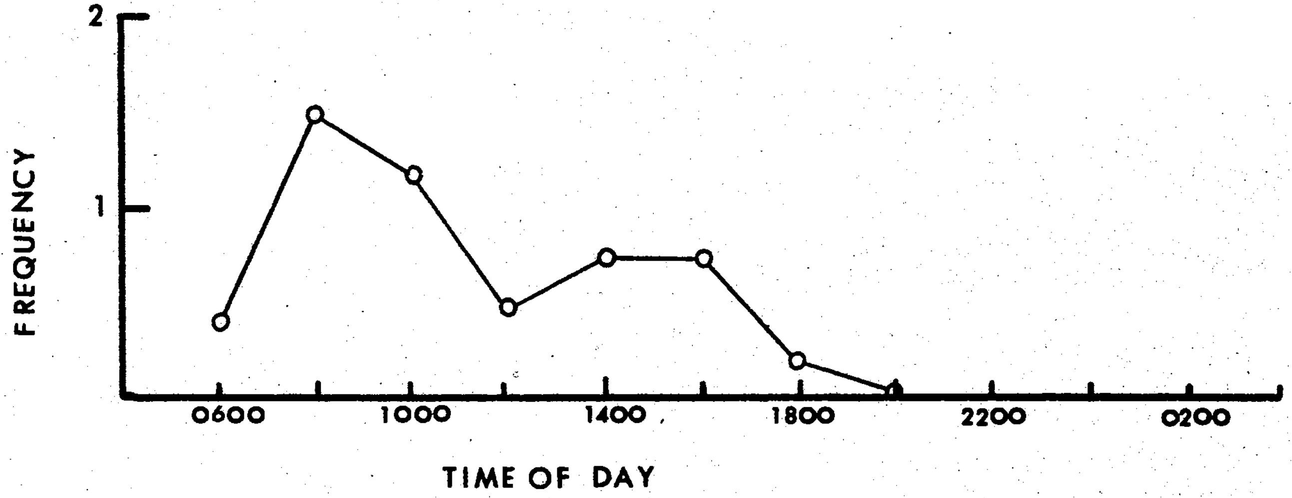


Figure 19. Average Frequency of Mouth Fight Behavior

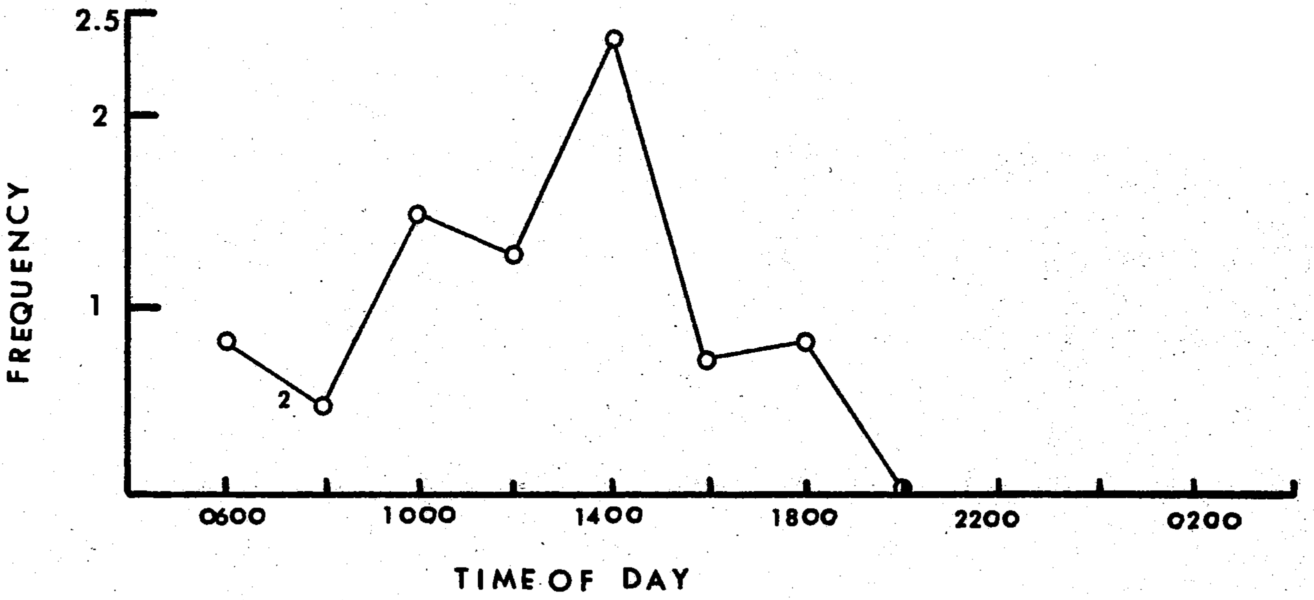


Figure 20. Average Frequency of Lateral Display Behavior

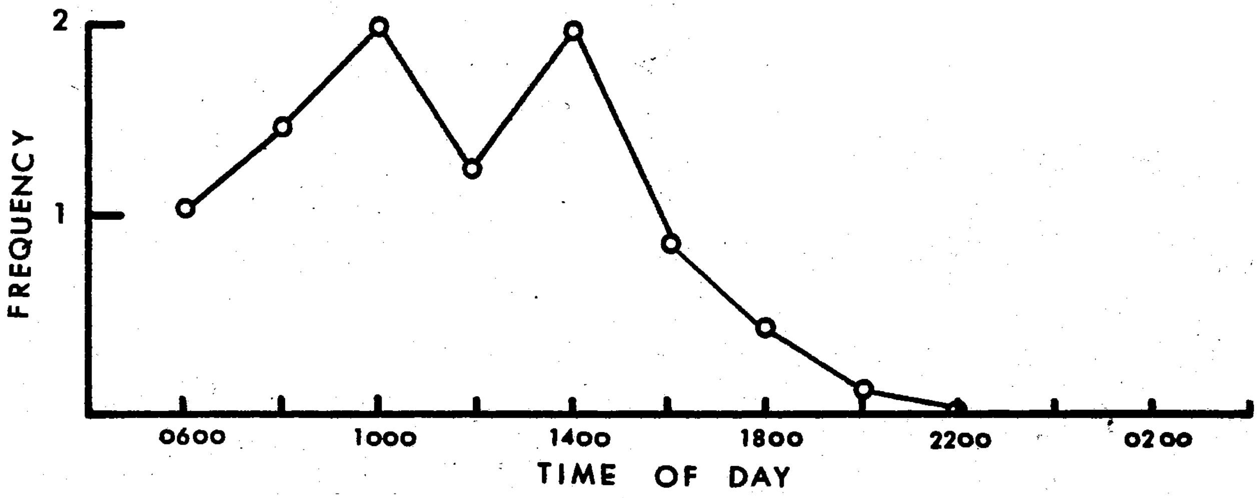


Figure 21. Average Frequency of Bite Behavior

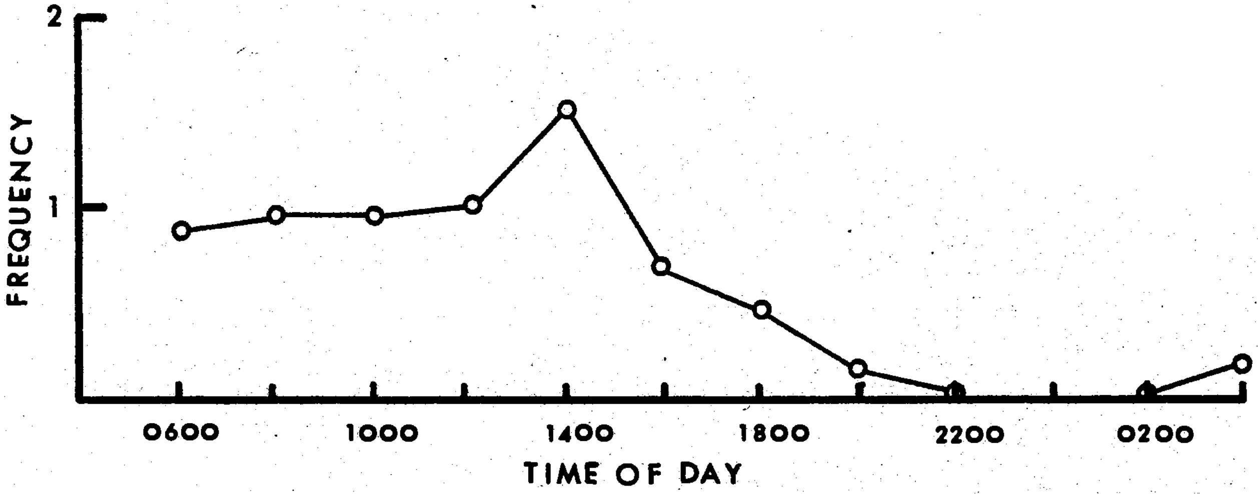


Figure 22. Average Frequency of Approach Behavior

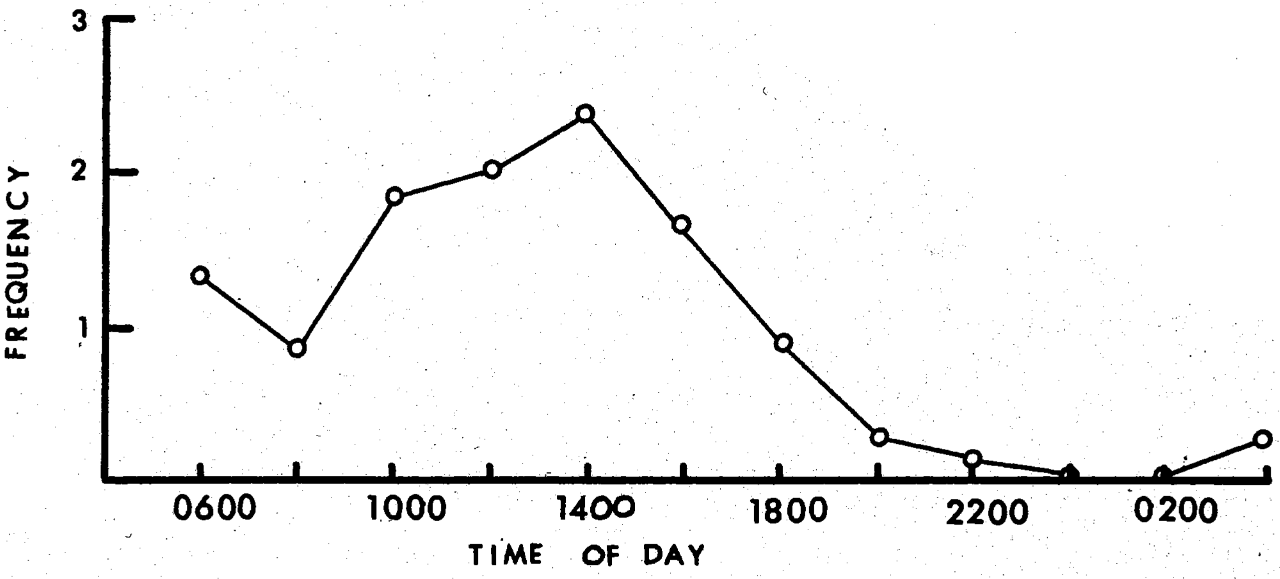


Figure 23. Average Frequency of Chase Behavior

Approach frequency (Figure 22) remained fairly constant in the morning hours but displayed the same (1400) afternoon peak as previous behaviors followed by a gradual decline until 2400 (0.17 approaches/10 min.). This gradual decline was in turn followed by a slight increase at 0200 (0.42 approaches/10 min.), continuing until 0400 (0.75 approaches/10 min.).

Frequency of chase (Figure 23) dipped at 0800 (0.83 chases/10 min.) after being 1.42 chases/10 min. at 0600. A gradual increase occurs after 0800 to a peak at 1400 of 2.42 chases/10 min. followed by a steady decline to no chases at 2400. A slight increase occurs at 0200 and 0400.

Approach, bite, and chase frequency all follow the same general patterns. Typical agonistic encounters between a dominant male and subordinate female are characterized by the sequence of approach, bite, and chase, therefore the same patterns for the three behaviors might be expected. Overall the data do suggest a pattern of agonistic activity in male _T_. _pectoralis_. From an intermediate level in the morning