

AN ETHOLOGICAL STUDY OF THREE SPECIES OF
ANABANTOID FISHES (PISCES, BELONTIIDAE)

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PREFACE

The objectives of the present study were to: (1) adequately qualitatively describe and compare courtship and reproductive behaviors in three species of anabantoid fishes; (2) to establish phylogenetic affinities in behavior; (3) to understand the biological significance of observed behaviors; (4) to link these observed behaviors with underlying causal factors. Qualitative and quantitative data were obtained and analyzed for all three species.

Dr. R. J. Miller served as major adviser and spent much time assisting with various phases of the study. Drs. George A. Moore, Roy W. Jones, Larry T. Brown, and D. E. Bryan served on the advisory committee and criticized the manuscript. Fred Rainwater helped with various phases of the study and Mrs. Frank Roberts typed the manuscript. The assistance of all these people is greatly appreciated.

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CHAPTER I

INTRODUCTION

This study on the comparative ethology of paradise fish, Macropodus opercularis (Linnaeus); pearl gouramis, Trichogaster leerii Bleeker; and blue gouramis, Trichogaster trichopterus (Pallas) deals primarily with courtship and reproductive behavior of breeding pairs in aquaria. The study was conducted in two phases. The first dealt with observation of complete behavioral patterns in the three species. The second dealt with quantification, recording, and analysis of courtship and reproductive behaviors.

Relatively little detailed information is available on the courtship and reproductive behaviors of these fishes or the evolution and biological significance of these behaviors. Even less is known regarding underlying causal factors. Therefore, the objectives of this study were to adequately qualitatively describe courtship and reproductive behaviors in these three species; to compare behaviors and establish their phylogenetic affinities; to understand the biological significance of observed behaviors and to link these observed behaviors with underlying causal factors.

The sub-order Anabantoidae is comprised of 15 genera and approximately 50 species (Liem, 1963). This group is well-suited for laboratory studies in behavior since it provides much behavioral, morphological, and ecological diversity and is geographically widespread.

Social behavior in anabantoid fishes is characterized by the presence of many different stereotyped actions, and rather distinct temporal patterns of behavior. Most anabantoids are small, hardy, easily sexed, fast-growing, and require only simple foods. Most reach sexual maturity in less than twelve months (Forselius, 1957) and breed well in aquaria in limited space.

Few qualitative or quantitative behavioral studies have been done on the group. Courtship and reproductive behavior is often described as "similar in all species" or "typical of the family" with no reference to gross differences in elements of behavior or temporal differences in behavioral patterns.

Numerous studies dealing with many aspects of anabantoid behavior, morphology, embryology, and physiology have been reported in the past 50 years. Some of these are: Lissmann (1932); Amirthalingam (1939); Kulkarni (1943); Smith (1945); Scharrer, Smith, and Palay (1947); Steinbach (1950); Hodges and Behre (1953); Lindsey (1954); and Hisaoka and Firlit (1963). Some of the more useful works used in the preparation of this paper are listed below.

A monograph by Forselius (1957) deals primarily with behavior in the genus Colisa and especially the behavior of the hybrid between C. lalia and C. labiosa. Also included is a review of the systematics, distribution, endocrinology, and ecology of the anabantoid fishes.

Liem (1963) in a monograph dealing with the osteology and phylogeny of anabantoid fishes also reviews the systematics of the group and deals briefly with some ecological factors presumably involved in the evolution of the group.

Picciolo (1964) described sexual and nest discrimination in several anabantoid fishes, including Colisa and Trichogaster species.

Miller (1964) described social behavior in T. trichopterus and included data on motor patterns, nest-building, and reproductive behavior. Also included are references to certain aspects of courtship and reproductive behavior in T. leerii.

A major problem encountered was the determination and delimitation of discrete blocks and units of behavior for analysis. This problem probably deserves most attention since it is commonly encountered in ethological studies. Russell et al. (1954) have stated: "A single behavior pattern can be broken up into recognizable and stereotyped fragments of behavior," which they have called acts. A strict application and usage of the term act has not been attempted in this paper, but instead an attempt has been made to break the behavioral patterns into meaningful units for ease in discussion and analysis.

The problem of simultaneously obtaining both qualitative and quantitative data was circumvented by use of prepared data sheets, tape recorder, multiple observers, and other techniques.

An attempt was made to record and quantify courtship and reproductive behaviors in relevant units to facilitate and clarify the qualitative description of these behaviors. Through quantification, precise comparisons could be made between genera and species. The quantitative data obtained will serve as the basis for subsequent papers dealing with quantitative aspects of courtship and reproductive behavior in these fishes.

The problem of analyzing motor elements occurring in different

combinations in different, but closely related species, was partially solved by using still and motion picture analyses.

Variation in human interpretation of overt behaviors posed another problem which was eliminated by use of standard codes and predetermined criteria for delimiting certain blocks and units of behavior.

CHAPTER II

MATERIALS AND METHODS

This study was conducted in the Constant Temperature Room of the Oklahoma State University Aquatic Biology Laboratory. The temperature of this room was held at approximately 24-27 C for the duration of the study.

Materials

At least 6 pairs of T. leerii, 5 pairs of M. opercularis, and 10 pairs of T. trichopterus were maintained during the study. All fishes were breeding or near-breeding age when paired. Sizes ranged from approximately 40 to 90 mm standard length for all species. An attempt was made to pair males and females of equal size to prevent aggression and lessen the danger of infection and mortality. Most fishes used in the study were obtained from aquarium dealers in Stillwater and Oklahoma City. Some fishes were reared at the laboratory for latter parts of the study. Fishes were fed mainly Daphnia, dried foods, and midge larvae.

The thirty-seven aquaria used ranged in size from 57 x 30 x 16 cm to 77 x 42 x 33 cm with volumes of 31.7 to 126.8 liters, respectively. Most fishes were kept as pairs, but in a few cases 2 pairs, 2 males and 1 female, or 2 females and 1 male were maintained in large aquaria.

The gravel bottom of each tank was planted with Vallisneria and Ceratophyllum. Each tank was equipped with at least one standard aquarium thermometer and one thermostatically-controlled electric aquarium heater.

Lighting was provided by overhead fluorescent and incandescent lights, as well as individual aquarium reflectors with 25-40 watt incandescent lamps. A 12-hour photoperiod was maintained by means of electric appliance timers. No effects on behavior or spawning efficiency due to photoperiod, lighting, or aquarium size were discernible.

Qualitative observation was facilitated by use of notebooks, prepared data sheets, stopwatches, and a "Mohawk 400" tape recorder. Photographic analysis was provided by the following: 4 x 5 Polaroid Press Camera; Exakta 35 mm camera with flash attachment; Bolex 16 mm Movie Camera with electric motor; Bell and Howell Time Motion Analysis 16 mm Movie Projector; rheostat, photographic hoods, and photoflood lamps. Quantitative data were obtained, transformed, and analyzed by use of an Esterline-Angus Event Recorder, Esterline-Angus Tape Reader, "time ruler" (an ordinary ruler with divisions marked in seconds corresponding to divisions of record charts), graph paper, data sheets, and summary charts.

Methods

Written data were obtained primarily by daily or twice-daily 15-minute observations per tank. These periods were long enough to determine if anything significant was happening, but short enough so that little time was wasted if no significant behavior was in progress.

Data were recorded for water temperature, barometric pressure, form and structural features of bubble-nests (if present), colors of male and female, and general types of behavior occurring during the observation period. These observation periods were useful adjuncts to quantitative recording because of observed indicators of spawning readiness.

Quantitative data were obtained mainly by use of the Esterline-Angus Event Recorder during the 2-5 hour-long spawning sequences. The primary advantage in use of the Event Recorder lies in the fact that complete, permanent behavioral records for both male and female can be obtained simultaneously. This method of recording provides information on frequency and duration of the behavioral element, its temporal relation to other elements in the same series, and intervals between bouts over a given period of time. Once precise units of behavior were determined, standard keyboard codes were used for each species throughout the study. Most recordings of courtship and reproductive behavior were made at a chart speed of 1 1/2 inch per minute, which was adequate for resolution of all types of behavior occurring in such bouts. Recording was facilitated by placing symbols in a logical sequence on the keyboard, i.e., keys were coded in a linear series corresponding to observed behaviors and could be easily manipulated as the series continued from one type of behavior to another. Recordings were made of 15 partial or complete spawning sequences in T. leerii, 6 sequences in M. opercularis, and 3 sequences in T. trichopterus. Of these, 15, 1, and 3, respectively, were transformed into analyzable terms and used to describe qualitatively courtship and reproductive behaviors in the three species.

CHAPTER III
STRUCTURAL AND BEHAVIORAL CHARACTERISTICS
OF ANABANTOID FISHES

Taxonomy

The anabantoid fishes are Old World fishes ranging from Africa to China. Most are tropical or sub-tropical in distribution and occur throughout Southern Asia, India, and Central Africa. Most are inhabitants of lower altitudes with few species found above 1000 meters (Forselius, 1957).

The sub-order Anabantoidei is comprised of four families: Anabantidae, Belontiidae, Helostomatidae, and Osphronemidae (Fig. 1). Forselius (1957) lists 17 genera and approximately 50 species for the sub-order. The family Belontiidae is comprised of 3 sub-families, 10 genera, and approximately 22-25 species (Liem, 1963). The three species considered here belong to the sub-families Trichogasterinae and Macropodinae of the family Belontiidae.

The two Trichogaster species are sympatric, whereas M. opercularis is a more northerly species and shows little if any geographical overlap with the Trichogaster species.

Unifying Characteristics in the Family Belontiidae

In general, there are three unifying characteristics in the family

Belontiidae. These are: presence of a labyrinth, construction of a bubble-nest which is used as a repository for the eggs, and utilization of a nuptial embrace or clasp to effect fertilization of the eggs at spawning. One finds exceptions with regard to these characteristics, but they are true for most of the 22-25 members of the group.

Labyrinth. The labyrinth is an arborescent organ located in the preopercular, dorsolateral region of the head. It is comprised of bilaterally arranged, dorsomedially oriented, pharyngeal outpocketings enclosing four bony lamellae, all covered with heavily vascularized epithelium (Alpert and Ebeling, 1963). The labyrinth is derived from the epibranchial of the first gill arch and lies within a moist chamber above the gills, i.e., within the suprabranchial cavity.

The gills are functional, but appear to be inadequate to sustain life for prolonged periods of time. Most, if not all, members of the family are directly dependent upon atmospheric oxygen to some degree for respiration. Accessory respiratory organs are probably an adaptation for the habitat in which these fishes are found: shallow, stagnant, anoxic waters. In order to ventilate a respiratory system with small quantities of oxygen diffused in water, large quantities of water must be moved over the gills. High concentration of oxygen in air permits fulfillment of aeration with lower energy expenditure by air-gulping.

Bubble-Nest. The beginning of a reproductive cycle in males of all three species is usually marked by color changes, increased aggressiveness, formation of a territory, and initiation of bubble-blowing behavior that eventually results in the formation of a nest of varying size, shape,

and depth at the air-water interface. The bubbles are formed from air inspired at the surface, which is then transformed into small bubbles in the oral cavity and coated with mucus which is secreted by unicellular glands that line the cavity. The bubbles are then expelled in groups of 2-10 large bubbles in M. opercularis or as clouds of tiny bubbles in T. leeri and T. trichopterus. Various bubble-blowing motor patterns are observed in males of these three species.

In T. leeri the following patterns were observed: surface blowing; gulp-drop below nest blowing; opercular emission of many small bubbles; jetting; and opercular emission of a few large bubbles. Surface blowing is typical during early nest-building stages or during the parental phase following hatching of eggs. This behavior entails the gulping of air at the surface and immediately expelling bursts of bubbles which tend to form diffuse, shallow, "raft type" nests. Gulp-drop-below-nest blowing involves inspiration of air at the surface, moving to a position below the nest by use of the caudal and pectoral fins, and expulsion of clouds of small bubbles. This is typical of prespawning males and usually results in deepening of the nest. Opercular emission of several small bubbles was also observed. After inspiring air at the surface and moving to a position below the nest, bursts of bubbles were emitted from beneath the opercles. This occurred at the termination of a spawning sequence and may aid in aeration of eggs. Jetting (emitting bursts of air and water through the nest) has been observed in postspawning males. This is accomplished by projecting the snout above the surface, gulping air, moving to a spot below the nest, and forcefully squirting air and water through the nest. This may function in providing a frothy nest

for eggs and fry. Opercular emission of a few large bubbles was seen in prespawning males. This differs from the other form of opercular emission in number and size of bubbles, as well as the context in which it was used. It may also function in creating a deeper, frothier nest.

At least four types of motor patterns are involved in T. trichopterus bubble-blowing. These are: surface blowing; gulp-drop-below-nest blowing; jetting; and opercular emission of a few large bubbles. The motor patterns are quite similar to those observed in T. leerii. Opercular emission of many small bubbles has not been observed in this species.

