# AN ETHOLOGICAL STUDY OF THE MOONLIGHT GOURAMI,
# TRICHOGASTER MICROLEPIS (GÜNTHER)

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# AN ETHOLOGICAL STUDY OF THE MOONLIGHT GOURAMI,
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# PREFACE

The objectives of the present study were to: (1) describe qualitatively the major behavior patterns of Trichogaster microlepis; (2) compare behavior patterns with those of congeneric species; (3) support qualitative descriptions with quantitative data when appropriate; (4) correlate observed behaviors with possible causal factors; and (5) determine the biological significance of the observed behaviors.

Dr. R. J. Miller served as major advisor and furnished invaluable suggestions and assistance throughout the study. Drs. L. T. Brown, L. H. Bruneau, B. P. Glass, R. I. Smith, served on the advisory committee. Drs. L. H. Bruneau, B. P. Glass, and H. C. Miller criticized the manuscript. The assistance of all these people is greatly appreciated.

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# CHAPTER I

# INTRODUCTION

Anabantoid fishes possess involved and highly stereotyped behavior patterns in both reproductive and nonreproductive situations. The similarity of behavior patterns in closely related groups suggests that phylogenetic affinities could be determined by comparison of behavior. Many species of even the most closely related forms, however, show marked behavioral differences and suggest a need for more scrupulous observation to determine the evolutionary or biological significance of these subtle variations in behavior.

Trichogaster microlepis is of interest since rather exhaustive qualitative behavior studies have been carried out on T. trichopterus by Miller (1964) and on T. leeri by Hall and Miller (1968). An opportunity thus exists to compare T. microlepis with two of its congeners.

The purpose of this study is to describe qualitatively the behaviors of T. microlepis and when possible compare them to other species of Trichogaster in an attempt to interpret the significance of the observed behaviors. Some quantitative data are included where deemed necessary to support the qualitative data.

The sub-order Anabantoidei was divided by Liem (1963) into four families: Anabantidae, Belontiidae, Helostomatidae, and Osphronemidae, and includes fifteen genera and approximately fifty species.

*Trichogaster* is a belontiid of the sub-family trichogasterinae and comprises four species: *T. microlepis* (moonlight gourami), *T. trichopterus* (blue gourami), *T. leeri* (pearl gourami), and *T. pectoralis* (snake-skin gourami). The Belontiidae contains ten genera and is wide spread in distribution throughout Southeast Asia, the Indonesian Archipelago, India, and Africa. The four species of *Trichogaster* are sympatric over most of their ranges, the center of distribution being in Southeast Asia including Borneo and Java (Forselius, 1957). *T. microlepis* is most abundant in central Thailand.

*Trichogaster* like most species of anabantoids inhabit a variety of fresh water environments, from streams and canals to the still, stagnant waters of ponds and swamps.

*Trichogaster* species reach a large size compared to most other members of the family, with maximum lengths in *T. microlepis* of 15 cm, *T. trichopterus* of 12 cm, *T. leeri* of 12 cm, and *T. pectoralis* of 20 cm (Smith, 1945). Most are economically important food fish, especially *T. pectoralis*.

Anabantoids vary in color from the dull browns to brilliant reds and purples. Some species change color with changes in aggressiveness and reproductive cycle and some do so only slightly or not at all.

In *Trichogaster* color varies from silver-blue to dark tan-green in *T. microlepis* and *T. pectoralis* respectively. These two also exhibit only subtle color changes during the reproductive cycle. In the former, increased aggressiveness produces change from light blue-gray to a dark blue-black and in the latter, darkening of the spotted brownish-red coloration results. Females of the genus show lesser color change than do males.

The basic coloration of _T. microlepis_ is silver becoming a silver-blue dorsally. A dark gray-black lateral stripe which becomes more indistinct posteriorly extends from the operculum to the caudal peduncle, where there may be an ocellus. Both the spot and the stripe vary greatly in intensity in the same individual, becoming lighter in dominant fish and in older fish. At the onset of the reproductive cycle the males in particular and to a much lesser degree the females, develop a blush of pink on the margins of the anal fins and occasionally the ventral margin of the caudal. The breast and pelvic fins of the males change most extensively.

The possession of a labyrinth organ, construction of a bubble nest, and use of a nuptial embrace are unifying characteristics of most anabantoids.