hours (0600) a general increase until an afternoon peak at 1400 occurs. This afternoon high is followed by a decrease until lights out, after which a continued decrease until 2400 is seen. A gradual increase from 2400 until 0400 follows.

CHAPTER X

TAXONOMY, PHYLOGENY, AND PHYLOGENETIC RELATIONSHIPS AMONG SPECIES OF THE GENUS TRICHOGASTER

Taxonomy

Anabantoid fishes are tropical or sub-tropical in distribution and occur throughout Southeast Asia, India, and parts of Central Africa (Smith, 1945; Liem, 1963). Present day nomenclature has relegated the anabantoids to the suborder Anabantoidei included in the order Perciformes. Previously they were considered a separate order Labyrinthici (Regan, 1909; Smith, 1945). In its present form, the suborder Anabantoidei consists of four families: Anabantidae, Belontiidae, Helostomatidae, and Osphronemidae (Figure 24). Liem (1963) lists 15 genera and approximately 50-55 species for the suborder.

The genus *Trichogaster* with which this study is concerned is a member of the family Belontiidae which is comprised of three sub-families, 10 genera and 22-25 species (Liem, 1963). Hall (1965) listed three main unifying characteristics in the family Belontiidae. These are: presence of a labyrinth organ, construction of some type of bubble nest used as a repository for eggs, and utilization of a nuptial clasp or embrace to effect fertilization of the eggs at the time of fertilization. The species of the genus *Trichogaster* belong to the sub-family Trichogasterinae.