Three motor patterns have been observed in male M. opercularis bubble-blowing. These are: gulp-drop-below-nest blowing; jetting; and opercular emission of a few large bubbles. Surface blowing and opercular emission of small bubbles has not been observed in this species. A variation in bubble-blowing behavior occurs in M. opercularis in which females regularly take part in nest-building activities. Nest-building by Trichogaster females was almost never observed. An M. opercularis female may work side by side with the male under his nest or may work on a separate nest, usually small and ill-formed. Nest-building by M. opercularis females may be inhibited by overly large and/or aggressive males. Gulp-drop-below-nest blowing was the only form of bubble-blowing observed in females of this species.

Variation occurs in number of inspirations preceding expulsion of bubbles. T. leerii males inspire 1-9 times, T. trichopterus males from 1-40 times (Miller, 1964) and M. opercularis males 1-5 times.

Vegetation may be included in bubble-nests of all three species,

but is not essential. Spawning may occur in all three species in the absence of a bubble-nest, but nest construction by males usually follows in such cases. It appears that the bubble-nest serves several functions. It provides a means of maintaining the developing eggs and young at the air-water interface where atmospheric oxygen is available for respiration; it serves to localize eggs and young for ease in tending by the male; and it serves to keep him in a limited area, thus making him more conspicuous to females and possibly facilitating repeated spawnings with one or more females.

A major disadvantage may be the vulnerability of the male (or M. opercularis female) because of the contrast in color with the nest, i.e., a dark male or female beneath a white bubble-nest would seem to offer a well-defined target for predation. This problem may be minimal in nature where the bubble-nest is built in areas with dense aquatic vegetation.

Even though most anabantoid genera use a bubble-nest as an egg repository, the form of the nest, materials, and methods used to construct the nest vary greatly, even at the species level.

Clasp. A spawning clasp is not unique to anabantoid fishes. Barlow (1962) stated that various members of the families Nandidae, Cyprinidae, Percidae, and Cottidae also utilize a clasp or spawning embrace during the reproductive act. Most, however, are very different from the anabantoid clasp. The clasp is an efficient method of reproduction insuring maximum fertilization of eggs. The high degree of fertilization is presumably brought about by the close juxtaposition of the genital pores during the nuptial embrace. The clasp may also facilitate egg

release through pressure of the male's enfolding body on that of the female. The clasp duration and form varies greatly among these three species, but the following elements are usually observed immediately preceding and during the clasp: approach of the female or proper orientation by the female if already present under the nest, female butting or thrusting, preliminary male clasp as female mounts, firm clasp, roll of clasped pair, quivering by both individuals, ejaculation and egg release, and clasp release.

In all three species clasping and spawning usually occur directly under the bubble-nest. The clasped pair may remain close to the surface or sink far below the nest before ejaculation and egg release occur. In the Trichogaster species buoyant eggs float upward into or near the bubble-nest. Trichogaster males usually gather floating eggs and consolidate these into a small, deep nest. Trichogaster males usually move actively about the nest area blowing bubbles, moving eggs within the nest, and defending the nest against intruders. Trichogaster females usually hide, or remain far away from the nest and do not retrieve eggs or aid in nest-care.

M. opercularis eggs are somewhat demersal when released and may sink to the bottom if not retrieved by male or female. Eggs of this species are less adhesive than those of Trichogaster species and are easily dislodged by movements under the nest. Egg retrieval appears to be facilitated by joint efforts of both sexes, but the added movements of the female appear to dislodge eggs, thus creating more work for both male and female. The female often retrieves eggs from the bottom, carried them to a spot below the nest, and spits them out. The male

then mouths and spews these into the bubble-nest with small bubbles attached. Little or no female bubble-blowing has been observed during postspawning egg retrieval. Eggs are often not concentrated into compact, deep nests. Density of eggs, lack of adhesiveness, and random female egg-retrieval movements probably account for the diffuse, shallow post-spawning nests and scattering of eggs often observed in this species.

No correlation between size of male (or female) and size or form of nest was detected in these three species. Neither was there evidence for a "critical nest size" (Braddock and Braddock, 1959) necessary for spawning. Spawning in the absence of a nest and under small, ill-formed nests argues against such a "critical nest size" phenomenon in these fishes.

Morphological Characteristics

Morphological, osteological, and general characteristics of the three species are summarized in Table I. Examination of these and foregoing characters will provide a general description of the fishes and activities studied.

Phylogenetic relationships of the various groups within the suborder are indicated in Fig. 1 (adapted from Liem, 1963).

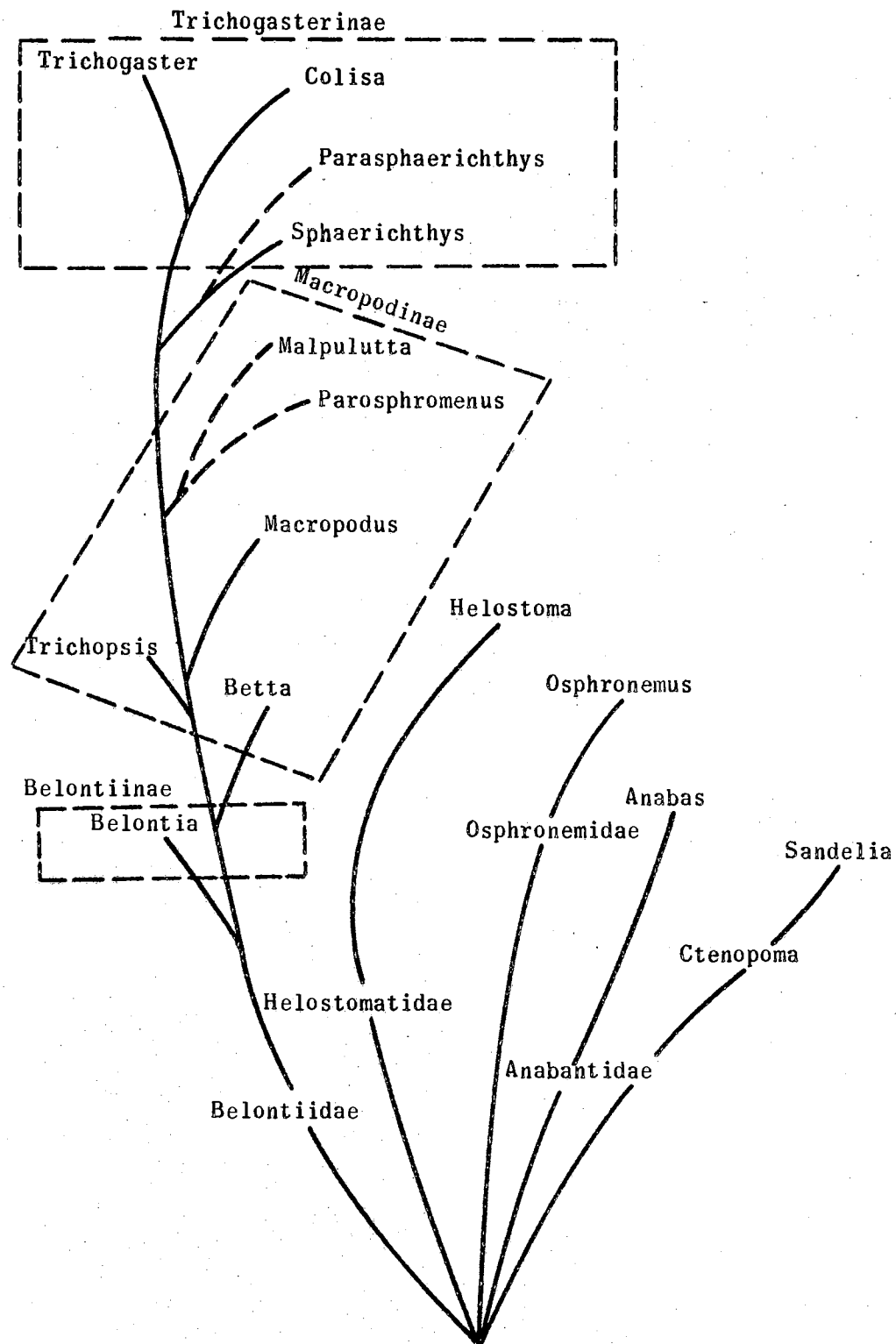


Fig. 1. Proposed Phylogenetic Relationships Within the Sub-Order Anabantoidei (from Liem, 1963).

TABLE I
SUMMARY OF STRUCTURAL AND GENERAL CHARACTERISTICS OF *T. leeri*,
T. trichopterus, AND *M. opercularis**

Characteristic	<i>T. leeri</i>	<i>T. trichopterus</i>	<i>M. opercularis</i>
Habitat	Malay Peninsula, Sumatra, S. E. Asia	Cochin China, Thailand, Malay Peninsula and Archipelago	China, Cochin China, Formosa, Loo Choo Islands
Depth of Body	2.25-2.67 in the length	2.00-2.67 in the length	2.80 in length to base of caudal fin
Dorsal Fin	V-VII, 8-10	VI-VIII, 8-9	XIII-XVII, 6-8
Anal Fin	XII-XIV, 25-30	X-XII, 33-37	XVII-XX, 11-15
Pectoral Length	as long as head	as long as head	not as long as head
Scales in Lateral Line	30-36	30-40	30-40
Scales in Longitudinal Series Above Lateral Line	44-50	40-52	35-40
Color	body and vertical fins with pale greenish spots enclosed in a reddish-brown network; much orange, red, violet, brown and green	head and body with or without somewhat oblique dark crossbands, which may be broken up into spots; much gray, blue, and black	body with or without dark crossbars; sometimes with irregular silvery bars; much blue, red, black, orange, silver
Marks	dark lateral horizontal band from base of caudal fin through eye to tip of snout; spot at base of caudal fin	a round black spot on the middle of the side and another at the base of the caudal fin; small, pale, and dark spots in dorsal, caudal, and anal fins (may form reticulations)	a round black or greenish-blue spot at the rear extremity of the operculum
Size	up to 100 mm in total length	up to 120 mm in total length	up to 80 mm in total length
Diameter of Eye	1.60 in the length of the post-orbital part of head (in 100-200 mm specimens)	2.00 in length of post-orbital part of head (in 100-200 mm specimens)	3.90 in length of head (in 36 mm standard length specimens)
Special Features	first pelvic ray produced into a long, unarticulated filament; lateral line present and steeply elevated anteriorly; anal and dorsal soft-ray extensions in breeding males	first pelvic ray produced into a long, unarticulated filament; lateral line present and steeply elevated anteriorly	long extensions on median fins; small scales on the fins in addition to the basal sheath; soft vertical fins sometimes produced when caudal becomes bilobed
Number of Trunk Vertebrae		10	9
Number of Caudal Vertebrae		20-21	17-19
Total Number of Vertebrae	30-31	30-31	26-28
Number of Interneurons	9	6-10	3-4
Number of Dorsal Pterygiophores	14		20-21
Number of Anal Pterygiophores	44		29-34
Number of Pleural Ribs	24		15-16
Number of Epipleural Ribs	10		15
Number of Pelvic Fin Rays	5 (and spine present)	5 (and spine present)	5 (and spine present)
Number of Branchiostegal Rays	5 (all joined to ceratohyal)	5 (all joined to ceratohyal)	6 (all joined to ceratohyal)
Number of Teeth on Parasphenoid	0	0	2-5

*Partially adapted from Liem (1963), Smith (1945), and Nichols (1943)

CHAPTER IV

MOTOR PATTERNS AND TERMS USED IN THE STUDY

Forselius (1957) and Miller (1964) have described in detail motor patterns of several anabantoid species. These descriptions will serve as a basis for the subsequent discussion of motor patterns in the species considered here.

Motor Patterns

Frontal Display and Opercular Erection. Frontal display with concomitant opercular erection is commonly observed in M. opercularis, but is rare in the two Trichogaster species. The displaying fish may be in front of or may face the other fish. Mutual display is commonly seen if neither fish is clearly dominant. In full display the median fins are usually fully erected, gill covers maximally extended, and branchiostegal membranes extended. Opercular ocelli are well developed in M. opercularis and attacks are commonly directed at the side of the head in the region of these spots. Frontal display often develops into biting, butting, mouth-fighting, tail beating, chase, and other aggressive behaviors.

Lateral Spread Display and Sigmoid Display. The lateral spread display is one of the most common displays in courtship and fighting behavior in these fishes. The displaying fish may be oriented at any angle to

the other fish, but usually is either directly in front of or parallel to it. At its lowest intensity there is a slight erection of the median fins and a slight spreading of the caudal fin. At high intensity median fins and caudal fin are maximally spread. At high intensity in T. trichopterus males the caudal fin and caudal peduncle are arched upward creating a bowed condition (Miller, 1964). At maximum intensity the body is curved laterally into an S-shape (sigmoid posture) and the display often develops into other activities, such as tail beating, biting, mouth-fighting, and butting. These also often occur simultaneously with lateral spread display. Sigmoid display in M. opercularis is more pronounced because of long dorsal, anal, and caudal fin extensions and the elongate body.