The labyrinth organ is a bilateral branched out-pocketing of the pharynx and is derived from the epibranchial element of the first gill arch. The organ occupies much of the preopercular dorsolateral head region and is covered with respiratory epithelium. The gills of anabantoids are functional and vary from species to species in their ability to furnish sufficient oxygen to the organism without the aid of the labyrinth organs. Most species of the belontiids are dependent to some degree on these organs. Fish inhabiting sluggish, oxygen deficient waters rely on air taken into the labyrinth organ as a supplementary oxygen supply. It is questionable whether a _Trichogaster_ in oxygeneated water would survive if kept from aerial respiration.

Wayne F. Hadley in unpublished work done at Oklahoma State University in 1966, determined that _T. trichopterus_ can survive periods of at least 173 hours in water containing 8.4 to 8.5 ppm oxygen at

22 C without access to a surface for aerial respiration. Fish undergoing these conditions responded by resting on the bottom in a sigmoid flexure tail up, and on their side.

The bubble nest, usually begun at the onset of the reproductive cycle, is constructed on the surface of the water usually by the male. However, females cooperate in nest building in some species. Air is taken into the mouth at the surface and converted within the mouth into bubbles, which are then coated with mucus secreted by unicellular glands lining the walls of the oral cavity. These bubbles are then expelled at, or as many as several centimeters beneath the surface of the water and form rafts from one to many layers in thickness. The nest is usually anchored to some stationary structure such as plants or debris and varies in size from less than an inch to over a foot in diameter. Some species incorporate vegetation into the nest while others do not. Nest construction involves highly stereotyped behavior by both sexes and varies considerably among the species of Trichogaster.

The nuptial embrace, or clasp, is exhibited by all known belontiids and is an effective way of assuring maximum egg fertilization, since the release of male and female gametes is accomplished at the instant during which both genital openings are in juxtaposition. Release of gametes occurs as the male clasps his body about the anterior one half of the female's, and in many anabantoid species as the pair turns over orienting the genital pore upward toward the water surface and nest. As in nest construction, there is a complex stereotyped series of behaviors leading to and involved in the nuptial embrace. These vary greatly even among the species of Trichogaster.

Some additional papers dealing primarily with the qualitative aspects of anabantoid behavior are: Braddock and Braddock (1955) and (1959), Hall (1965), Kühme (1961), Lissman (1932), Piciolo (1965), and Smith (1937). The first comprehensive paper on quantitative aspects of anabantoid behavior was presented by Miller and Hall (1968) which dealt with the reproductive behavior of _T. leeri_ and emphasized the causal mechanisms influencing various behaviors.

# CHAPTER II

## MATERIALS AND METHODS

Early phases of the study were carried out using 22 young adults, 7 males and 15 females. Two males possessed secondary sexual characteristics when received at the laboratory but all were identified as to sex by the end of the second month. All fish appeared to be the same age group and were at much the same state of maturity. Twenty-seven fry, 8 males and 19 females, from spawns early in the study were raised to adults and were included in most later phases of the study.

In most cases a male was maintained in a tank with 1-2 females. Tanks possessing other social groupings were also maintained.

The aquaria in which the fish were kept ranged in size from 60 to 135 liters. Two 500 liter steel tanks and a plastic wading pool 1.83 meters in diameter and 0.5 meters deep were used for rearing fry and observing various behaviors.

With few exceptions, light was provided in each tank individually by two incandescent bulbs which were used on a 12-hour on and a 12-hour off photoperiod. Two different wattages (15 and 25) were used in order to produce more light at one end of the tank than at the other. During part of the study two additional centrally located ceiling light sources were used. One 5-watt bulb burned continually and one 40-watt bulb was illuminated an hour before the tank lights were turned on and an hour after the tank lights were turned off. The small bulb furnished sufficient light to make entering the room and moving about possible without introducing additional light. The 40-watt light furnished enough illumination to make the outlines of the fish barely distinguishable in the tank and was an attempt to make the transition between light to dark and vice versa less abrupt.

Tanks were maintained at various ranges of turbidity and pH by addition of peat moss. Water in some tanks became so turbid that fish were scarcely visible in the darker areas of the tank. In tanks of greatest turbidity sediments accumulated on the bottom up to a depth of 7 cm.