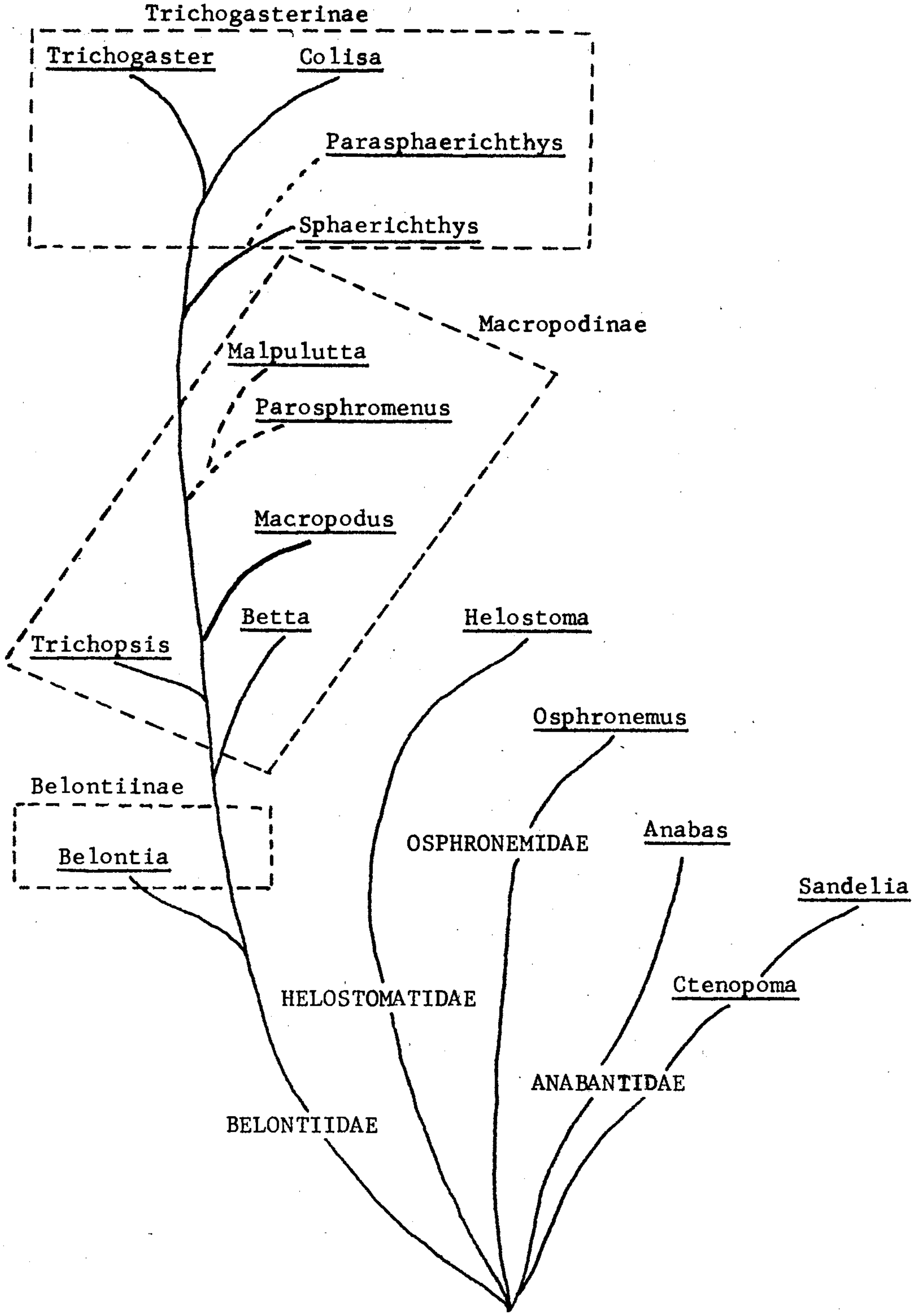


Figure 24. Proposed Phylogenetic Relationships Within the Suborder Anabantoidei (from Liem, 1963)

Phylogeny

Ancestral anabantoid fishes probably originated from percoid stock during the Upper Cretaceous or Paleocene in the tropical portion of the oriental region (Liem, 1963). The tremendous diversity and abundance of anabantoids in Asia supports this hypothesis (Darlington, 1957). That the suborder Percoidei is an ancestor of the anabantoids is a reasonable intuitive guess due to its central position in the order Perciformes (Liem, 1963). Romer (1945) reported that all major teleost groups were established by the Eocene; however, no fossil records for any species of the Belontiidae exist.

Three main divergent lines (Osphronemidae, Helostomatidae, and Belontiidae) radiated from the ancestral stock. Three new subfamilies were proposed within the Belontiidae, which included (1) Belontiinae (*Belontia*), (2) Macropodinae (*Macropodus*, *Betta*, *Trichopsis*, *Parashronemus*, *Malpulutta*, *Ctenops*), and (3) Trichogasterinae (*Trichogaster*, *Colisa*, *Sphaerichthys*, *Parasphaerichthys*).

The Trichogasterinae form a rather homogeneous complex probably evolved from a *Macropodus*-like ancestor by intensification of trends already present in Macropodinae (Liem, 1963). The subfamily Trichogasterinae represents the most specialized group of the Belontiidae. Myers (1958) listed the deepening and compression of the body as one of the evolutionary trends leading from generalized to more specialized teleosts. This trend culminates in the Trichogasterinae. Other evidence for specialization includes reduction in dentition of the prevomer, palatine, and parasphenoid (Liem, 1963).

The genus *Trichogaster* consists of four well-defined species: *T. leeri*, *T. microlepis*, *T. trichopterus*, and *T. pectoralis*.

Phylogenetic Relationships

The concept that behavioral differences or similarities may provide clues to evolutionary affinities was recognized by early behaviorists such as Whitman and Heinroth and more recently this concept has been applied to an ever increasing number of animal groups. Used in conjunction with morphological data, this form of evaluating taxonomic relationships within groups has become increasingly popular. Simpson (1958) has pointed out that similarity of behavior tends, like structural similarity, to be proportional to phylogenetic affinity. Because behavior evolves as species evolve, phylogenies of behavior may be as useful as those based on structure (Johnsgard, 1967; Hinde, 1970).

The use of behavioral characters, like taxonomic characters, requires the collection of data on homologous features that can be compared among species (Johnsgard, 1967). Hinde and Tinbergen (1958) stated that the comparative method itself basically depends on the establishing of homologies, i.e. grouping together of elements having a common evolutionary origin. Recently Atz (1970) discussed the dangers inherent in establishing "homologies of behavior." Atz contends that homologizing behavior or establishing homologies of behavior is risky, but admits "the only reliable homologies of behavior have been confined to closely related forms." Baerends (1958:411) and Tinbergen (1963:428) stated that to be reliable, homologous behaviors must be limited to closely allied forms. The viewpoint taken in this study is that while the idea of homology has traditionally been a morphological concept, it nevertheless may be used with reasonable assurance in closely related species, i.e. species of the same genus.

Within an animal group it is possible to find species exhibiting more generalized or "primitive" conditions of behavior than are found in other species of the group due to the differential rate of evolution in different animals. By using the technique of comparative analysis of behaviors it is possible to provide a tentative description of the course evolution has taken by studying closely related animal species and then comparing the more specialized forms with the less specialized ones. It must be remembered, however, that behavior "is much more difficult to treat comparatively than is structure due to its variability, continuity, extended ontogeny, and the evanescence of each behavioral act" (Atz, 1970).

The question of the part of the animal's behavioral repertoire to be recorded and measured is a profound one. Successful use of the comparative method depends on the selection of characters to be compared (Hinde and Tinbergen, 1958). Because fixed action patterns may be as characteristic of a species as any of its morphological characters and are directly observable, they have been the most useful behavioral characters for systematic study (Hinde, 1970). Behavior has provided valuable clues to systematic relationships in many studies (Mayr, 1958; Simpson, 1958; Cullen, 1959; Marler, 1959). Fixed action patterns are reasonably constant within a group, yet exhibit moderate diversity within members of the group forming the basis for the comparative study. Atz (1970) reported the most convincing examples of homologous behaviors comprise patterns of motor activity peculiar to a single group and found in all members of the group.

Stereotyped threat and courtship movements have provided a rich source of material for studying the evolution of behavior (Hinde, 1970). Because of the stereotypy of social behavior in anabantoid fishes, this set of behaviors is probably the most useful for comparison in this group. Maintenance and comfort movements are very similar if not identical in all species of *Trichogaster*, thus of no use in a comparative study. Hinde and Tinbergen (1958) have pointed out that all characters of the living animal, both behavioral and morphological are products of environmental factors as well as inherent potentialities and care must be taken to ensure that behavioral differences are in fact indicative of genetic diversity and not merely of dissimilar environments. Because all species of *Trichogaster* were spawned under similar laboratory conditions, behavioral differences in courtship and reproductive behavior are thought to be indicative of genetic diversity.