Vibrating. Vibrating (Forselius, 1957) has been observed only in M. opercularis. "It is a spasmodic vibration that pervades the whole fish body from head to caudal fin ...," (Forselius, 1957). This undulatory movement usually occurs with the pair in a head to head or head to tail position. The pectoral and pelvic fins flutter rapidly as both individuals vibrate, producing a jerky and uncoordinated movement. Vibrating may be brief or prolonged and may be repeated several times in succession. It often occurs prior to and after spawning periods. Sexually non-receptive females commonly show this response to male lateral spread display.

Biting and Butting. Biting appears to be the most effective aggressive behavior. The mouth is open, the fish attacks and grasps body or fins with its teeth. Butting is a thrusting with the lips against the

opponent's body without attempts to bite. Butting and biting vary in force and frequency with the situation. Butting usually occurs in less aggressive situations while biting usually indicates high aggressiveness. Butting and biting were observed in males and females of all species. T. leerii females appear to be more docile than other females with little biting or butting directed at males in agonistic situations. M. opercularis females appear to be most aggressive and often show biting, butting, and other aggressive behaviors toward males.

Chasing. Chasing involves fleeing of one fish with another in pursuit, usually biting or attempting to bite the pursued. The fleeing fish usually swims away from the attacker at moderate to high speed with fins folded. Male chasing commonly occurs after spawning in the Trichogaster species when the female recovers from swimming inhibition and swims slowly away from the nest. Chases may be brief or prolonged, single or repeated.

Tail Beating. Tail beating occurs during the lateral spread display in all species and is usually performed when the displaying fish is directly in front of or alongside the other fish. It typically consists of undulating thrusts of the tail and caudal peduncle toward the other fish. The undulating movements vary in force and duration and may be performed by one or both fish. Reverse beats of the pectoral fins prevent forward movement. Tail beating is often seen in agonistic situations, but also occurs during courtship and reproductive behavior, particularly during pre- and postspawning phases when a lateral-displaying male is not receiving an appropriate sexual response (following, courtship butting, mounting) from a female.

Circling. Circling, curving, and clasping appear to comprise a functionally related group of activities. After preliminary courtship activities in the Trichogaster species, the male curves his body and begins to circle slowly. The female usually remains within the semi-circle of the male's body with her snout near his dorsum. Clasping occurs simultaneously as the female mounts. The head and caudal fin of the male are brought closer together to clasp the anterior half of the female's body. Little or no circling or preliminary courtship activity is observed in M. opercularis. The male usually curves the body, the female mounts immediately, and clasping follows. Prolonged circling often leads to incomplete bouts in the Trichogaster species. "The more a male circles, the greater is the chance that the female will lose her orientation to him, and the greater the chance he will cease behaving sexually and chase her," (Miller, 1964). Circling movements are effected primarily by means of the pectoral fins. Degree of median fin erection is variable, but in most cases these fins are partially or fully erected.

Appeasement Postures. Several behaviors with some appeasing function are observed in the three species. Appeasement is seen most often in females being harassed by males, but dominated males may also show it. Median fins are folded, the caudal fin often droops, and the fish often tilts laterally. Sometimes the body is tilted vertically, either upward or downward. Appeasement appears to be only mildly successful in inhibiting male aggression. Lateral and vertical appeasement are commonly seen in M. opercularis females while approaching males under the nest. Lateral and vertical tilting are seen in males and females of all species.

Head-snapping is sometimes seen in T. leerii. The head is snapped sporadically sideways. Median fins are completely folded and the caudal fin droops as it occurs. It is seen most often in females during conflict situations, but has also been seen in males while attempting to lead-to-the-nest. J-shape and waggle dance appeasement were seen only in M. opercularis. J-shape appeasement commonly occurs in females, but may also be shown by inferior males. It is usually performed with the longitudinal axis of the body perpendicular to the bottom of the tank with the head pointing upward. Flexure of the caudal fin and caudal peduncle results in a distinct J-shape which is usually maintained for 1-2 seconds. This often develops quickly into the waggle dance, consisting of low frequency undulating movements of the caudal fin and caudal peduncle of a fish in vertical or near vertical position. Waggle dancing resembles tail beating, an aggressive behavior, except that the body is oriented differently and the frequency of undulation is less than that of aggressive tail beating.

Leading- and Driving-to-the-Nest. Leading-to-the-nest was observed in males of all species. This commonly occurs in early phases of a spawning cycle, but is sometimes seen in postspawning males. Typically, the male approaches a female, gives a lateral spread display, then turns and swims slowly back to the nest with fins erected and the body in a sigmoid curve. Leading can be carried out in stages with the male stopping, backing up, or turning and moving back to the female to begin again. A sexually responsive female may follow the male to the nest where leading then changes to other courtship activities. In T. trichopterus the male sometimes gets the female to the nest by swimming beside her while in

full lateral spread display and pushing her with head and body toward the nest (Miller, 1964). Driving-to-the-nest was not observed in T. leeri or M. opercularis. "Zigzag leading" as described by Forselius (1957) for Colisa lalia males was not seen in Trichogaster or M. opercularis males.

Female Courtship Butting. Almost all Trichogaster spawnings are preceded by female butting. In T. leeri the male caudal ocellus and lateral horizontal band do not appear to serve as targets for female butting. In T. trichopterus fewer female butts are seen and these are usually directed at the area between the lateral and caudal spots. The spots on the side and caudal peduncle do not appear to serve as targets for female butting (Miller, 1964). A highly sexual Trichogaster female can often inhibit the attack of a male that has turned to chase her by butting him ("self protection butting"). Female courtship butting is greatly reduced or absent in M. opercularis females. In most spawnings no contact is made prior to the clasp.

Female courtship butting appears to release leading, lateral spread display, and curving in sexually responsive males. Female thrusting in M. opercularis apparently serves the same functions as butting in Trichogaster females.

Rubbing. Rubbing occurs only in T. trichopterus. After male and female are under the nest the male drops under the breast of the female and slowly moves back and forth. Orientation is variable, but both usually face in the same direction. The male's dorsal fin is completely depressed. The dorsum and folded fin often brush against the venter of

the female. The anal fin is partly or fully spread and the pelvic fins extend forward and outward. The female's dorsal fin is partially folded, her anal fin is spread wide and pelvic fins are held diagonally backward (Miller, 1964).

Mounting, Clasping, and Roll. As the male circles (curves) the female moves into the U-shaped flexure with her snout protruding beyond the male's back just anterior to the origin of his dorsal fin. A slight lateral tilting of the male's body may occur as she mounts. If movements are executed properly he then clasps her tightly. In all species quivering of body and fins was observed after initiation of the clasp. In T. leeri the soft-rayed portion of the male's dorsal fin may be flexed to cover the eye of the female nearest his caudal peduncle. The clasped pair may remain "upright" for a few seconds (Trichogaster species) or may roll over almost immediately (M. opercularis). The roll appears to be effected primarily by movements of the male's free pectoral fin and movements of the female's caudal fin, caudal peduncle, and anal fin. After the roll the genital pores of both male and female are usually close to the bottom of the bubble-nest. Quivering continues as sex products are released. Clasp release follows and both male and female enter swimming inhibition.

Terminal Squeeze. This unique phase of the clasp motor pattern was observed only in T. leeri males. Near the end of a spawning bout, a relaxation of the clasp is followed immediately by a convulsive tightening of the male's body on that of the female. The forceful muscular contraction is presumably associated with ejaculation by the male. It may promote egg release by mechanical pressure on the female's abdomen.

Swimming Inhibition. This occurs in all three species. Immediately after spawning and pseudospawning bouts the male loosens the clasp and both male and female enter a 2-10 second period of swimming inhibition. Both are relatively immobile and tend to lose their orientation to one another. Both may sink far below the nest before recovering. Females of all species tend to recover first. In Trichogaster, swimming inhibition often ends abruptly with female fleeing and subsequent male aggression. In M. opercularis the female often remains and aids in nest-care and egg retrieval.

Terms

Bout. Any social interaction. It may contain any combination of the activities noted above.

Sexual Bout. This term will be used to denote only male-female interactions that contain sexual responses by one or both partners. Female approach, following-to-the-nest, courtship butting, and waggle dance were behaviors used to judge sexual responsiveness in females. Rubbing, leading-to-the-nest, driving-to-the-nest, lateral spread display, sigmoid display, curving, and clasping were used as sexual response criteria in males.

Spawning Sequence. This refers to the complete series of male-female interactions (bouts) comprising prespawning, spawning, and postspawning activities. These sequences are of variable duration, but usually last 2-5 hours. These are comparable to "mating cycles" of Forselius (1957).

Spawning Bout. This term will be used to refer only to sexual bouts

in which gametes are released by both partners. It is a collective term including all movements and activities between male and female in connection with the fertilization process. This is comparable to a "spawning cycle" of Forselius (1957).

Pseudospawning Bout. This refers to a sexual bout, similar in form to a spawning bout, in which one or both sexes fail to release sex products.

Incipient Spawning Bout. Sexual bouts that do not reach the spawning or pseudospawning stage have been termed "incipient spawning acts" by Forselius (1957). These bouts vary from mild female butting to attainment of the clasp.

CHAPTER V

QUALITATIVE DESCRIPTION OF COURTSHIP AND REPRODUCTIVE BEHAVIOR

Schiller (1957) defined the term "ethogram" as, "A broad and detailed description of the normal behavior of a species." Since a complete description of all the behaviors of any species has not yet been made it is probably legitimate to use the term for a "broad and detailed description of any phase of normal behavior," such as courtship and reproduction.

An "ideal spawning bout" may be defined as a sexual bout in which gametes are released and there appears to be an economy of effort and little male or female aggression. Constituents of such a bout are difficult to determine precisely for T. leeri, but the following ethogram (Table II) is an attempt to describe qualitatively the stages or phases judged basic. Of the approximately 7% of all sexual bouts that reach the spawning stage, few follow the exact form outlined in the ethogram.

The divisions of the following ethograms do not represent acts in the sense of Russell, et al. (1954), but are designed only for a meaningful discussion of the reproductive actions observed in the three species. Obviously, some of the units of the ethograms could have been broken down further, but such a detailed analysis was not deemed appropriate at this stage of the study.

TABLE II
TRICHOGASTER LEERI ETHOGRAM

Male		Female
1a. acquires nuptial coloration; establishes a territory; initiates nest-building; attains physiological readiness to spawn		1b. acquires nuptial coloration; attains physiological readiness to spawn ↓
2. stops nest-building; often gives brief lateral spread display; may show aggressive behavior	←	2. female approach (variable in form and duration)
3. male curving (U-shape posture)	↗	3. female butts male on anal fin, sides, and dorsal half of the body
4. male preliminary clasp	↘	4. female mounts
5. roll and quivering	↗	5. female curves body into sigmoid posture as male initiates clasp
6. male terminal squeeze and ejaculation	↘	6. female quivering
7. male clasp release	↗	7. egg release
8. swimming inhibition	↘	8. swimming inhibition ↓
9. male chases, bites, and butts	↗	9. female swims slowly away from nest
10. male bite, butt, and lateral spread display	↘	10. fleeing and/or appeasement
11. returns to nest-building and nest-care	↗	11. remains stationary on bottom away from male's nest with occasional surfacing and feeding

Discussion of T. leerii Ethogram

Stages 1a and 1b. These are necessary preliminary phases in both male and female and vary greatly in duration. In T. leerii nest territoriality and nest-building appear to be functions of males only.

2. Female Approach. The female approach typically consists of a quick movement up to the male under the nest, but often takes the form of apparently hesitant, stop and go movements toward the male. The female may also swim up and down ("fluttering") along a wall of the aquarium while far away from the male. This may continue for a minute or more and may be terminated by a male approach, often followed by male aggression, or direct approach. She may, however, stop and return to the bottom of the tank. Fluttering occurs mainly in pairs where the male is highly aggressive and the female has a low threshold for flight responses.

The male stops nest-building and folds the dorsal fin during or subsequent to the female approach. Approach appears to be facilitated when the male turns so that the female does not have to approach head-on. This is a critical stage in reproductive bouts and male aggression (biting, butting, chasing) is common at this stage. The sexually responsive male gives the lateral spread display which is usually followed by female courtship butting.

3. Female Courtship Butting. Much female butting usually precedes a spawning. Between 20-30 butts are directed at the anal fin, sides, and the dorsal half of the male's body. Female butts on the dorsal half of the body are typically followed by curving and/or circling by the male.

Prolonged male circling frequently indicates a forthcoming breakdown of the sexual bout. Often the male circles behind the female and attempts to bite and/or butt her on the anal and caudal fins. Male curving or simply forming a U-shaped posture appears to be the ideal situation. Curving usually involves a slight lateral tilting of the male's body as the female mounts. The female usually mounts immediately as the male forms the U-shape posture. Failure to mount may result in more male circling and male aggression, or more female butting and ultimately more curving by the male.