Tanks filled with unaltered tap water maintained a pH of between 7.8 and 8.4. The pH was reduced artificially in some tanks to as low as 5.3 by addition of peat moss or potassium bisulphate crystals. Water was maintained with few exceptions from 25 to 29 C by electric heaters in each tank. In some tanks in which spawning was being encouraged the temperature was maintained up to 32 C.

An attempt was made to keep food available at all times in the tank to eliminate variations in behavior due to artificial feeding practices. Fish were fed liberal amounts of commercial dry food morning and evening and live *Daphnia* and midge larvae were maintained in the tanks continuously. Fry were fed powdered egg yolk, yeast, and infusoria.

The sand and gravel bottoms were planted along the back and sides with *Vallisneria* and *Sagittaria*. *Ceratophyllum* was grown on the surface of all tanks up to a depth of 15 cm. Dense areas of vegetation, broken pots, shells, and plastic plants furnished shelter.

Water was changed irregularly and was usually done with the purpose of stimulating the commencement of reproductive behavior.

The fish showed extreme timidity on arrival in the laboratory and it was necessary to enclose the front of some of the tanks with hoods with a viewing aperture of approximately 5 square cm. Fish eventually became accustomed to the distractions of the laboratory and the hoods were removed. _T. microlepis_, however, never became as unaffected by laboratory disturbance as other species of the genus. Their temperamental behavior made it impossible to take motion pictures and reduced the possibility of description by the use of this technique. Notebooks, data sheets, tape recorders, and dictaphones were used to aid in recording qualitative descriptions as well as some quantitative data.

Most quantitative data were taken using a twenty-pen Esterline-Angus multiple event recorder, on which were recorded 46 different behaviors. Some quantitative data, however, were obtained by use of stop watch and counter and placed directly onto data sheets.

Observation periods varied in duration and frequency according to the specific behavior being observed. Usually observation periods for determinations of nest construction were 10 minutes in length, once each hour from onset of nest construction continuously through spawning or abandonment of construction. Maintenance pre-spawning and post-spawning behavior usually was observed for 10 minute periods twice daily for several weeks on each pair or group. Spawning behavior necessitated continual observation and varied from 5 to 24 hours of continuous observations.

Nest sizes were difficult to measure in most instances without disturbing the fish; therefore, dimensions were estimated by tracing the outline of the nest on tissue paper placed on the glass cover.

# CHAPTER III

# ACTIVITY PATTERNS

Rather than describing in detail the numerous activity patterns possessed by *T. microlepis*, only those patterns unique to *T. microlepis* or those showing a dissimilarity with other species of *Trichogaster* will be comprehensively described, while others will be defined briefly.

Delimitation of activity patterns into specific units of behavior is difficult since they vary in complexity from simple fin erections to highly complex behaviors involved in courtship and nest building behavior.

Miller (1964) and Hall and Miller (1968) have described in detail most of the activity patterns (motor patterns) of *T. trichopterus* and *T. leeri,* respectively. These studies will furnish a basis for the behaviors described for *T. microlepis*.

## General Agonistic Activity Patterns

General agonistic activity patterns are found wherever social encounters occur and are characterized by behaviors which apparently indicate varying degrees of aggressive and flight motivation.

### Lateral Spread

The lateral spread is common in aggressive and reproductive encounters between two fish and varies from partial to full median fin erection. One or both fish may perform such a behavior and may be in almost any relative position to each other although it is most common for the pair to be relatively close and in view of each other. Most agonistic behaviors include some degree of lateral spread.

## Lateral Display or Sigmoid Display

The lateral display as used in this paper refers to a lateral spread in which the median fin erection is complete and the body has been curved into a sigmoid position with the head slightly away and the tail toward the adjacent fish. This behavior is more aggressive than the lateral spread and often develops into an attach, chase, or tail beating. Miller (1964) defined the lateral display as a maximum intensified lateral spread and Hall and Miller (1968) referred to this behavior as a sigmoid display.

## Tail Beating

Tail beating usually develops from the lateral display position by a fish one to several centimeters from a second fish. The caudal peduncle and fin are beat laterally back and forth, forcing water against the other fish. Tail beats are common in courtship as well as agonistic situations and often terminate in attack, chase or flight.