This study is based on data collected on courtship and reproductive behavior of members of the genus *Trichogaster*. Phylogenetic relationships will not be assessed on the basis of behavioral observations alone, but will be used in conjunction with morphological and meristic data compiled on the species involved.

Species of *Trichogaster* existing sympatrically may largely depend primarily on courtship and reproductive behavior as an isolating mechanism. It is reasonable to assume geographic separation at some time in the past, with sympatry occurring subsequent to the development of behavioral isolating mechanisms. Behavioral isolation may be the most effective isolating mechanism (Spieth, 1958). *Trichogaster* species all follow a generally similar pattern of breeding, but they are quite effectively sexually isolated even when breeding in the same tank. Spieth (1958) commented that in many species exhibiting territorial behavior, specific and unique recognition ornamentation and movements have evolved. That such is the case in *Trichogaster* is easily seen.

Nest Building in the Genus Trichogaster

Most anabantoid genera utilize a bubble nest for spawning, but the form and composition of the nest, and nest building behavior vary even at the species level (Miller, 1964). Species specific variation in nest building behavior is readily apparent in the genus *Trichogaster* (Table VIII). Perhaps the most apparent difference in nest building behavior is in the use of vegetation in nest construction by the four species. *T. leeri*, *T. trichopterus*, and *T. pectoralis* utilize plant material as a means of anchoring nests if such material is present. In some instances other such structures as the corner of the tank, or feeding rings are used. *T. trichopterus* and *T. pectoralis* never seek out vegetation and transport it back to the nest area. *T. leeri* occasionally adds plant fragments as well as detritus and sand to its nests. *T. microlepis*, however, not only always uses plant material in its nest construction, but it actively seeks out vegetation and either uproots such vegetation if planted or snips off leaves of plants and carries the leaves back to the nest area where incorporation into the nest follows (Wimmer, 1970). Such behavior is prominent in members

TABLE VIII

COMPARISON OF NEST BUILDING AMONG SPECIES OF THE GENUS TRICHOGASTER

	leeri	microlepis	trichopterus	pectoralis
Male Nest Building	Present	Present	Present	Present
Female Nest Building	Absent or Very Rare	Absent	Absent or Very Rare	Absent
Active Incorporation of Vegetation into Nest	Rare	Always	Absent	Absent
Nest Pushing	Absent	Present	Absent	Absent
Surface Inspiration with Surface Release	Present	Absent or Rare	Present	Present
Surface Inspiration with Subnest Release	Present	Present	Present	Present
Opercular Air Emission	Present	Rare	Present	Present
Jetting	Present	Present	Present	Present
Inspirations Preceding Expulsion of Bubbles	1-9	?	1-40	1-35

of the genus *Colisa* such as *C. lalia*. Because this behavior represents an extreme found nowhere else in the genus *Trichogaster*, it probably represents a specialization of *T. microlepis*.

Differences are also found in *Trichogaster* in motor patterns used in nest building. With regard to motor patterns used in bubble blowing during nest construction, *T. leeri*, *T. trichopterus*, and *T. pectoralis* exhibit fairly similar patterns, however certain behaviors are rare or lacking entirely in *T. microlepis*. While *T. leeri*, *T. trichopterus* and *T. pectoralis* use surface inspiration with surface release and opercular air emission to blow bubbles during nest building, apparently this motor pattern is rare or even absent in *T. microlepis*. All species use surface inspiration with subsurface release.

Another unique behavior exhibited by *T. microlepis* is nest pushing (Forselius, 1957:222), a behavior not found in other *Trichogaster* species (Wimmer, 1970) but found in *Colisa* species. Nest pushing is accomplished as the fish shoves its snout against the nest, perhaps influencing the arrangement of vegetation or dispersal of bubbles throughout the mass of plant growth (Wimmer, 1970). The absence of this behavior in other species of *Trichogaster* may be due to less extensive use of vegetation in nest construction as Miller (1964) suggested for *T. trichopterus*.

Quantitative data on nest building will probably provide for a more exact differentiation among species, but such data are unavailable at present. Nest size is so variable even among individuals of the same species that comparisons among species offer little in the way of differentiation.

Qualitative Comparison

Related species are generally characterized by more or less pronounced differences in reproductive behavior, frequently accentuated by the evolution of different markings and color patterns in the different species (Forselius, 1957). That such is the case in *Trichogaster* is readily apparent, as every species has its own characteristic markings and color patterns. Such differentiation is particularly important during the reproductive cycle because closely related species may exhibit much more similarity in execution of sexual behavior (Forselius, 1957). Because the fishes of this genus are highly territorial and thus stationary during the reproductive cycle, it is particularly advantageous for them to have distinctive nuptial coloration.

A wide range of nuptial coloration exists in *Trichogaster*. *T. microlepis* males exhibit little if any nuptial coloration while *T. leeri* in the reproductive phase is quite brilliantly colored (Hall, 1966b). Nuptial coloration in male *T. trichopterus* is also quite intense and in its most intense form is a dark inky blue, almost black in color. While not as startling as *T. leeri* or *T. trichopterus*, *T. pectoralis* undergoes pronounced color changes, characterized by the darkening of vertical reticulations, lateral band of the body, fins, and eyes. It is interesting to note that the vertical anastomosing reticulations so prominent in *T. pectoralis* are exhibited to a large degree in both highly motivated male and female *T. trichopterus*, perhaps indicating close relationship.

The lateral band is worth commenting on in these four species (Figure 25). At one end of the spectrum is *T. microlepis* which has almost no band remaining on its silvery body while *T. leeri* has an almost solid lateral line. The band in *T. microlepis* is difficult to see but becomes slightly more pronounced in older adults. Richter (1970) also observed the presence of this band. Two ocelli are present on the lateral portion of the body (where the lateral band occurs in other species) in *T. trichopterus*. One is a caudal ocellus observed in all species of *Trichogaster* (very faint in *T. microlepis* and *T. leeri*) while the other is situated approximately below the dorsal fin halfway between the dorsal and ventral edges of the body. *T. leeri* presents a narrow lateral band that darkens and becomes more pronounced when individuals assume nuptial coloration.

Just as each species has its own characteristic nuptial coloration each species also possesses certain unique behaviors displayed during the reproductive cycle (Table IX). For example, rubbing occurs in *T. trichopterus*, rubbing position is found in *T. pectoralis*, while postcircling pause is characteristic of *T. microlepis* and terminal squeeze is found only in *T. leeri*.