4. Female Mounting. The female swims into the curve with her snout just anterior to the origin of the male's dorsal fin. Male clasping occurs simultaneously with female mounting. The female anal spines are usually erected during mounting. The male operculum in contact with the female's body is usually extended toward her and may exert pressure on her abdomen, possibly facilitating egg release. The pelvic fins of both fish do not appear to be used in any special way during mounting or subsequent clasping. Proper mounting and proper orientation of the female within the clasp are important for continuation of the spawning bout. Some adjustments are possible by both male and female, but not to the extent observed in M. opercularis. Some of the factors that appear to be responsible for breakdowns at this point are: improper orientation of either male or female, hyperaggressiveness in either male or female, loud noises, sudden movements outside the tank, and sudden increases in illumination.

5. Female Sigmoid Posture. Female sigmoid posture is usually observed

as the male initiates the clasp. In this position the female fits tightly into the male clasp. The exact function of the posture has not been determined, but may be important in facilitating egg release. It may also be of value in rolling the clasped pair or may aid the male in attaining a firmer clasp on the body of the female. The female remains upright for several seconds with the male clasping the anterior half of her body. The enfolded pair then rolls over, accompanied by movements of the female's caudal peduncle and caudal fin, as well as movements of the male's free pectoral fin and caudal fin.

6. Female Quivering. Female quivering of body and fins may be pronounced, especially as the moment of egg release approaches. During egg release the female is usually in an inverted position directly beneath the bubble-nest with her genital pore in close proximity to that of the male and to the bottom of the nest. The male terminal squeeze occurs just prior to female egg release.

7. Egg Release. Egg release is usually quickly completed following the terminal squeeze and ejaculation. However, in a few instances eggs were observed emerging from the female genital pore for a few seconds after the subsequent clasp release, while both fish were in swimming inhibition.

8. Swimming Inhibition. Immediately following male clasp release, both fish usually float downward for a few seconds with little movement or orientation until recovery.

9. Female Fleeing. The female usually regains her orientation first and begins to swim slowly away from the nest. Male chasing and biting

at the anal and caudal fins generally follow.

10. Female Appeasement. Male aggression usually results in more active female fleeing and in the appearance of appeasement postures which inhibit male aggression only slightly. Male biting and butting usually occur during and after the chase and during female appeasement, then the male often gives a brief lateral spread display which in some cases elicits a sexual response such as approach and/or courtship butting. This generally results in more male aggression. The male lateral spread display in this context appears to be a threat or agonistic element of behavior.

11. Nest-Care. Following postspawning aggression the male usually returns to the nest and resumes nest-building and cares for the eggs. After spawning the eggs float to the surface. Those not floating directly into the bubble-nest are sucked into the mouth by the male and deposited in the nest. Eggs are usually consolidated in a small area of the nest. Thinner, peripheral areas of the nest are usually allowed to dissipate, leaving only a small, deep nest containing the eggs. Both fish may eat the eggs, usually after the spawning sequence is over.

After spawning, the female usually remains motionless on the bottom of the tank, as far away from the male as possible, surfacing occasionally to gulp air. Her surfacing rate appears to be effected by the level of male aggressiveness as well as by actual physiological needs. Postspawning females sometimes spend prolonged periods gulping with the snout at or just above the water surface. This behavior may be related to physiological needs, but may also be an attempt to eat

eggs which may have floated away from the nest. The female may also feed, especially at or near the end of a spawning sequence.

To summarize: in the T. leerii ethogram six major phases are represented. These are:

1. prespawning preparatory phase (1a and 1b)
2. courtship phase (2, 3, 4)
3. clasp (5, 6, 7)
4. swimming inhibition (8)
5. postspawning aggression phase (9, 10)
6. interval between bouts (11)

The reproductive actions (stages 2-10) are somewhat stereotyped, but much variation in form and duration is evident.

Reproductive behavior can be terminated by inappropriate responses at several stages. Some of these (stages 2, 3, 4, 5) appear to be more critical than others. The male seems to be responsible for most of the interrupted bouts. This is not entirely unexpected since the female presumably does not approach the male until she has reached a high level of sexual motivation. She therefore, appears ready to spawn, whereas the male is not necessarily at the same peak of readiness. This is probably a major factor contributing to the low spawning efficiency (less than 7% of all bouts) observed in this species.

Reproductive Color Changes in T. leerii

Color changes during the reproductive cycle are striking and are useful guides in determining the motivational states of the sexual partners. Changes in color patterns are shown in Fig. 2. The following

text numbers correspond to the male diagram numbers.

1. Dorsal Fin Ocellus. Some, but not all, breeding males develop a small spot (or spots) in the soft-rayed portion of the dorsal fin. The functional significance of this characteristic has not been determined.

2. Post-Opercular Ocellus. The formation of a dark post-opercular ocellus is characteristic of breeding males. It is not a "remnant of the horizontal band" as Forselius (1957) stated because the horizontal band is still present, although somewhat diffuse and the diameter of the ocellus is greater than the width of the original horizontal band. The functional significance is unknown as it does not appear to serve as a target for female courtship butts.

3. Eye Color. The eye of a breeding male becomes uniformly dark at the time of spawning, in contrast to the gray eye, traversed by a dark horizontal band observed in non-breeding males. This is one of the best indicators of spawning readiness in males, but is not present in all.

4. Ventral Coloration. Most breeding males acquire a deep yellow or orange coloration on the ventral surface, especially on the throat, breast, and pelvic fins. The intensity of coloration varies in and between individuals.

5. Dorsal and Anal Fin Extensions. Filamentous extensions of the soft rays of the dorsal and anal fins are characteristic of breeding males. These streamers are broken and disappear at or near the end of the spawning cycle. The functional significance of the streamers is unknown, though their growth is presumably related to the phenomenon of

general increase in rate of mitosis associated with increased gonadal hormone levels (Bullough, 1961).

6. Caudal Ocellus. The caudal spot also changes in form and intensity, but it is less marked than most other changes. The well-defined, usually circular caudal ocellus of non-breeding males anastomoses with the melanophore network of the caudal peduncle and becomes diffuse and less distinct.

7. Horizontal Band. In breeding males the horizontal band anastomoses with reticulations of the body melanophore system and usually becomes diffuse and somewhat shortened. Instead of reaching almost to the caudal ocellus it may extend only one-half to two-thirds the original length. The horizontal band does not include the lateral line, except posteriad on the caudal peduncle, and does not appear to serve as a target for female courtship butts. Most female butts are directed at the base of the anal fin, sides and the base of the dorsal fin.

The following text numbers correspond to female diagram numbers in Fig. 2.

Non-breeding females are marked much like non-breeding males. Breeding females may acquire some yellow coloration ventrally, but not the intense gold and reddish-orange colors which characterize breeding males.

1. Caudal Ocellus. Diffusion of the caudal ocellus is usually more pronounced in breeding females than in males and in some cases no remnant of it can be seen. This marking usually disappears during or shortly before the onset of a spawning sequence, but normally begins

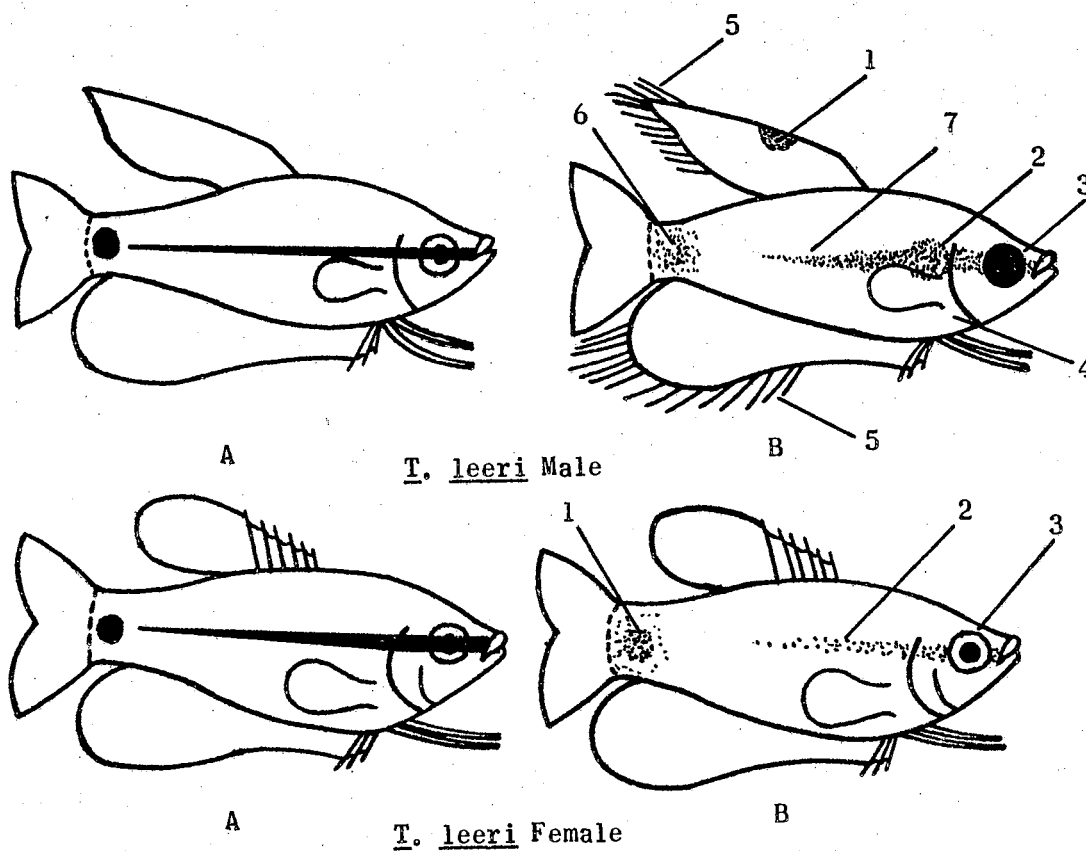


Fig. 2. Structural, Color, and Body Marking Changes in T. leerii Male and Female. A. Non-Breeding. B. Breeding.

to reappear at or near the end of the sequence and remains quite distinct until the onset of the next spawning sequence.

2. Horizontal Band. The horizontal band usually disappears completely during spawning and reappears at or near the end of the spawning sequence. The body color usually becomes uniformly pale with vague reticulations.

3. Eye Color. One of the most striking color changes in females is

the change in eye color associated with spawning. Although the male's eye becomes uniformly dark, the female's eye, with few exceptions, becomes uniformly light with no trace of the original horizontal band.

The functional significance of many of these changes is unknown. Picciolo (1964) found that sex and species discrimination are dependent upon visual stimuli in T. leeri. He stated that, "No conclusive evidence was obtained to support the hypothesis that the horizontal band displayed by males and females of T. leeri functioned as a cue for sex or species discrimination." Furthermore, "No evidence was obtained to indicate that the reddish-orange throat and abdomen displayed by the males of T. leeri functioned as a cue for sex discrimination." These statements, however, are based on model experiments involving only males of apparently indeterminate reproductive condition, with a maximum of 30 trials. Inasmuch as approach frequency was the only criterion measured, there is some doubt as to the nature of the response itself and the causal factors involved. The nature and quantity of the data seem not to justify strong confidence in the conclusions stated. Present observations strongly suggest that body markings, color, and body configuration all are highly important stimulus sources for sex recognition in T. leeri.

Discussion of T. trichopterus Ethogram

The T. trichopterus ethogram is shown in Table III.

Stages 1a and 1b. These two preliminary phases in male and female are quite similar in T. leeri and T. trichopterus. As in T. leeri, the male establishes a nest territory and constructs the bubble-nest.

TABLE III
TRICHOGASTER TRICHOPTERUS ETHOGRAM

Male		Female
1a. acquires nuptial coloration; defends territory; approaches female; nest-building; some aggression; attains physiological readiness to spawn		1b. acquires nuptial coloration; usually stays away from nest ↓
2. stops nest-building; gives lateral spread or sigmoid display; drops down below female for rubbing posture	←	2. female approach (generally quite swift); usually terminates in female butting
3. male rubbing	↗ ←	3. female assumes rubbing orientation to male
4. male curving and circling	↗ ←	4. female maintains rubbing orientation
5. male preliminary clasp	↗ ←	5. female mounting; maintains snout on or near dorsum of male
6. roll and quivering	↗ ←	6. female sigmoid curve; quivering begins; movements initiate roll
7. ejaculation ↓	↗ ←	7. female quivering and egg release
8. loosening of clasp; swimming inhibition	↗	8. swimming inhibition ↓
9. male chases, butts, and bites ↓	←	9. swims slowly away from nest; flees actively; appeasement; rarely counter-aggression
10. male nest-building and nest-care	↗	10. female usually remains in hiding; surfaces rarely; occasionally feeds

Some leading-to-the-nest may occur, but the "ideal spawning bout" appears to be one in which the female approaches of her own volition. A sigmoid display by T. trichopterus males is also seen in prespawning aggression, but is relatively uncommon in T. leerii males. T. trichopterus females, if not ready to spawn, usually hide far from the nest and feed on surface rarely.