## Approach

An approach is any behavior which brings a fish directly toward or into the path of a second fish. It is executed most frequently by a dominant swimming toward a subordinate although the reverse is common. Usually the more rapid the approach the greater the degree of median fin erection and vice versa. An aggressive approach is often accompanied by an open gape and forwardly extended pelvics which may be thrashed toward and/or against the fish being approached. A mild approach is usually accomplished slowly with median fins relaxed and gape closed.

Opercular spreading, often found accompanying this behavior in other anabantoids, has not been observed in *T. microlepis* and is reported to be rare in *T. trichopterus* and *T. leeri* by Miller (1964) and Hall and Miller (1968).

## Attack

The attack varies from the approach in that is is usually more vigorous and executed with greater speed and median fin erection. It may terminate in oral contact, lateral spreading, or tail beating and often elicits appeasement or flight by the subordinate fish. Attacks are most common in situations in which the attacking fish is clearly dominant over the one being attacked, especially during territorial defense accompanying nest construction and spawning.

## Biting and Butting

The former is rare except by the male while defending the nest at which time intruders may be viciously attacked. Butting is often used by the female when orienting during spawning and appears to help reduce male aggression.

While butting usually consists of ramming or nudging the opponent with closed mouth, biting is accomplished by closing the open mouth upon contact and may result in the tearing loose of scales and the severing of fins, particularly the pelvics.

## Mouth Fighting

This behavior has been described in detail by Miller (1964) for the blue gourami and was mentioned as a behavior of the pearl gourami by Hall (1966). Mouth fighting by the snake-skin is quite common and well developed, and was observed on two occasions by the author. No such behavior has been observed for the moonlight gourami.

## Appeasement Postures

Appeasement postures usually are performed by females or smaller males. Appeasement in *T. microlepis* varies considerably from other species of *Trichogaster*, especially with respect to fin positions. Appeasing females characteristically erect fins to some degree rather than folding them against the body as is usually done in *T. leeri* and *T. trichopterus*. One of the most characteristic appeasement postures of the female is one called "breasting."

Breasting is most frequent in situations when a subordinate fish, usually a female, is approached by a dominant, usually a male, from the front. The subordinate usually responds by raising the front of her body so that the breast is in line with the approaching fish. Median fins, especially the anterior spiny-rayed portion of the anal fin, are erected and pelvics are extended slightly forward. Contact is seldom made and the aggressor usually turns and swims away before the subordinate resumes other behaviors. If the breasting fish turns before the dominant leaves, it is attacked.

An approach often elicits "leaning" by the subordinate. If the approach is from the side and is not extremely aggressive, the female may erect her median fins and lean in such a manner as to expose as much of her side as possible. If the approach from the side is aggressive, she usually flees.

## Chasing

Chasing involves fleeing of one fish with another in pursuit. Male chases of females are common, but males seldom are chased by females except by larger females in nonreproductive situations. Degree of aggression shown in the chase varies and has been categorized in this study into three types. Type #3, the most aggressive, is the one in which the harassing fish aggressively follows the subordinate at least a distance of half the tank and may result in damage to the subordinate. In Type #2 the harassed fish is aggressively followed for less than the distance described for Type #3, and in Type #1 the harassing fish merely swims toward another causing the approached fish to turn and swim away.

Females generally show Type #1 or #2 chases while the males carry out extremely aggressive and often damaging Type #3 chases, especially during spawning and nest building.

Fins of both male and female fish are usually partly erected during the more aggressive chases and are erected fully while braking.

## Fleeing or Escape

Fleeing or escape is behavior during which a harassed fish swims away from an attacker. The typical fleeing posture of an aggressively chased fish is with the caudal region elevated slightly and with median fins erected. As the chase continues the median fins are relaxed and the fish becomes more horizontal. At each renewed burst of speed the former position is assumed. Aggressive chases are usually terminated when the harassed fish reaches shelter and assumes a breasting posture.

Less aggressive chases elicit flights with correspondingly lesser degrees of tilt and fin erection.

## General Non-Agonistic Patterns

General non-agonistic behavior is primarily concerned with maintenance behaviors and other non-social activities.

### Inspiration

Inspiration of air is accomplished by two distinctly different methods, stationary-at-surface and dashes-to-surface.