Differences among species manifest themselves with regard to agonistic behavior during the spawning sequence. Male agonistic behavior in *T. microlepis* lacks opercle spread and mouth fighting and shows reduced postspawning aggression and low female bite frequency upon approach (1-6), all suggesting reduced agonistic behavior in this species. *T. pectoralis*, conversely, demonstrates enhanced agonistic behavior as mouth fighting is quite common, males show opercle spread behavior, and there is severe postspawning aggression. *T. leeri* and

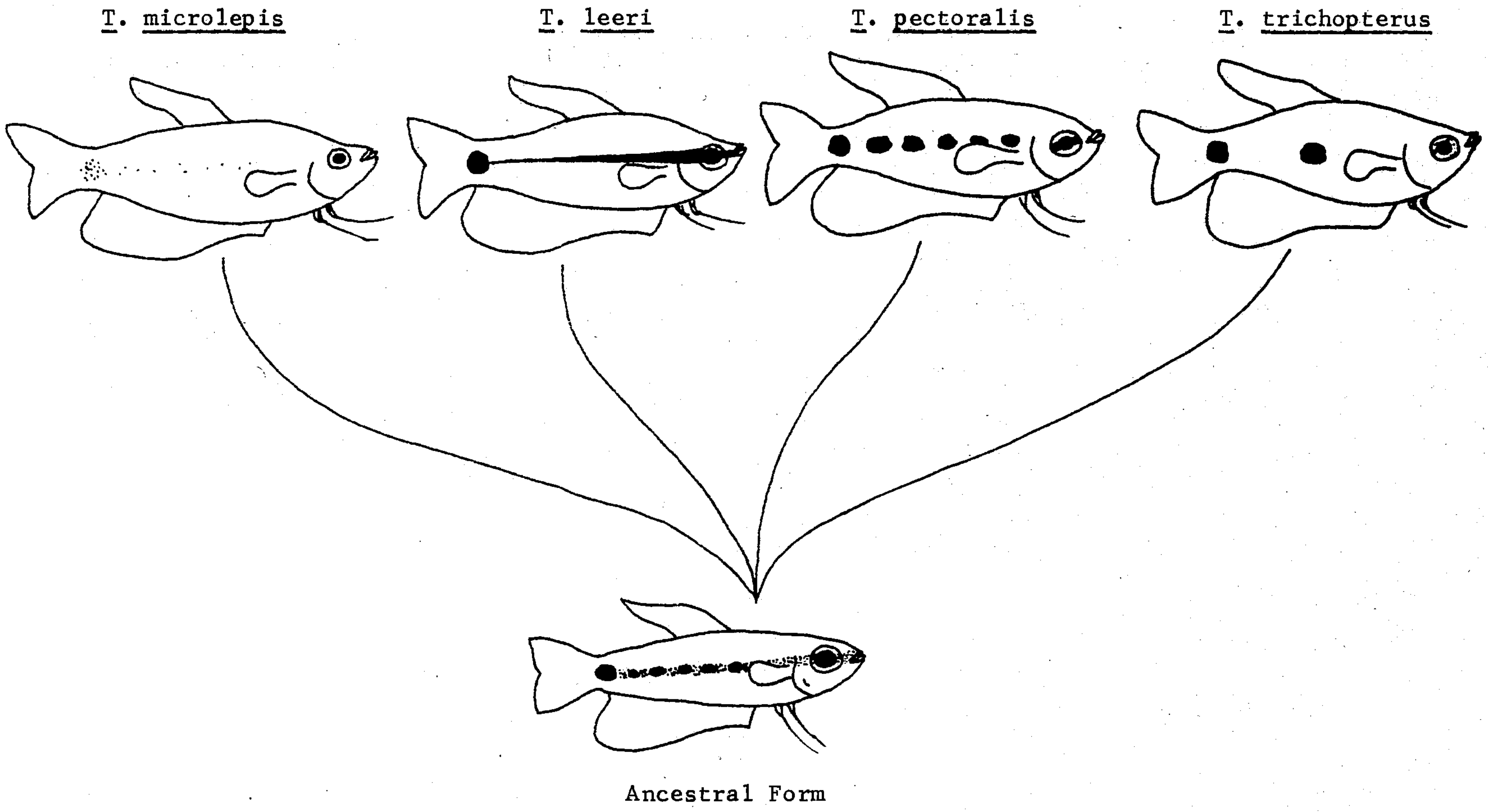


Figure 25. Evolution of Lateral Band in the Genus Trichogaster

TABLE IX

QUALITATIVE COMPARISON OF COURTSHIP AND REPRODUCTIVE BEHAVIOR IN *TRICHOGASTER*

Behavior	*leeri*	*microlepis*	*trichopterus*	*pectoralis*
Male Nest Building	+	+	+	+
Female Nest Building	- r	-	- r	-
Tail Beating (Male	+	+	+	+
Opercle Spread	- rd	-	rd	rd
Mouth Fighting	r	-	r	c
Head Jerking	r	r	r	r
Male Lateral Display	+	+	+	+
Male Sigmoid Display	r	+	c	c
Male Lead to Nest	c	c	c	r
Female Courtship Butting	+	+	+	+
Rubbing	-	-	+	-
Rub "Position"	-	-	-	+
Male Circling or Curving	+	+	+	+
Post Circling Pause	-	+	-	-
Male Terminal Squeeze	+	-	-	-
Vibrating	-	-	-	-
Swimming Inhibition	+	+	+	+
Male Postspawning Aggression	c	rd	c	c
Female Appeasement	+	+	+	+
Male Postspawning Nest Care	+	+	+	+
Female Postspawning Nest Care	-	-	-	-
Mouth Snapping	r	r	r	c
Jetting	+	+	+	+
Opercular Air Emission	+	r	+	+
Egg Predation by Female	r	r	r	r

TABLE IX (continued)

Behavior	leeri	microlepis	trichopterus	pectoralis
Nest Pushing (Male)	-	+	-	-
Surface Inspiration with Surface Release	+	-	+	+
Active Incorporation of Vegetation into Nests	r	c	-	-
Sub-nest Release of Bubbles	+	+	+	+

+=present, -=absent, r=rare, rd=reduced, c=common

T. trichopterus appear to be intermediate between these two extremes with regard to agonistic behavior.

Differences in spawning temperatures, hatching and free swimming durations, and eggs per spawning bout show little clear-cut differentiation (Table X); however, it should be noted that T. microlepis apparently has more eggs per spawning sequence and is typically a night spawner.

In an attempt to illustrate similarity among species in the genus Trichogaster a matrix was constructed based on a total of 41 behavioral characters. These characters have not been weighted even though some are obviously more important than others. Many of the behavioral differences are quantitative, involving the magnitude of the behavior performed rather than its presence or absence. Table XI shows the number of ethological characters shared by each species. The higher the numerical value (out of 41) the greater the similarity.

From Table XI it is seen that the greatest similarities in behavior occur between T. trichopterus and T. pectoralis, which are similar or share 33 of 41 behaviors. Next closest are T. trichopterus and T. leeri which are similar in 27 ethological characters. T. trichopterus is least similar to T. microlepis as they share only 18 characters.

T. microlepis is almost equally dissimilar to the other three species, sharing 22 characters with T. leeri but only 18 characters with T. trichopterus and T. pectoralis. This suggests the great divergence represented by T. microlepis, which is behaviorally the most unique of the four anabantoid species of Trichogaster.

TABLE X

COMPARISON OF *TRICHOGASTER* SPECIES WITH REGARD TO SPAWNING DATA

	$\bar{x}$ No. Spawning Bouts	Optimum Temp. at Spawning	$\bar{x}$ No. Eggs/Spawning Sequence	Eggs/ Spawning Bout	Hatching (age in hrs.)	Free-Swimming (Days)	Time of Spawning
T. leeri	6	84°F	955	135	24	2-3	10AM-2PM
T. microlepis	27*	84°F	2000+	5-100	18-26	3	After 7PM
T. trichopterus	6	84°F	1000	10-80	24-36	2-3	10AM-5PM
T. pectoralis	6	82°F	1000+	8-70	20-32	2-3	9AM-6PM

*This figure includes spawning and pseudospawning bouts.