2. Female Approach. The female approaches the nest, usually rapidly, and butts the male 1-10 times on the sides or caudal peduncle as he gives a brief lateral spread display.

3. Male Rubbing. Following female butting, the male drops below the female and begins a unique motor pattern called rubbing (Miller, 1964). The male, with dorsal fin partially or completely folded, moves back and forth beneath the belly of the female. This movement may serve as a tactile or mechanical stimulus (Miller, 1964), though contact during rubbing is not absolutely essential for spawning to occur. The motor pattern of rubbing presumably is mutually stimulating and probably is of value in keeping the pair in close proximity and in proper orientation for subsequent curving and clasping. As the male rubs, the female usually remains in a stationary position directly above the male.

4. Male Curving and Circling. After a long period of rubbing (approximately 70 seconds in spawning bouts) the male curves to form a semi-circle with his body. In spawning bouts T. trichopterus males circled for an average of 5.6 seconds (Miller, 1964). Circling time appears to be related to the level of aggressiveness of males and, as in T. leerii, prolonged circling often leads to incomplete bouts. Improper

female orientation and circling too rapidly appear to cause most of the terminations at this point.

5. Female Mounting and Male Preliminary Clasp. The female mounts with the snout just anterior to the origin of the male's dorsal fin and as she mounts the male brings his head and tail together to clasp her tightly. Improper orientation of the female within the clasp commonly causes terminations at this stage.

6. Female Sigmoid Posture. As the male clasps, the female flexes her body into the sigmoid posture. Quivering by both male and female usually commences at this stage and fin and body movements by both partners appear to cause the roll of the clasped pair.

7. Female Quivering and Male Ejaculation. Female quivering continues after the roll and male ejaculation usually follows a few seconds after the roll is completed. Male ejaculation is usually accompanied by violent quivering and muscular contractions, but these movements appear to differ from the terminal squeeze of T. leerii both in form and intensity. Egg release by the female follows male ejaculation and is usually completed within a few seconds.

8. Loosening of the Clasp and Swimming Inhibition. Immediately following ejaculation and egg release the male loosens the clasp and both sexes enter a 2- to 10-second period of swimming inhibition. As in T. leerii, the female tends to recover first and begins to swim slowly away from the nest after regaining equilibrium.

9. Female Fleeing and Male Chase. Sight of the fleeing female elicits

male chasing, butting, biting, and other forms of aggression. Female appeasement is commonly observed in this situation, but does not appear to be highly successful in inhibiting male aggression. Counter-aggression by females is rarely observed and then usually only in cases where the female is markedly larger than the male (Miller, 1964).

10. Male Nest-Care and Female Hiding. Following postspawning chase, the male usually returns to the nest and tends the nest and eggs. The female typically remains in hiding and/or as far away from the nest as possible. Female feeding may occur at or near the end of a spawning sequence, but feeding by Trichogaster males during the reproductive cycle is less common.

Basically, the courtship and reproductive behavior in T. trichopterus is quite similar to that of T. leerii. Major differences observed in behavior preceding the clasp were the reduced number of female courtship butts and presence of male rubbing. One may also observe male sigmoid display and driving-to-the-nest which are relatively uncommon or absent in T. leerii and M. opercularis.

Discussion of the M. opercularis Ethogram

The M. opercularis ethogram is shown in Table IV.

Stages 1a and 1b. M. opercularis differs conspicuously from the Trichogaster species. In well-coordinated pairs the female commonly shows bubble-blowing and nest-building behavior. She may work with the male or construct a nest of her own, usually in the opposite end of the aquarium. Most females do not spend much time in hiding or on

TABLE IV
MACROPODUS OPERCULARIS ETHOGRAM

Male		Female
1a. acquires nuptial coloration; establishes a territory; initiates nest-building; approaches female; some courtship and aggression; attains physiological readiness to spawn		1b. acquires nuptial coloration; may assist with nest-building; or may stay away from male in opposite end of tank ↓
2. male stops nest-building; may give brief lateral spread display	←	2. female stops nest-building; approaches male; often shows waggle dance appeasement
3. curves body (invitation posture)	↗	3. female butts or thrusts (1-2 or absent)
4. preliminary clasp	←	4. mounting with snout just anterior to origin of male's dorsal fin
5. firm clasp	↗	5. sigmoid posture
6. roll, quivering, and ejaculation	←	6. roll, quivering, and egg release (may continue after clasp release by male) ↓
7. loosening of clasp and swimming inhibition	↓	7. swimming inhibition ↓
8. male egg retrieval	↓	8. egg retrieval, bubble-blowing and nest-care
9. bubble-blowing and nest-care		OR
		9. swimming inhibition may be followed by male chase with butts and bites; female then flees, returning to separate nest or remains quietly in opposite end of tank

the bottom as in Trichogaster, but instead play a much more active role in prespawning activities. The waggle dance and J-shape appeasement postures are commonly shown by females during the prespawning phase and the median fins are usually partly or completely folded during nest-building. Female movements during nest-building are generally slow and deliberate and are effected almost entirely by means of the pectoral fins.

2. Female Approach and Male Lateral Spread Display. If the female is not already present under the male's nest she approaches, usually in appeasement posture with the median fins folded. The male often gives a brief lateral spread or sigmoid display. Approach is effected primarily by use of the pectoral fins.

3. Female Courtship Butting and Male Invitation Posture. Female butting, if it occurs, usually consists of 1-2 strong thrusts at the opercular or post-opercular region of the male's body. The male's opercular ocellus does not appear to be a target for female butts. In well-coordinated pairs the female often does not butt at all, but mounts immediately as the male curves his body and forms the U-shape invitation posture. Little or no circling is observed in most spawning bouts.

4. Female Mounting and Male Preliminary Clasp. As in the Trichogaster species, mounting by the female consists of swimming into the U-shape flexure of the male's body with the snout just anterior to the origin of the dorsal fin. Both male and female appear to be capable of more adjustments than the Trichogaster species if the preliminary clasp is faulty. Even so, many bouts end at this point because of various difficulties.

5. Female Sigmoid Posture and Male Firm Clasp. As the female mounts, the male brings his head and tail together to clasp her tightly. As she mounts and as the male clasps, her body is bent into the S-shaped flexure as in the Trichogaster species.

6. Roll, Ejaculation, and Egg Release. The roll occurs quickly after the firm clasp and male ejaculation usually follows soon after the inversion of the pair. No terminal squeeze has been observed in males, however, both male and female tremble perceptibly prior to ejaculation and egg release. The clasped pair may sink far below the nest before egg release occurs. More sinking was observed than in the Trichogaster species. More male clasping after the female had slipped out of the clasp also occurred. Egg release also differs from the Trichogaster species in that females commonly continue to extrude eggs for several seconds after the clasp release by the male while in swimming inhibition.

7. Swimming Inhibition. Swimming inhibition occurs after spawning and pseudospawning as in the Trichogaster species.

8. Egg Retrieval. After swimming inhibition, male aggression is often absent and the female may aid in egg retrieval and nest-care activities. The male usually spends much time directly under the nest, whereas the female searches for and retrieves eggs. These eggs are brought to, or very near the nest by the female and either placed in the nest or spat out for the male to put into the nest. As in most other phases of courtship and reproduction, the female's median fins are usually partly or completely folded and movement is effected primarily by means of the pectoral fins. Appeasement postures are commonly shown by females during

the postspawning phase. Male postspawning aggression does occur in some pairs and female egg retrieval and nest-care may be inhibited by large and/or aggressive males. Little egg eating by either sex has been seen in this species. It does occur, but apparently not to the extent observed in the Trichogaster species. Males will vigorously defend a clutch of eggs and strike at foreign objects introduced into the aquarium.. Trichogaster males rarely showed any aggressiveness when eggs and nests were removed from aquaria.

9. Female Postspawning Behavior and Male Nest-Care. The male usually does not consolidate the eggs into a central area of the nest, but continues to add bubbles to the nest creating a shallow, diffuse nest for the eggs. Eggs that float away from the nest are usually mouthed by the male and expelled back into the nest with one to several small mucus-coated bubbles attached.

The spawning bout in M. opercularis is usually marked by greater cooperation between male and female than is observed in the Trichogaster species. Several behavioral differences occur such as: waggle dance appeasement, J-shape appeasement, female nest-building, female egg retrieval, and reduced number or absence of female courtship butts.

The major behavioral similarities and differences in the three species are listed in Table V.

TABLE V
QUALITATIVE COMPARISON OF COURTSHIP AND REPRODUCTIVE BEHAVIOR
IN T. LEERI, T. TRICHOPTERUS, AND M. OPERCULARIS*

Behavior	T. leeri	T. trichopterus	M. opercularis
Male Nest-Building	present	present	present
Female Nest-Building	absent or very rare	absent or very rare	common
Male Lateral Spread Display	present	present	present
Male Sigmoid Display	rare	common	common
Male Circling or Curving	variable (usually brief)	variable (usually brief)	very brief
Female Waggle Dance Appeasement	absent	absent	present
Female Vertical and Lateral Tilt Appeasement	present	present	present
Female Courtship Butting	many butts	few butts	none or very few butts
Swimming Inhibition	present	present	present
Male Postspawning Aggression	almost always	almost always	rare
Rubbing	absent	present	absent
Duration of Spawning Bouts	intermediate	long	short
Female Postspawning Nest-Care and Fry Retrieval	absent	absent	common
Male Leading-to-the-Nest	present	present	present
Male Terminal Squeeze	present	absent	absent
Vibrating	absent	absent	present
Tail Beating	present	present	present
Frontal Display and Opercular Erection	absent or reduced	absent or reduced	present

*Well-coordinated pairs used as standard for comparison

CHAPTER VI

FUNCTIONS OF COURTSHIP

Desmond Morris (1957) has defined courtship as, "The heterosexual reproductive communication system leading up to the consummatory sexual act." Burton (1953) has defined courtship as, "A relatively stereotyped sequence of actions or events without which reproduction will not normally take place." Miller (1964) defined courtship in T. trichopterus as, "Those activities that appear to attract and/or stimulate the spawning partner, thus facilitating successful spawning."

Mating behavior has been defined by Etkin (1964) as, "A complex series of movements bringing the sex openings of the mates close together and effectuating release of the sperm over the eggs as the latter emerge." This differs little from many definitions of courtship. Because of the difficulty in distinguishing between the two types of behavior it seems likely that they share at least some common causal factors.

There are at least six functions of courtship (with some overlap). Courtship can aid in: locating a mate; making sure the mate is of the right species; arousing the mate sexually; synchronizing sexual levels; advertisement (or attraction); and overcoming aggression.

Finding a Mate

Various cues are usually involved in mate location, but visual,

chemical, and auditory stimuli appear to be most important in teleost fishes. In his study of sexual and nest discrimination in anabantoid fishes, Picciolo (1964) found that visual cues are most important in sex recognition in T. leerii and T. Trichopterus. Visual cues also appear to be of primary importance in sex recognition in M. opercularis.

Making Sure Mate is of the Right Species

These fishes have developed a complex courtship reaction chain in which each reaction apparently releases the next action in the opposite sex. This highly species-specific chain of reactions precludes consummation of the reproductive behavior by individuals of different species. Closely related sympatric species often differ markedly in certain aspects of behavior and/or structure which play important roles in courtship and reproduction. For example: T. trichopterus pre-spawning behavior includes a lengthy (25-143 second) period of male rubbing (Miller, 1964). This behavior is not found in T. leerii.

Flexibility and adaptability in courtship behavior are observed in all three species, i.e., the form and temporal qualities of sexual bouts are not rigidly fixed, but variation within certain limits may be tolerated and/or compensated for. It seems unlikely that the patterns are flexible enough to permit interspecific mating in T. leerii and T. trichopterus.

Ethological barriers probably contribute only a part of the complex of factors preventing hybridization.

Arousing the Mate Sexually

According to one line of thought, motivational substrates are provided by at least three "tendencies" (sensu Tinbergen, [1959] or "drives" sensu von Iersel and Bol, [1958]) in operation in each individual at the time of courtship and reproduction: the tendencies to flee, attack, and mate (Morris, 1957). The first two must be inhibited or suppressed so that the tendency to mate predominates in both individuals. The arousal properties of courtship are difficult to measure but they may be instrumental in bringing about the consummatory act of spawning. Arousal in most cases is not limited to either sex, but mutual stimulation appears to be the result of sexual displays and other courtship activities (Burton, 1953).

Data on this aspect of courtship are sparse or mainly subjective in studies on lower vertebrates, and the present study sheds little light on the problem.