Stationary-at-surface air snapping is used in air intake for nest construction as well as at other times for respiratory purposes and is the exclusive type of inspiration used during darkness. During inspiration of this type, median fins, especially the anal, are partly to fully erected and the fish maintains itself at the surface of the water by undulations of the pectoral and anal fins. Pelvics are usually held slightly forward as the fish maintains itself with anterior end elevated at an angle of 20 to 30 degrees with the surface of the water. Although 1-5 snaps are most common in nonreproductive behavior as many as 50 snaps have been observed in nest building.

Dashes-to-surface is the most common type of inspiration during daylight hours except when the male is constructing or guarding a nest. Although they are usually continued by the female during nest construction, neither sex executes them during parental care, since the female is forced to hide from the male throughout most of this period. Dashes-to-surface start in two ways: either by erratic dashes often covering much of the tank and culminating in a nearly vertical dash to the surface or by a slow hesitant ascent up to within 10-20 cm of the surface, ending in a dash upward. The latter method is most common while the former is practiced mainly by dominant fish during early reproductive behavior. Air is expired through the mouth and opercula an inch or so beneath the surface and inspired as the mouth of the fish is out of the water. The entire body of the fish leaves the water several centimeters during more energetic surfacings. After returning to mid-water the fish usually remains stationary for several seconds before assuming other behavior. Surfacing by either the dominant or subordinate fish often has an allelomimetic effect on other fishes in the tank and adjacent tanks where there is visual contact.

## Shelter Seeking

Shelter is usually sought by a fish which is being severely harassed by a dominant, although shelter seeking is common in other situations. It is most common during reproductive periods when chases by the male are frequent and usually violent.

Although broken pots were placed in each tank for shelter, the harassed fish commonly chose to swim into thick vegetation against the side of the tank to escape attack. Almost invariably median fins were folded, with the body head up or down at an angle between 20 to 70 degrees to the tank bottom. When approached while in this position median fins were erected. Flight of a fish from shelter usually was not elicited by the harassing fish; occasionally, however, contact was made or movement of water caused by the tail beating actually forced the subordinate from its place of shelter. Generally, however, a harassed fish was safe from damaging attack if it did not flee and remained in shelter. A hiding fish became most vulnerable when surfacing for air and harassment was often renewed at that time.

## Chafing

Chafing is the contacting of the fish's body against a stationary object followed by a rapid push away usually by means of a lateral undulation of the body. Chafing by the male is more common than by the female. Generally the behavior immediately prior to the chafe becomes hesitant and forward progress slows or stops. As the object to be chafed against is neared or contacted, the fins are folded and the body is leaned toward the object, while at the same instant a lateral undulation propels the body against the structure in a glancing blow. As the plant or other structure is left the fins again are erected and the fish glides along often with no additional propulsion until it becomes stationary. After remaining stationary for several seconds, the fish resumes other behaviors. On occasion several chafes are performed in succession and are frequently followed by erratic dashes about the tank and to the surface. Although chafing is a common occurrence, it becomes more frequent in early reproductive behavior.

## Feeding

Dry food was eaten throughout the tank at any depth. The most common method of ingestion occurred at the surface where fish remained stationary while sucking the floating food into the mouth with currents of water. When food is available, a hungry fish may remain feeding at the surface for over 60 seconds without cessation. While a fish is actively feeding, food may occasionally be carried out through the opercles. Fin and body position of surface feeding fish is similar to those during stationary inspiration at the surface. Sinking food is eaten almost as readily as that at the surface. Food reaching the bottom is usually not taken until larger pieces of suspended food have been consumed. On numerous occasions food from previous feedings could be observed on the bottom while food was presented and consumed readily at the surface. Feeding from the bottom is most infrequent perhaps because the superior mouth makes this an awkward procedure. When bottom feeding occurs, however, the fish commences nibbling at the substratum with head down at approximately a 45 degree angle to the bottom. As feeding continues the fish becomes perpendicular to the substratum as it nips the bottom. It is not uncommon for a fish to fall over backward while so feeding. Balance appears to be maintained mainly by the caudal and pectoral fins with stabilization added by the erected median fins.

Small moving organisms such as Daphnia were preferred to larger slow moving foods such as midge larvae and pieces of Lumbricus. Although several fish learned to take the latter, they showed preference for Daphnia when the two foods were presented simultaneously.