TABLE XI

MATRIX OF ETHOLOGICAL CHARACTERS SHARED BY EACH SPECIES*

	T. leeri	*T. microlepis*	*T. trichopterus*	*T. pectoralis*
T. leeri	-	22	27	21
T. microlepis	22	-	18	18
T. trichopterus	27	18	-	33
T. pectoralis	21	18	33	-

*Based on 41 possible behavioral characters

This method of analyzing similarity of behavior is fairly objective, although the characters chosen are of necessity subjective. In this manner, however, each character is given equal weight or value, thereby distinguishing the possible importance of certain behaviors which may be highly indicative of close relationship, i.e. rubbing and rubbing position in *T. trichopterus* and *T. pectoralis*, respectively.

Quantitative Comparison

Miller (1964) pointed out that courtship and sexual behavior in anabantoid fishes is organized into discrete bouts which may contain numerous types of display postures, intention movements, and non-ritualized agonistic or sexual actions. He further stated that the duration and nature of these bouts are quite distinctive in all species and seem to reflect specialization and modification of a more generalized pattern. Thus insight into phylogenetic relationships should be gained by analyzing courtship and reproductive bouts of the species of *Trichogaster*.

Data used in this comparison are presented in Table XII and will serve as the basis for the following discussion. Similarities and differences will be noted, but no attempt will be made to evaluate causal or motivational aspects of the behaviors analyzed. Data has been analyzed in the manner of previous studies, i.e. placing behaviors into arbitrary, artificial categories that facilitate dealing with the data available. Definition of bout types was presented in Chapter III.

Bouts/spawning sequence varies widely in species of the genus *Trichogaster*, from a low of 44 bouts/spawning sequence in *T. microlepis* to a maximum of 85.5 bouts/spawning sequence in *T. leeri*. *T. trichopterus* and *T. pectoralis* are very similar with 69.7 and 70.3 bouts/spawning sequence, respectively.

It was impossible to compare directly spawning bouts and pseudospawning bouts per sequence for all species, unfortunately, due to night spawnings in *T. microlepis* in which spawning and concomitant release of eggs could not be differentiated from pseudospawning with no release of eggs. However, a comparison taking this into consideration could be made by using a category of spawning plus pseudospawning bouts. Again *T. microlepis* demonstrates an extreme of 27 spawning and pseudospawning bouts. *T. trichopterus* and *T. leeri* are relatively similar with 11.8 and 11.5 spawning plus pseudospawning bouts, respectively. *T. pectoralis* has 9.7 spawning plus pseudospawning bouts per spawning sequence.

Clasp bouts/spawning sequence show considerable variation in the genus. An average of 3.0 clasp bouts/spawning sequence is found in *T. microlepis* and *T. pectoralis*, while *T. trichopterus* has a slightly

TABLE XII

QUANTITATIVE COMPARISON OF COURTSHIP AND REPRODUCTIVE BEHAVIOR AMONG SPECIES OF THE GENUS <u>TRICHOGASTER</u>

	<u>leeri</u>	<u>microlepis</u>	<u>trichopterus</u>	<u>pectoralis</u>
Spawning Sequences	15	2	5	3
Average Bouts/Sequence	85.5	44.0	69.7	70.3
Average Spawning Bouts/ Sequence	6.5	-	6.2	6.3
Average Pseudospawning Bouts/Sequence	4.9	-	5.6	3.3
Average Spawning Plus Pseudospawning Bouts/ Sequence	11.5	27.0	11.8	9.7
Average Clasp Bouts/ Sequence	21.9	3.0	4.8	3.0
Average No Clasp Bouts/ Sequence	52.7	14.0	51.2	57.7
Average Duration of Spawning Bout*	55.3	-	199.8	263.6
Average Duration of Pseudospawning Bouts	74.7	-	221.4	251.3
Average Duration of Spawning Plus Pseudospawning Bout	63.7	54.0	210.6	259.3
Average Duration of Clasp Bout	45.5	35.0	253.3	279.8
Average Duration of Clasp During Spawning Bouts	25.3	9.3	47.1	60.8
Average Duration of Clasp in Clasp Only Bouts	4.0	3.4	7.1	19.3
Average Interval Between Bouts	131.4	189.0	90.4	73.7
Swimming Inhibition	2-5	2-6	2-5	2-12
Average Circling Duration	0.9	10.4	5.6	6.4

*All durations are in seconds.

higher average of 4.8 clasp bouts/spawning sequence and *T. leeri* has an extreme of 21.9 clasp bouts/spawning sequence. With its large number of bouts/spawning sequence (85.5), *T. leeri* may need more clasp bouts for pairs to become properly synchronized before successful spawnings take place.

As might be expected with its low number of bouts/sequence (44), *T. microlepis* exhibits a much lower number of no clasp bouts/spawning sequence (14) than *T. leeri*, *T. trichopterus*, and *T. pectoralis*, with 52.7, 51.2, and 57.7 no clasp bouts/sequence, respectively.

Duration of spawning and pseudospawning bouts could not be compared directly for all species due to the previously mentioned circumstances in *T. microlepis* spawnings, thus average duration of spawning plus pseudospawning bouts was calculated. *T. pectoralis* exhibits the maximum spawning and pseudospawning bout duration with 259.3 seconds, followed closely by *T. trichopterus* with 210.6 seconds. There is a decided drop in duration in the other species. Spawning plus pseudospawning average duration is 63.7 seconds in *T. leeri*, and 54 seconds in *T. microlepis*.

Mean circling duration in spawning bouts is shortest in *T. leeri* (0.9 seconds) and longest in *T. microlepis* (10.4 seconds). *T. pectoralis* has a circling duration of 6.4 seconds while circling duration in *T. trichopterus* is 5.6 seconds.

Duration of clasp bouts during a spawning sequence varies from 35 seconds in *T. microlepis*, to 45.5 seconds in *T. leeri*, 253.3 seconds in *T. trichopterus*, and 279.8 seconds in *T. pectoralis*. Duration of the actual clasp in spawning bouts is lowest in *T. microlepis*, which exhibits an average of 9.3 seconds, followed by *T. trichopterus* at

22.5 seconds, T. leeri with 25.0 seconds while T. pectoralis has the longest mean clasp duration of 60.3 seconds.

Duration of clasp in clasp only bouts shows a decrease in duration compared to clasps in spawning bouts. T. leeri has an average of four seconds, as does T. microlepis. T. trichopterus has a clasp duration of 7.1 seconds while T. pectoralis demonstrates the highest clasp duration of 19.3 seconds in clasp only bouts.

T. pectoralis exhibits the shortest interval between bouts, 73.7 seconds, followed by T. trichopterus with an average of 90.4 seconds, while T. leeri has an average interval of 131.4 seconds and T. microlepis with 189 seconds. This suggests that T. pectoralis and T. trichopterus have longer reproductive bouts but overall spawning sequences are shorter due to shorter intervals between bouts.