Synchronizing Sexual Levels

Synchronization of sexual levels appears to be an important function of courtship and may be intimately related to arousal. Both male and female must be at a peak of sexual receptivity, i.e., appropriate behavior by both male and female is essential if spawning is to occur. If one partner is not ready or is unwilling to spawn, the other continues courtship activities until the "poorly motivated" individual begins to respond. The subsequent chain of interactions results in a close synchronization of activity that culminates in successful spawning.

Advertisement

Mating in fishes often depends upon an exchange of signals between potential mates. Signaling devices such as brightly colored structures, special movements and postures, emission of chemicals, sound production, and tactile responses may be employed. Most of these are found in certain members of the sub-order Anabantoidei, but sound production and chemical signals were not detected in the species considered in this study.

Signal movements are common in these fishes and include such behaviors as lateral spread display, sigmoid display, frontal display, female courtship butting, appeasement postures, invitation postures, leading-to-the-nest, and other behaviors. Some signals, such as female courtship butting and male circling appear to involve aggressive elements of behavior. Degree of fin erection, color changes, and opercular erection may also indicate the motivational state of an individual at a given time.

Advertisement may take the form of attraction displays. Two types are common in these fishes: change in mode of swimming and acquisition of breeding color. The former is commonly seen in males of the three species in the behavior called leading-to-the-nest. This is often a stop and go movement toward the nest apparently functioning to entice the female to follow to the nest. The latter is a common occurrence in male anabantoid fishes at the peak of the breeding cycle.

Overcoming Aggression

Overcoming male aggression is primarily a female problem in these

fishes because they must ordinarily enter the male's territory in order to spawn. The male is aggressive in defense of territory, protection of the nest, competition for food, and in social interactions with others of the same species, including courtship.

The degree of male aggressiveness varies greatly and in rare cases females may defend a territory and show aggressive behavior toward males. Great size difference is usually a contributing factor in this situation and in most pairs with fish of equal or near equal size it is the male which acts as the aggressor. Less male aggression is usually seen during prespawning and spawning periods in M. opercularis than in the Trichogaster species. Consequently, M. opercularis females play a greater and more conspicuous role in courtship and reproductive activities than in the Trichogaster species. Trichogaster females may initiate sexual bouts, but in general they appear to be more timid and almost never show nest-building behavior. In general, M. opercularis exhibits greater cooperation and "peacefulness" during spawning than do the Trichogaster species, in which the females enter the male's territory, spawn, and then leave immediately or are driven away by male attacks.

Rapid, direct approaches to the male from the bottom of the tank are characteristic of sexually motivated Trichogaster females. The manner of approach, along with morphological features may serve to identify them as females and thus inhibit male aggression. Shape of fins, abdominal plumpness, and general body form appear to be important sex recognition characters in the Trichogaster species (Picciolo, 1964). Female appeasement postures are commonly associated with the approach.

CHAPTER VII

FACTORS INVOLVED IN ANABANTOID REPRODUCTION

Breeding Cycles in T. leerii Males

It appears that most T. leerii males spawn for approximately one month, then enter a period of dormancy for several weeks or months. This dormancy appears to be determined by an innate rhythmicity independent of diet, lighting, temperature, or other observable external factors.

The onset of the quiescent period in males is signaled by cessation of nest-building, lack of nest territoriality, breaking and eventual loss of the dorsal and anal streamers, and a gradual loss of breeding colors. Upon entering the quiescent phase, external shocks such as cooling the water followed by a rapid increase in temperature, removing vegetation, addition of a gravid female, addition of fresh water, and heavy feeding appear to have little or no rejuvenating effect. Males still showing some breeding color, intact streamers, etc. may in some cases be stimulated to resume nest-building upon addition of a gravid female to the tank. For example: a T. leerii male spawned with a female on 29 June, 6 July, and 12 July, 1964. Then followed a period of 11 days in which nests became smaller, then absent, and male color became poorer until 21 July, when a young, gravid female was placed in the tank. Within 24 hours a large nest was constructed, breeding

color became excellent and on 27 July spawning occurred with the newly introduced female.

Breeding Cycles in T. leerii and M. opercularis Females

Table VI, showing intervals between spawning sequences in T. leerii females, shows that intervals between successive spawning sequences tend to increase in length. Secondly, intervals of at least 14 days were observed in 4 of 8 females for which records were available. It appears that after numerous spawning sequences (as many as 6 in 26 days by one female) T. leerii females undergo a "rest period" or period of rejuvenation. In the 4 females that showed a prolonged "rest period," at least one spawning sequence followed and in three females, two spawning sequences followed.

A comparison with intervals in M. opercularis females (Table VII) does not show a similar pattern, however, extensive records over a long period were not available for M. opercularis females. There does appear to be a gradual increase in length of intervals between spawning sequences in M. opercularis females, but this is not as clear-cut as in T. leerii. A prolonged "rest period" (19 days) was observed in only 1 of 5 M. opercularis females. This does not necessarily mean that M. opercularis females do not show a rejuvenation period similar to that observed in many T. Leerii females.

Seasonal reproductive cycles have been studied little in tropical species of animals and this is especially true of fishes. In other tropical vertebrates seasonal cycles have been observed and it is suspected that many tropical fishes also exhibit seasonal reproductive cycles (Bullough, 1961).

TABLE VI

INTERVALS (DAYS) BETWEEN SPAWNING SEQUENCES IN T. LEERI FEMALES

Tank #31

old female -- 7, 6, 17, 5

new female -- 6, 10, 5

Tank #33

resident female -- 3, 4, 14, 22, 6

Tank #35

old female -- 3, 4, died

new female #1 -- 2, 4, 15

new female #2 -- 4

Tank #14

resident female -- 2, 3, 3, 4, 4, 10, 67, 10

Tank #25

resident female -- 5, 4, 4

TABLE VII

INTERVALS (DAYS) BETWEEN SPAWNING SEQUENCES IN M. OPERCULARIS FEMALES

Tank #27

resident female -- 4, 9

Tank #28

resident female -- 2, 19

Tank #29

resident female -- 4, 7, 7, 3, 4, 3

Tank #34

resident female -- 3, 5, 7

Tank #36

resident female -- 4, 8, 5

Diel Rhythmicity of Spawning Activity in T. leeri

A definite diel rhythmicity of spawning activity was observed in T. leeri. Both sexes were more active during the morning and practically all spawning sequences began before noon. Much of this activity consisted of prespawning courtship activities and most spawnings (80%) occurred during the period 10:00 a.m.-2:00 p.m. (Fig. 3).

Afternoons were usually characterized by less activity in both sexes, little or no male nest-building (unless spawning had occurred), hovering near the bottom of the tank or in vegetation, bottom feeding, and other low threshold activities.

Diel Rhythmicity of Spawning Activity in M. opercularis

In M. opercularis a different diel pattern of spawning activity was observed. Most spawning sequences began after noon and a peak in spawning activity was observed between 4:00-5:00 p.m. with 38 of 136 spawnings occurring during this period (Fig. 3). A decrease was noted in each of the three succeeding hourly intervals with 27 spawnings occurring between 5:00 and 6:00 p.m.; 22 spawnings between 6:00 and 7:00 p.m.; and 20 spawnings between 7:00 and 8:00 p.m. No spawnings were recorded prior to 1:00 p.m. and none after 8:00 p.m. Spawning, however, does occur at night in this species. Spawning was observed at 10:32 p.m. on one occasion and on 3 other occasions eggs were discovered in the morning that, on the basis of development and observed time until hatching, could only have been spawned the preceding night. No night spawning was observed nor was there any indication that this occurs in T. leeri.

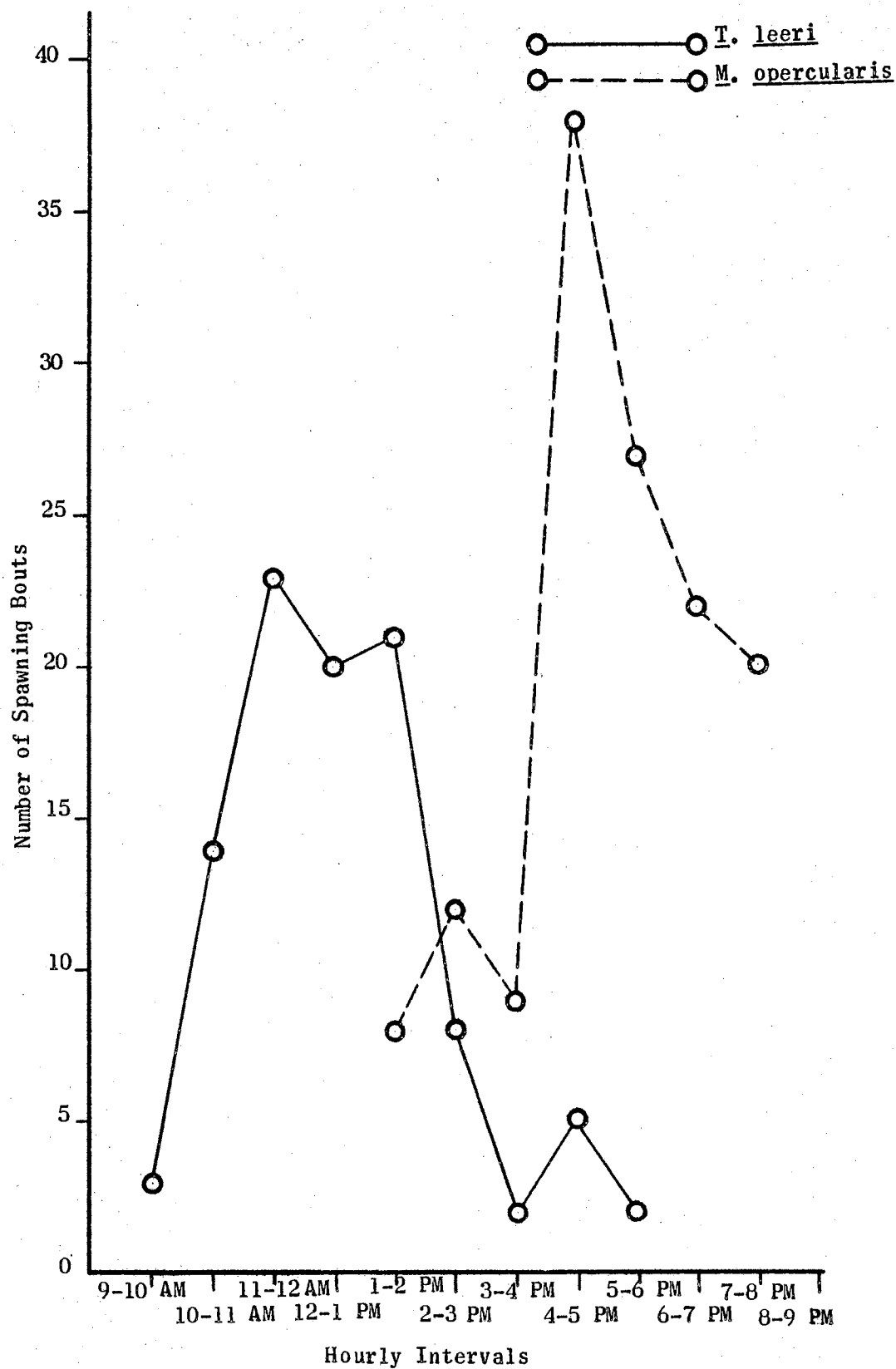


Fig. 3. Diel Spawning Activity in *T. leerii* and *M. opercularis*

Caution should be exercised in applying these results to what may happen in nature. The cycles and rhythmicities observed in these two species may occur in nature, but they may have been imposed, in part, by the laboratory conditions and may have been influenced by methods of lighting and photoperiod employed during the study, as well as other factors not easily discernible.

Number of Eggs Released Per Spawning Sequence in T. leerii
and M. opercularis Females

Data regarding number of eggs released per spawning sequence in these two species are listed in Tables VIII and IX.

To obtain egg counts, eggs and nests were removed from aquaria with syringes, eye droppers, and watch glasses immediately after the termination of all spawning bouts. Increased male aggressiveness, pseudospawnings, color changes in both sexes, female feeding, female hesitation in approaching the male, and other criteria were used in determining the completeness of spawning sequences. Eggs were removed, counted, and placed in aerated, small aquaria for hatching. No egg counts were made if either sex was observed eating eggs prior to completion of the spawning sequence.

The number of eggs released per spawning bout in T. leerii is highly variable, ranging from 1-2 eggs to clouds of eggs. The average number of spawnings per spawning sequence was approximately 7-8. The number of eggs released during a given spawning sequence appears to be relatively constant for a given female, but variation between females is great. In one T. leerii female, 644, 711, 607, and 752 eggs were released

TABLE VIII
NUMBER OF EGGS RELEASED PER SPAWNING SEQUENCE
BY T. LEERI FEMALES

Tank	Date	Number of Eggs
Tank #1	6-19-64	953
Tank #14	6-16-64	644
	6-19-64	711
	6-27-64	607
	7- 7-64	752
Tank #32		
new female	8-12-64	1818
resident female	8-13-64	764
new female	8-17-64	1371
resident female	8-18-64	976
Total		8596
Average Number of Eggs Per Spawning Sequence		955

TABLE IX
NUMBER OF EGGS RELEASED PER SPAWNING SEQUENCE
BY M. OPERCULARIS FEMALES

Tank	Date	Number of Eggs
Tank #29	8- 4-64	873
	8- 9-64	521
Tank #27	8-17-64	1354
Total		2758
Average Number of Eggs Per Spawning Sequence		916

during successive spawning sequences. Another T. leerii female liberated 1818 and 1371 eggs in successive sequences.