Feeding on *Daphnia* is usually accomplished by the selection of an individual organism somewhat isolated from the main aggregation, then approaching and opening the mouth an instant previous to ingestion. Slight chewing movements usually follow ingestion and larger *Daphnia* are often spit out and ingested a second time or ignored.

Small *Lumbricus* and pieces too large to be taken whole into the mouth, although bitten, were never torn into pieces suitable for swallowing.

Pelvic fins appear to be used in searching for food as well as in the investigation of change in the physical consistency of the water. This was evident in several tanks in which broken pots were placed so that *Daphnia* tended to congregate behind them out of view of the fish. Passing fish often extended pelvics behind these structures and usually proceeded to swim behind and feed when *Daphnia* were present but did not do so if none were there. Aggregations of *Daphnia* in open water also often are approached with outstretched pelivcs which can be moved independently of one another and reach out simultaneously in opposite directions. Pelvics are normally pulsated singly or in pairs toward or against the investigated substance and may be extended forward, laterally, or backward. Thrusts delivered at objects above the fish are accomplished by tilting the body to the side or by raising the anterior part of the body.

Fish reacted to the addition of silt or peat moss to the tank by approaching the dense cloud of turbid water with pelvic fins extended forward. After some fin pulsating into the encroaching water mass they usually entered with little hesitation.

Social hierarchies, although existing in some tanks, often appear to break down and are not evident during feeding. The longer the fish continue to feed, however, the greater the possibility that dominant-subordinate relationships will be reformed. When a hierarchy is evident during feeding, the dominant fishes generally occupy the surface areas and subordinate fish feed at lower levels of the water or not at all.

## Patrolling or At-Random-Swimming

Patrolling is behavior in which a fish moves about the tank showing no interaction with other fish. Slow patrolling is accomplished by alternate pectoral beats. Increased speed is effected by lateral undulations of the body and caudal fin. Body undulations are usually followed by glides during which pectorals are adducted to the body except for turning or stopping at which time they are extended. Pelvics, dorsals, and anals are partially erected and become slightly depressed with each sudden forward movement and erected as the fish slows or stops.

## Resting

The term resting is used in this study to describe a stationary fish showing no movements other than those necessary to maintain position and to respire.

Fish rest at any depth but most frequently in the upper two-thirds of the tank. They rest with dorsal and anal fins relaxed, pectorals beating alternately, and the dorsal section of the caudal slowly undulating. The pelvics vary considerably in the degree by which they are abducted from the body both anteriorly and laterally and when the fish is resting near an object such as a plant or tank side, they are often held out and used as braces against such structures thus aiding the fish to remain stationary. When pelvics are used as braces the pectoral and caudal often cease to move. Normally, however, pelvics are abducted outward at an agnle approximately 45 degrees or more with the sagittal plane of the body and held forward at an angle of approximately 30 degrees with the frontal plane of the body. The head is usually held about a centimeter higher than the tail. Differences in resting during light and dark will be discussed in the section on diurnal activity.

### Posting

Forselius (1954) uses this term to describe all the occasions when a male has taken up a position. This behavior differs from resting in that during posting the median fins are often partly to fully erected and pelvics are abducted from the body at a slightly greater angle. Respiration rate is more rapid and the fish assumes a more alert appearance. This behavior is typical of a stationary male guarding a nest or defending a territory.

## Non-Agonistic Patterns Most Common in Pre-Spawning Phase

Several days prior to nest building there is an increase in maintenance behavior of both sexes. The following behaviors occur infrequently throughout nonreproductive phases but become somewhat more frequent during the early phase of reproductive behavior.

### Vertical Posturing or Head Standing

Vertical posturing or head standing appears much like bottom feeding. Median fins are erected and the fish orients with mouth on the bottom of the tank and may bounce several centimeters up and down off the bottom, primarily by use of pectoral fins. As in feeding there is often a loss of balance and the fish falls backward.

### Yawning

Yawning usually is performed by a stationary or a slowly moving individual and is followed by a more energetic behavior such as a dash-to-surface for air or rapid swimming to another part of the tank. Yawning is accomplished by extending the jaws forward and increasing the gape. The opercles are slightly extended and median fins which are partly to fully erected during the yawn are relaxed as the fish moves off.