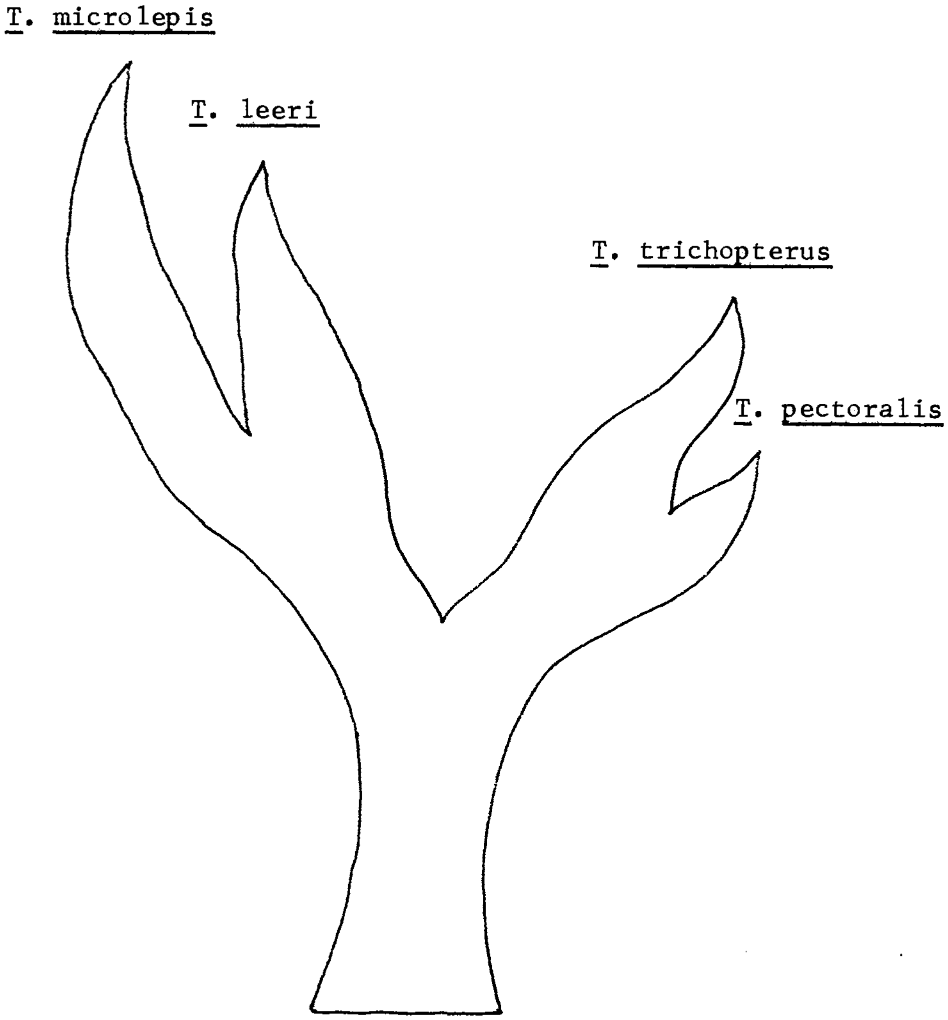
Swimming inhibition is fairly constant among species, ranging from 2-17 seconds.

Evolution of Trichogaster Species: An Hypothesis

Direct evidence concerning the behavior of ancestral forms of the genus Trichogaster is not available, quite obviously because behavior does not fossilize. Therefore, primitive as well as specialized conditions of behavior must be hypothesized by comparison among living taxonomic units. Hinde and Tinbergen (1958) have pointed out that the comparative method is the only method available for such analysis and it is naturally indirect. Because of the lack of fossils in the Belontiidae, even morphological characters of ancestral belontiids are unknown. The following account represents an hypothesis of the formation of species in the genus Trichogaster with Figure 26 depicting the proposed scheme.

Liem (1963) has reviewed the suborder Anabantoidei and proposed a Macropodus-like ancestor for the genus Trichogaster. It is clear that as species diverge phylogenetically, as determined by structure, ecology, and distribution, observable reproductive behavior also diverges so that species from different species groups exhibit different reproductive behavior (Spieth, 1958). Since all species of Trichogaster are sympatric, each species must have evolved isolating mechanisms to keep populations from hybridizing.

Behaviorally, two separate "types" seem to have emerged in the genus Trichogaster. These groups include the "long spawners" which have long spawning, pseudospawning, and clasp bouts and the "short spawners" which have short spawning, pseudospawning, and clasp bouts. Long spawners also exhibit long clasp durations in spawning and clasp only bouts, shortened intervals between bouts, and the presence of rubbing or rubbing position. Short spawners, conversely, have shortened clasp durations in spawning and clasp only bouts, long intervals between bouts and no rubbing behavior. These differentiations probably are more important evolutionarily than are such characters as bout numbers. Differentiation in bout numbers seems to be primarily a species specific character that each species has evolved to fit its own particular pattern of reproductive behavior. Bout numbers would be little help in acting as isolating mechanisms between species. Durations however, play a critical role in synchronizing pairs in the actual spawning act.



Macropodus-like Ancestor

Figure 26. Hypothetical Phylogenetic Arrangement Within the Genus *Trichogaster*

It seems likely that two distinct groups of the *Macropodus*-like ancestor of the genus *Trichogaster* diverged behaviorally along the lines of short and long spawners. Morphologically, this division is evidenced by the long spawners possessing 6-8 dorsal spines while the short spawners have only 3-5 dorsal spines.

The group containing the long spawners (*T. trichopterus* and *T. pectoralis*) seems to have remained fairly homogeneous in courtship and reproductive behavior. Because rubbing and rubbing position are found nowhere else in the entire suborder Anabantoidei, this characteristic probably should be accorded special systematic significance in establishing natural relationships among species. Rubbing position may be older phylogenetically than the more complicated rubbing behavior, so *T. pectoralis* probably is the more primitive of the two species. It is reasonable to assume that rubbing position is intermediate between no rubbing and rubbing. *T. pectoralis* evidently found it advantageous to use rubbing position to stimulate females during spawning, but never progressed to the level of actual movement, while *T. trichopterus* added movement producing rubbing.

Short spawners (*T. microlepis* and *T. leeri*) are more specialized forms. Due to its reduction in dorsal spines, habit of night spawning, high number of spawnings per sequence, and low durations, *T. microlepis* is believed to be the most specialized of the short spawners, probably of the entire genus. The remaining short spawner, *T. leeri* seems to be fairly similar to *T. trichopterus* and *T. pectoralis* in many of its behaviors indicating it diverged less from the long spawners than did *T. microlepis*.

Conclusion

It is generally accepted that the more closely related species are the more their behavior patterns are similar (Spieth, 1958). Species that are very closely related may have almost identical reproductive behavior. The great similarities in courtship and reproductive behaviors of *T. trichopterus* and *T. pectoralis* suggest that these two species are the most closely related of the *Trichogaster* species. The unique motor pattern of rubbing in *T. trichopterus* and the intermediate form of rubbing position in *T. pectoralis* indicate definite close relationship. In addition, the two species exhibit approximately the same frequency of total bouts/spawning sequence, spawning bouts/ spawning sequence, intervals between bouts, and are the only two forms with extremely long spawning, pseudospawning and clasp bouts in the genus.

Morphological data support this contention, with *T. trichopterus* and *T. pectoralis* having relatively close meristic and morphological measurements, although great overlap exists in counts and measurements in the genus *Trichogaster*. Morphologically, *T. microlepis* seems to diverge from the other species more than they do from one another. *T. microlepis* possesses a reduced number of dorsal spines (3-4) whereas *T. leeri* has 4-5 dorsal spines, with *T. trichopterus* and *T. pectoralis* each having 6-8 dorsal spines. Myers (1958) listed reduction in spine number as a specialization in teleost fishes. Thus there seems to be a distinct differentiation between the *pectoralis*-*trichopterus* group at 6-8 dorsal spines and the *leeri*-*microlepis* group at 3-5 dorsal spines. Smith (1945) in his key to the species of *Trichogaster*, presented *T. microlepis* as the most distinctive form, whereas *T. leeri*, *T. trichopterus*, and *T. pectoralis* were separated on minor structural differences. He presented *T. trichopterus* and *T. pectoralis* as the two species most similar to each other. Regan (1909) merely listed the species and counts of each and did not indicate similarity.