Size of female does not appear to be highly significant with regard to number of eggs released per spawning sequence. This conflicts with Forselius (1957) who states that, "... the age and size of the female has an influence on the total amount of eggs." No evidence was found to support this statement. For example: a small (approximately 60 mm standard length) female released 1818 and 1371 eggs in successive spawning sequences, whereas an older and larger (approximately 75 mm standard length) female in the same aquarium released 764 and 976 eggs in successive spawning sequences. All four sequences occurred within a period of 7 days and all spawnings occurred with one male.

The average number of eggs released per spawning sequence in T. leerii was 955, with a minimum of 607 and a high of 1818. This does not agree with Forselius (1957) who stated that approximately 2000 eggs are released per spawning sequence by T. leerii females.

Average number of eggs released per spawning sequence in M. opercularis was 916 with a low of 521 and a high of 1354. This, again, conflicts with Forselius (1957) who lists an average of approximately 200-500 eggs per spawning sequence for M. opercularis females.

On the basis of these egg counts the average number of eggs per spawning bout was about 135 in T. leerii and approximately 60 in M. opercularis.

Reduction in number of eggs released during successive spawning sequences does not appear to be the rule in T. leerii or M. opercularis, however, data are insufficient to make definite statements in regard to this aspect of spawning.

Male Fertility in T. leerii

Male fertility appears to decline when repeated spawnings occur in a short period. On 12 July, 1964 a male spawned with a newly introduced female. Of 1818 eggs released, over 90% hatched. On 13 July, 1964 the male spawned with the resident female. Of 764 eggs released, fewer than 25% hatched. Many became moldy and were apparently infertile. A similar pattern was observed on 17 July and 18 July, 1964 in two successive spawning sequences involving these same fish. Peripheral tissue changes are apparently less important in T. leerii males than females since they may continue clasping even though unable to fertilize eggs. Barlow (1962) also noted this phenomenon in Badis badis males.

In general these findings indicate that: the presence of sperm or seminal fluid apparently is not a prerequisite for clasping and spawning in T. leerii males; in successive spawning sequences that occur within a period of 1-2 days a decrease in fertilization may be noted; and the number of eggs released during successive spawning sequences may be relatively constant for a given T. leerii female, but may vary greatly between individuals.

Spawning Temperatures in T. leerii and M. opercularis

Various factors are known to be of importance in spawning in fishes. Some of these are: food, temperature, barometric pressure, changes in water quality, photoperiod, presence of vegetation, and suitable nesting sites (Bullough, 1961).

Spawning temperature data were obtained for 41 spawning sequences in T. leerii and 22 sequences in M. opercularis. Data were obtained

from 7 pairs of T. leerii and 5 pairs of M. opercularis. Standard aquarium thermometers were used. Spawning temperature data for these two species are shown in Tables X and XI. A graphic comparison is shown in Fig. 4.

The optimum temperature range for T. leerii spawning appears to be 80-86 F with 38 of 41 spawning sequences (93% of total) occurring within this range. The optimum spawning temperature appears to be 84 F with 11 spawning sequences (27% of total) at this temperature.

The optimum range for M. opercularis appears to be 78-83 F with 16 of 22 spawning sequences (76% of total) occurring within this range. No clear-cut optimum spawning temperature is evident in this species, but 80, 81, and 82 F appear to be near optimal with 12 of 22 spawning sequences (55% of total) occurring at these temperatures.

Both T. leerii and M. opercularis are capable of spawning over a wide temperature range. T. leerii data show, in general, a near-normal distribution pattern, but M. opercularis data do not show such a pattern. Limited data may account, in part, for the absence of a well-defined central tendency in M. opercularis.

Temperature appears to be an important factor in spawning success in these two species, though it is but part of a complex of factors influencing spawning. It appears that the reproductive cycles in these fishes are determined by an innate rhythmicity which is acted upon and made more precise by various environmental factors.

TABLE X
SPAWNING TEMPERATURES IN T. LEERI

Temperature (°F)	Tank #1	Tank #14	Tank #25	Tank #30	Tank #31	Tank #32	Tank #33	Total
78.0			1					1
78.5	1							1
79.0								0
79.5								0
80.0	2		1					3
80.5								0
81.0		1		1	1			3
81.5								0
82.0	1	2			1		1	5
82.5					1			1
83.0	1	1			1		1	4
83.5		1						1
84.0	2	1	1	1	2	3	1	11
84.5	1	1					1	3
85.0	1		1		1			3
85.5		1			1		1	3
86.0					1			1
86.5								0
87.0							1	1
Total	9	8	4	2	9	3	6	41

TABLE XI
SPAWNING TEMPERATURES IN M. OPERCULARIS

Temperature (°F)	Tank #27	Tank #28	Tank #29	Tank #34	Tank #36	Total
78.0	1					1
78.5						0
79.0	1		1			2
79.5						0
80.0		1	1	1	2	5
80.5						0
81.0	1			1	1	3
81.5						0
82.0		1	1	1	1	4
82.5						0
83.0		1	1			2
83.5						0
84.0			1	1		2
84.5						0
85.0						0
85.5						0
86.0			2			2
86.5						0
87.0			1			1
Total	3	3	8	4	4	22

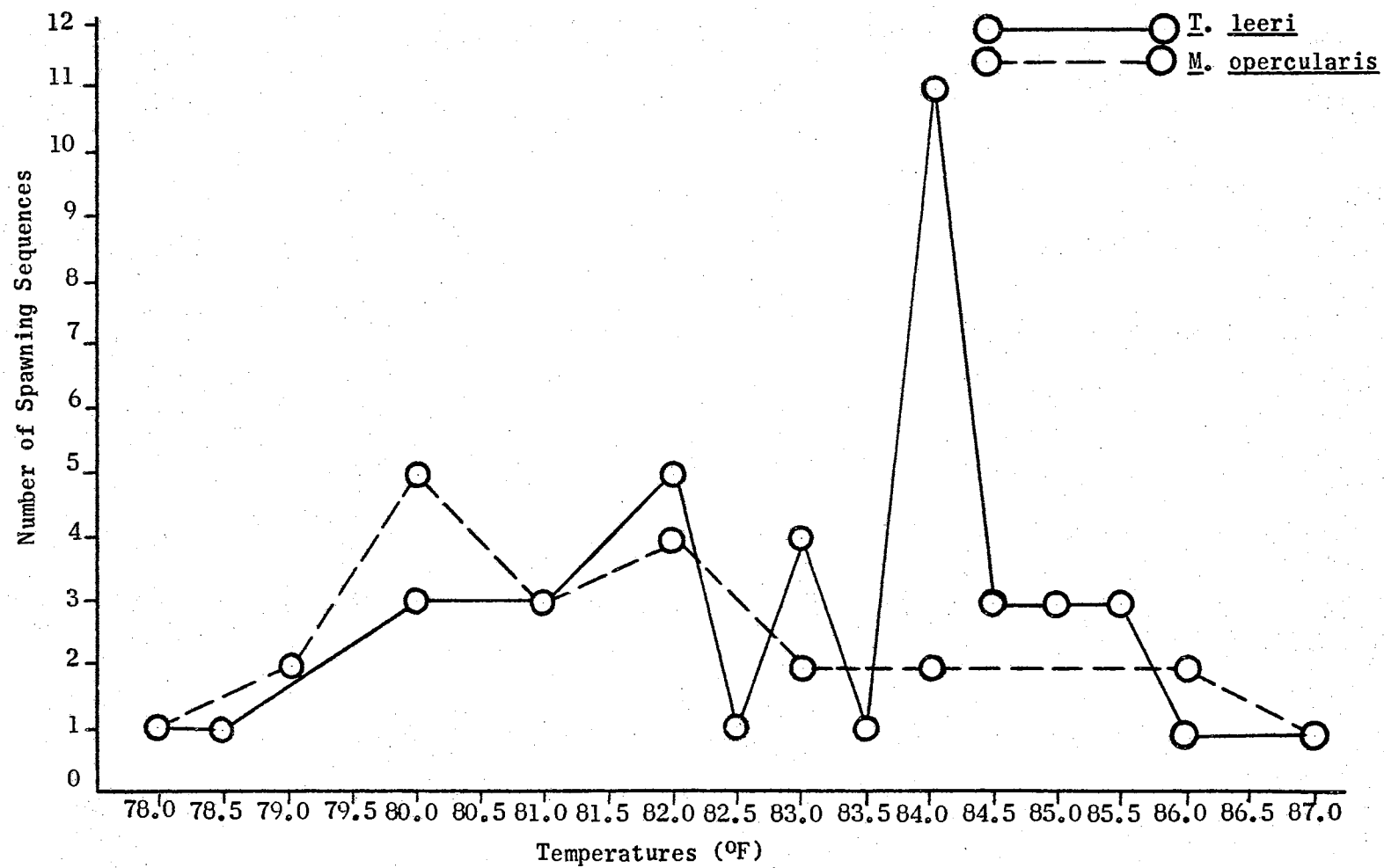


Fig. 4. Comparison of Spawning Temperatures in *T. leerii* and *M. opercularis*

CHAPTER VIII

QUANTITATIVE ASPECTS OF ANABANTOID COURTSHIP AND REPRODUCTION

Tables XII and XIII will serve as bases for a general discussion of quantitative aspects of sexual bouts in the three species. T. leerii data were obtained from 15 recorded spawning sequences which include a total of 1287 bouts. T. trichopterus data were obtained from 3 spawning sequences with a total of 205 bouts and M. opercularis data from 1 spawning sequence with a total of 355 bouts. Major similarities and differences will be noted. Little attempt will be made to deal with motivational aspects or causal factors. Data are limited in certain areas and are subject to revision subsequent to further analysis. Quantitative aspects of courtship and reproduction will be treated in detail in a subsequent paper.

Behaviors in the three species tend to occur in discrete units separated by intervals of varying duration. Bouts differ in duration, complexity, and "success." "Success" refers to the degree of completeness of sexual bouts as reflected by the level of sexual activity attained during the bout. Bout types are arbitrary, artificial categories that attempt only to deal with and make meaningful the available data.

In the following discussion, spawning bout will refer to a sexual bout in which gametes are released by both partners. Pseudospawning refers to a sexual bout, similar in form to a spawning bout, in which

one or both partners fail to release sex products. Clasp only refers to sexual bouts involving sexual responses by both partners that culminate in one (or more) clasp(s), but no higher level sexual activity. Courtship only refers to bouts involving sexual responses by one or both partners. These bouts do not reach the clasp stage. In the three species they may include male lateral spread display, sigmoid display, leading-to-the-nest, driving-to-the-nest, rubbing, and curving. Female responses include approach, following-to-the-nest, courtship butting, thrusting, and waggle dance. Aggression only bouts are male-female interactions not containing sexual responses by either partner. Components of such bouts include male and female biting, butting, chasing, lateral spread display, sigmoid display, frontal display, tail beating, and vibrating. All of the above "bout types" may be male or female initiated.

General quantitative comparisons are listed in Table XII.

Complete spawning sequence average duration is remarkably similar in all three species, ranging from 229.50 minutes in T. trichopterus to 249.00 minutes in M. opercularis. T. leerii shows an average duration of 236.37 minutes per sequence.

A comparison of male vs. female initiated bouts shows that T. leerii males initiate approximately 55% of all bouts and females about 45%. In T. trichopterus and M. opercularis the figures are 60% vs. 40% and 51% vs. 49%, respectively. This shows that Trichogaster males initiate well over half of all bouts, whereas M. opercularis males initiate almost exactly half. This exemplifies the conspicuous role that M. opercularis females play in courtship and reproductive activities.

TABLE XII

GENERAL QUANTITATIVE COMPARISONS IN T. LEERI, T. TRICHOPTERUS,
AND M. OPERCULARIS

	<u>T. leeri</u>	<u>T. trichopterus</u>	<u>M. opercularis</u>
1. Total Duration (complete spawning sequences only)*			
a. minutes	2836	459	249
b. seconds	170187	27540	14940
c. average duration per complete spawning sequence (minutes)	236.37	229.50	249.00
2. Total Number of Bouts	1287	205	355
a. male initiated	714	122	182
b. percent of total initiated by male	55.47	59.51	51.00
c. female initiated	573	83	173
d. percent of total initiated by female	44.53	40.49	49.00
3. Total Duration of All Bouts (Seconds)	36985	13111	2503
4. Average Sexual Bout Duration (Seconds)	31.29	75.99	10.61
5. Total Interval Duration Following Bouts (Seconds)	167759	20373	12437
6. Average Interval Duration Following Bouts			
a. minutes	2.18	1.66	0.58
b. seconds	131.36	99.86	35.03

* Based on 12 complete spawning sequences in T. leeri, 2 complete sequences in T. trichopterus, and 1 complete sequence in M. opercularis

Average sexual bout duration is 31.29, 75.99, and 7.05 seconds per bout in T. leerii, T. trichopterus, and M. opercularis, respectively. Longer average duration in T. trichopterus is primarily due to rubbing, a component of most sexual bouts. Short average duration in M. opercularis is due to absence or reduced nature of certain elements of behavior. Average interval following bouts shows, again, the high degree of similarity between T. leerii and T. trichopterus. Average interval duration is 2.18 minutes in T. leerii and 1.66 minutes in T. trichopterus. It is 0.58 minutes in M. opercularis, indicating the faster tempo of spawning sequences.

Bout categories are analyzed in Table XIII.

Average number of bouts per spawning sequence is quite similar in T. leerii and T. trichopterus with means of 85.50 and 68.33 bouts per sequence, respectively. M. opercularis shows an average of 355.00 bouts per sequence.

Spawning bouts in T. leerii and T. trichopterus comprise 7.61% and 8.78% of all bouts. M. opercularis shows even less efficiency with only 3.09% of all bouts culminating in spawning. Most spawnings in all species are female initiated, indicating the importance of female sexual receptivity and readiness to spawn. Average spawning bout duration varies from 14.10 seconds in M. opercularis to 194.44 seconds per bout in T. trichopterus. T. leerii is intermediate with an average of 55.23 seconds per bout. Shortened duration in M. opercularis is due to reduced leading, short female approach, few female courtship butts, little or no male circling, rapid clasp and roll, and short clasp duration. The long duration in T. trichopterus is due to male rubbing,

TABLE XIII

**BOUT CATEGORY ANALYSIS OF SEXUAL BOUTS IN T. LEERI,
T. TRICHOPTERUS, AND M. OPERCULARIS***

	<u>T. leeri</u>	<u>T. trichopterus</u>	<u>M. opercularis</u>
1. Total Number of Bouts	1287	205	355
a. average number of bouts per spawning sequence	85.50	68.33	355.00
2. Total Number of Spawning Bouts	98	18	11
a. male initiated	10	5	0
b. female initiated	88	13	11
c. (male and female) percent of total bouts	7.61	8.78	3.09
3. Average Duration of Spawning Bouts (Seconds)	55.32	194.44	14.10
4. Total Number of Pseudospawning Bouts	74	16	1
a. male initiated	8	3	0
b. female initiated	66	13	1
c. (male and female) percent of total bouts	5.74	7.80	0.30
5. Average Duration of Pseudo- spawning Bouts (Seconds)	74.65	215.37	28.00
a. male initiated	69.13	183.31	0
b. female initiated	75.32	222.77	28.00
6. Total Number of Clasp Only Bouts	329	16	31
a. male initiated	45	2	7
b. female initiated	284	14	24
c. (male and female) percent of total bouts	25.56	7.80	8.73
7. Average Duration of Clasp Only Bouts (Seconds)	45.49	241.46	16.15
a. male initiated	42.00	212.50	13.90
b. female initiated	46.04	245.64	16.80
8. Total Number of Courtship Only Bouts	450	43	95
a. male initiated	331	25	56
b. female initiated	119	18	39
c. (male and female) percent of total bouts	34.96	20.93	26.76

TABLE XIII (Continued)

	<u>T. leerii</u>	<u>T. trichopterus</u>	<u>M. opercularis</u>
9. Average Duration of Courtship			
Only Bouts (Seconds)	21.30	38.74	9.92
a. male initiated	15.34	16.72	7.30
b. female initiated	37.91	69.33	13.70
10. Total Number of Aggression			
Only Bouts	219	78	164
a. male initiated	212	59	114
b. female initiated	7	19	50
c. (male and female) percent of total bouts	17.01	38.00	46.19
11. Average Duration of Aggression			
Only Bouts	5.11	6.65	3.94
a. male initiated	4.81	5.58	3.30
b. female initiated	14.14	10.00	5.40

*Based on 15, 3, and 1 spawning sequences, respectively

lateral and sigmoid displays, circling, and long clasp duration.

Pseudospawnings were observed in all species. In the Trichogaster species these comprise 5-8% of all bouts, but in M. opercularis they form less than 1%. Average duration of pseudospawning bouts ranges from 28.00 seconds in M. opercularis to 215.37 seconds in T. trichopterus. T. leerii pseudospawnings average 74.65 seconds per bout. Pseudospawnings show greater average duration than spawning bouts in the same species.

Clasp only bouts comprise 25.56% of all T. leerii bouts, but form only 7.80% and 8.73% of T. trichopterus and M. opercularis bouts, respectively. If a T. trichopterus female remains near the male through the prolonged courtship activities it appears likely that she will stay long enough to consummate the bout by spawning or pseudospawning. Higher spawning efficiency in T. trichopterus (8.78% vs. 7.61% and 3.09% in T. leerii and M. opercularis, respectively) may be due to this feature of courtship.

Courtship only bouts comprise 34.96% of all bouts in T. leerii, 20.93% of all bouts in T. trichopterus, and 26.76% of all bouts in M. opercularis. Males initiate most of these bouts. In general, male initiated bouts are much shorter than female initiated bouts, indicating rapid return to nest-care, bubble-blowing, and defense of territory if the female does not respond appropriately (follow, butt, etc.).

Aggression only bouts, usually male initiated in all three species, comprise a major portion of most spawning sequences. T. leerii males are relatively non-aggressive toward females in regard to percent of total number of bouts. In T. leerii they comprise only 17.01% of all bouts,

whereas in T. trichopterus and M. opercularis they form 38.00% and 46.19%, respectively. A comparison of male and female initiated aggression only bouts indicates the docile nature of most T. leerii females. Of 219 aggression only bouts in this species, 7 (3%) were female initiated. Conversely, in M. opercularis 30% (50 of 164 bouts) were female initiated, indicating comparatively higher aggressiveness. T. trichopterus females are intermediate, initiating approximately 24% of all aggression only bouts. These bouts are usually of brief duration and may consist of mild butting or biting, butting, chasing, tail beating, and other aggressive behaviors by male and/or female. Means of 14.14, 10.00, and 5.40 seconds per aggression only bout were observed in T. leerii, T. trichopterus, and M. opercularis, respectively.

Table XIV, based on features listed in Tables XII and XIII, is an attempt to graphically show the degree of similarity between the three species by use of lines ("links"). A "link" connecting two species indicates highest degree of quantitative similarity in regard to that feature. These "links" have not been weighted. Some, obviously, are more important than others. Dotted lines, used to connect T. leerii and M. opercularis, are not intended to show great phylogenetic similarity, but only greater numerical relationship caused by rubbing in T. trichopterus. Rubbing indirectly accounts for 5 of the 6 links between T. leerii and M. opercularis. Without this unique element, congeneric similarities in the two Trichogaster species, undoubtedly, would appear more pronounced. No special significance is intended by length of lines or positioning of categories within Table XIV. No statistical inference is intended or implied by use of this method.

TABLE XIV
BEHAVIORAL RELATIONSHIPS IN T. LEERI, T. TRICHOPTERUS,
AND M. OPERCULARIS

Feature	<u>T. leeri</u>	<u>T. trichopterus</u>	<u>M. opercularis</u>
Average Number of Bouts Per Spawning Sequence	0 ————— 0		0
Spawning Bouts as Percent of Total Bouts	0 ————— 0		0
Average Duration of Spawning Bouts	0 ————— 0		0
Pseudospawning Bouts as Percent of Total Bouts	0 ————— 0		0
Average Duration of Pseudospawning Bouts	0 ————— 0		0
Clasp Only Bouts as Percent of Total Bouts	0	0 ————— 0	
Average Duration of Clasp Only Bouts	0 ————— 0		0
Courtship Only Bouts as Percent of Total Bouts	0 ————— 0		0
Average Duration of Courtship Only Bouts	0 ————— 0		0
Aggression Only Bouts as Percent of Total Bouts	0	0 ————— 0	
Average Duration of Aggression Only Bouts	0 ————— 0		0
Average Duration of Complete Spawning Sequences	0 ————— 0		0
Percent of All Bouts Male Initiated	0 ————— 0		0
Average Sexual Bout Duration	0 ————— 0		0
Average Interval Following Bout	0 ————— 0		0
Total Number of <u>T. leeri</u> - <u>T. trichopterus</u> "Links" = 7			
Total Number of <u>T. leeri</u> - <u>M. opercularis</u> "Links" = 6			
Total Number of <u>T. trichopterus</u> - <u>M. opercularis</u> "Links" = 2			

CHAPTER IX

SUMMARY

A comparison of morphological features (Chapter III) shows much similarity between T. leeri and T. trichopterus and their dissimilarity to M. opercularis. Qualitative comparisons of courtship and reproductive behavior (Chapter V) again show the marked similarity in the Trichogaster species. Quantitative comparisons (Chapter VIII) also show congeneric similarities and intergeneric differences.

Onset of reproductive cycles in males is usually signaled by establishment of a territory, increased activity, bubble-blowing, acquisition of breeding color and certain morphological changes. The pre-spawning phase in females is usually marked by increased abdominal plumpness and changes in color and body markings. Nest-building is common in M. opercularis females, but rare or absent in Trichogaster. M. opercularis and T. trichopterus females may establish and defend territories, but this was not observed in T. leeri. Female sexual receptivity and readiness to spawn appear to be highly important factors in "success" of sexual bouts. Either sex may initiate sexual bouts, but most spawning bouts are female initiated. Sexual bouts may end at any point prior to spawning (incipient spawning bouts) or may continue through spawning or pseudospawning. The "success" of a sexual bout may be used as a rough indicator of the momentary sexual motivation of the fish (Miller, 1964).

Qualitative differences in courtship and reproductive behavior in the three species are evident. Distinctive features in T. trichopterus are male rubbing, driving-to-the-nest, and long clasp duration. T. leeri behavior includes much female courtship butting, head-snapping, and male terminal squeeze. M. opercularis reproductive behavior includes female waggle dance and J-shape appeasement postures, female nest-building, female parental care, little or no female courtship butting or thrusting, little or no male circling, vibrating, and short clasp duration.

Innate breeding cycles appear to be operant in T. leeri and M. opercularis and appear to be influenced by various external and internal factors. "Rest periods" in T. leeri males and females were observed. In females these varied from 14-67 days and were followed by one or more spawning sequences. These periods were not clear-cut in M. opercularis. Diel spawning rhythmicities were observed in T. leeri and M. opercularis. Other activities in T. leeri also appear to follow a diel rhythm. Spawning temperatures appear to be important in both T. leeri and M. opercularis, but both species may spawn over a wide temperature range. Number of eggs released per spawning sequence by a given T. leeri female appears to be relatively constant, but individual variation is great. A decrease in T. leeri male fertility was noted following repeated spawnings, although males continued to carry out spawning motor patterns in apparently normal fashion.

On the basis of this study some general statements can be made about the relationships between the three species.

1. Courtship and reproductive behavior in the Trichogaster species

shows some differences, but differences between these two species and M. opercularis are qualitatively and quantitatively greater. The differences in form and duration of courtship and reproductive behaviors appear to be of such magnitude so as to effectively reproductively isolate the sympatric Trichogaster species. The three species are characterized by distinctive courtship and reproductive patterns. These patterns vary in: temporal relationship of behaviors, inclusion and deletion of behavioral elements, and frequency and intensity of certain behaviors.

2. Courtship and reproduction in M. opercularis shows more female participation and greater male-female cooperation than observed in the Trichogaster species. Female postspawning nest-care and egg and fry retrieval are common, but rare or absent in Trichogaster females.

3. Spawning "efficiency," based on number of spawning bouts as percent of total number of bouts, is greatest in the Trichogaster species. The term "efficiency" may be misleading, however, since total time involved in spawning bouts per spawning sequence is lowest in M. opercularis. Average number of eggs released per spawning sequence is not greatly different in T. leeri and M. opercularis, but the average number of spawning bouts per spawning sequence is about 7-8 in T. leeri and approximately 15-16 in M. opercularis. Average number of eggs released per spawning bout is therefore less in M. opercularis. Spawning bouts are of much shorter duration in M. opercularis than in the Trichogaster species, thus making possible more spawning bouts in a comparable period. Intervals between bouts are also shorter in M. opercularis.

The net effect in all three species is the same - high rate of

fertilization of the many eggs produced - therefore, the term "efficiency" is used advisedly. The increased spawning "efficiency" in the Trichogaster species may be partially due to prolonged courtship activities which provide greater mutual stimulation for the sexual partners.

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