It is believed that *T. microlepis* and *T. leeri* represent an off-shoot from the *pectoralis-trichopterus* type and represent quite specialized forms. Because of its many differences (often extreme) with other species of the genus *Trichogaster*, *T. microlepis* probably is the most specialized member of the genus. This species is adapted by its relative loss of coloration to night spawning (or spawning in dark areas), absent in other species of *Trichogaster*. Its loss of several behavior patterns, notably opercle spread, mouth fighting, and surface inspiration with surface release, plus reduction of male agonistic behavior throughout the spawning sequence and use of active incorporation of vegetation into the nest all suggest this species has a highly specialized reproductive cycle. *T. microlepis* has greatly increased spawning efficiency. Of an average of 44 bouts/spawning sequence, spawning and/or pseudospawning is achieved in 27 of the 44 or almost one of every two bouts during the spawning sequence. This could be viewed as a tremendous specialization by a species in its reproductive phase to actually spawn in one of every two bouts during a spawning sequence.

T. leeri represents a specialized form although its exact relationships with *T. microlepis* remain unclear. Due to its high number of bouts/spawning sequence, clasp bouts/spawning sequence, low circling duration, and high number of female butts during a spawning sequence this form is viewed as more specialized than either *T. trichopterus* or *T. pectoralis*.

CHAPTER XI

SUMMARY

T. pectoralis individuals in aquaria primarily confine themselves to nonagonistic maintenance activities. Of the comfort movements exhibited, chafes were most common while fin flicking was second in occurrence. Other comfort movements including flexing, yawning, coughing, and mouth snapping were noted.

Fright behavior is indicated by three types of behavior, i.e. flight, movement suppression, and aggregating. Fright behavior is most common in situations where a dominant approaches a subordinate, in male-female encounters, and adult-juvenile encounters. Movement suppression is common after agonistic encounters. Aggregating behavior is exhibited only when fish are frightened or placed into a new environment. Young come together in a loosely organized aggregation only under conditions of fright.

Courtship and reproductive behavior in *T. pectoralis* is stereotyped, and occurs in distinct temporal patterns. Acquisition of nuptial coloration usually is associated with establishment of a territory, increased aggressiveness, and nest building activity. The bubble nest of *T. pectoralis* is a raft-like structure composed of various-sized bubbles and extremely variable in size, depth, and shape. Incorporation of plant material into the nest is absent or rare. Four principal types of motor patterns exist in bubble blowing.

These are: surface blowing, sub-nest blowing, jetting, and opercular emission of a few large bubbles. Sub-nest blowing is of major importance in T. pectoralis and is most frequently used. Surface blowing is reduced while jetting and opercular emission are scarcely used in bubble blowing.

Males and females undergo marked changes in coloration during the reproductive cycle and these changes are discussed in the text as are non-reproductive color changes, mainly fright and agonistic coloration.

Leading to the nest by the male is absent in T. pectoralis. Instead, the female approaches the nest area swiftly, terminating her approach with a series of rapid butts directed at the dorsolateral region of the male. Following approach and butting by the female the male assumes a position beneath the female partially or completely folding his dorsal fin. This unique behavior is described for the first time and termed "rubbing position." Rubbing position lasts from 4-103 seconds with an average duration of 30.2 seconds. Subsequent to assuming rubbing position the male begins to curve his body into a semicircle and swim in a rather tight circle as the female moves into the circle. Circling is an especially important stage because of the high frequency of disruptions occurring at this stage. As the female swims into the curve she is clasped by the male. The entwined pair turn over as a result of these movements and end up with the belly of the female directed upward and the head of the male folded over her with head directed downward. Several seconds after this turn or "roll" is completed male ejaculation occurs prior to egg release. From 8-70 eggs are released at the termination of each spawning bout. As the male loosens the clasp the pair then enter a 2-12 second period of swimming inhibition. Females usually recover first and either swim from the nest area or are chased by the male.

Spawning sequences of *T. pectoralis* are quite short for species of *Trichogaster*. Shorter intervals between bouts help explain these shorter spawning sequences as the action bouts are quite long. Spawning bouts averaged 263.6 seconds, longest of any species of *Trichogaster*. That aggressive behavior is important in the spawning sequence is indicated by the fact that aggression only bouts comprised 26.06 per cent of all bouts. Male approach is the most frequent agonistic behavior during the spawning sequence and mouth fighting between the pair is quite common.

Only males gather eggs and subsequently place them in a thickened portion of the bubble nest. Incubation period of eggs is 18-28 hours. Males remain on guard beneath the nest up to nine days after spawning orienting toward any movement. They will attack potential predators whether it be a snail, conspecific, or the hand of the investigator.

An attempt was made to determine if a diel activity pattern exists in *T. pectoralis*. Results indicated that patrolling, inspiration, and total activity all show some type of diel pattern over a 24 hour period generally increasing from 0600 (lights on) until about mid-morning and decreasing until lights out (1800) and into darkness. Agonistic behaviors including approach, bite, and chase exhibit the same general patterns, i.e. increasing from an intermediate level in the morning hours (0600) to an afternoon peak at 1400, followed by a decrease until lights out and afterwards. That the same patterns for the three behaviors might be expected is explained by the fact that typical agonistic encounters between a dominant male and subordinate female are characterized by the sequence of approach, bite, and chase.

Because stereotyped courtship and reproductive behaviors have provided a rich source of material for studying the evolution of behavior, these stereotyped behaviors were selected for comparison among species of the genus *Trichogaster*. Differences were found among the four species of *Trichogaster* even in nest building behavior and motor patterns used in bubble blowing. Each species possesses certain unique behaviors. For example, rubbing occurs in *T. trichopterus*, rubbing position is found in *T. pectoralis*, while postcircling pause is characteristic of *T. microlepis* and terminal squeeze is found only in *T. leeri*.

Quantitative and qualitative data analyzed for the four species suggest that *T. trichopterus* and *T. pectoralis* are the most closely related of the *Trichogaster* species. Morphological data also support this contention. Although their exact relationships remain unclear, *T. microlepis* and *T. leeri* represent specialized forms distinct from *T. trichopterus* and *T. pectoralis*.

Behaviorally, two separate "types" seem to have emerged in the genus *Trichogaster*. These include the "long spawners" (*T. trichopterus* and *T. pectoralis*) and the "short spawners" (*T. microlepis* and *T. leeri*). The group containing the long spawners seems to have remained fairly homogeneous in courtship and reproductive behavior. The short spawners diverged to become more specialized forms the most specialized of which is *T. microlepis*.

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VITA

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Thesis: AN ETHOLOGICAL STUDY OF THE SNAKESKIN GOURAMI, TRICHOGASTER PECTORALIS, WITH COMMENTS ON PHYLOGENETIC RELATIONSHIPS AMONG SPECIES OF TRICHOGASTER (PISCES, BELONTIIDAE)

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Education: Graduated from Gosnell High School, Blytheville, Arkansas in 1963; received the Bachelor of Science degree, Arkansas State University, Jonesboro, Arkansas, May, 1967, with a major in Biology; received the Master of Science degree, Arkansas State University, Jonesboro, Arkansas, August, 1968, with a major in Biology; completed requirements for the Doctor of Philosophy degree at Oklahoma State University in May, 1971.

Professional Experience: Graduate teaching assistant, Arkansas State University, 1967-68; Graduate teaching assistant, Oklahoma State University, 1968-1970; Research assistant, Oklahoma State University, 1969 and 1971; Museum assistant, Oklahoma State University, 1970.

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