### Head Jerking

Head jerking was observed four times. The head and anterior body is moved extremely rapidly to the left and right at which time large air bubbles may be expelled from the mouth and opercles. In each case the behavior was observed during the early phase of reproductive behavior.

### Mouth Snapping

This behavior is also rare and consists of rapid opening and closing of the mouth without sideward movement of the head. Clicking is sometimes audible during the snapping and air is sometimes released from the mouth and opercles.

### Pseudo-Clasping

This behavior is performed by both sexes but predominantly by the male following periods of inactivity of from several seconds to several minutes. The body is clasped so that the curved body forms an angle of 20 to 90 degrees. The pelvic fin on the outside of the curve is usually held away from the body and the inside pelvic is depressed backward against the body. Anals and pelvics are partly to fully erected. The body remains curved for a second or two at the most. As the fish straightens he moves forward in the direction which his head was turned and this often results in changes in direction.

### Rocking

This is a behavior most common, but not unique, to subordinate fish and is performed before leaving shelter to swim into a situation of increased danger of being attacked. A female about to leave cover to inspire air or approach a nest frequently performs such behavior. Median fins are partially to fully erected and rapid beating of the pectorals move the fish several millimeters back and forth.

## Nest Construction

Behaviors during nest construction are numerous and form complex patterns. Descriptions of the more prominent of these behaviors will be included in Chapter IV.

## Spawning

Activity patterns occurring in each spawning bout of the spawning series vary according to the location in the series and the state of spawning readiness of each fish and will be described in detail in Chapter VI.

## Terms

Bout. Any temporally defined interaction between two or more individuals.

Circling Bout. A male and female encounter beneath the nest during which one or more circling periods occur.

Circling Period. The period of time from the commencement of circling until the post-circling pause or until circling ceases. Several circling periods may be present in one circling bout.

Encounter. Used synonymously with bout.

Incipient Spawn. An incomplete spawn and an encounter preceding as a spawn but breaking up before rolling over or inhibition is achieved.

Multicircle Bout. A spawning attempt possessing two or more circling periods.

One (1)-Circle, 2-Circle, 3-Circle Bout. A bout containing 1, 2, or 3 circling periods, respectively.

Pseudospawn. A bout similar to a true spawn (including clasping and swimming inhibition) without release of gametes by either fish.

Spawning Bout or Spawn. An encounter between two fish in which gametes are released by both. In this study all bouts continuing through the roll were included in this category.

Spawning Series. All the spawns, pseudospawns, and incipient spawns between the spawning male and female from the first through the last spawning. Approximate duration of a spawning series is 3-6 hours.

Successful Spawn. Synonymous with a spawn or spawning bout.

Unsuccessful Spawn. Either a pseudospawn or an incipient spawn.

# CHAPTER IV

## NEST CONSTRUCTION AND DESCRIPTION

The nest of T. microlepis is a floating structure constructed by the male of mucous covered air bubbles, pieces of vegetation, and other materials. It is variable in size, usually considerably larger, and has more plant fragments than nests of T. leeri or T. trichopterus. The nest of T. pectoralis is poorly known but it also uses bubbles and vegetation. Egg release, ejaculation, care of eggs, and several other reproductive behaviors occur under the nest.

### Nest Size

Nest size usually is proportional to the amount of available vegetation suitable for construction. Usually by the end of the first active day of nest building most loose pieces of vegetation are incorporated into the structure. Since nest pushing and resecuring of nesting material is common, the nest, if maintained for several days, decreases in area and becomes more compact because of the breaking of larger pieces due to manipulation.

Fifteen nests varied in average diameter, immediately prior to spawning and ranged in diameter from 13 cm to 26 cm with an average of 19.4 cm. Thickness varied between 1 and 4 cm approximately two-thirds of which extended above the surface of the water. After a broad sparse foundation was formed the nest increased in thickness more rapidly than in diameter, due to the continual transfer of vegetation from the margins to more central positions.

In most cases at the time of spawning the nest was maximum size for that particular day and nest construction after completion of spawning, although continuing, was less intense and dimensions of the nest decreased. The most prominent factor responsible for deterioration in the nest is the rapid decline in the mass of bubbles which is almost completely gone by the time the fry hatch.

The rate of nest construction during the night appeared to be somewhat proportional to the amount of light available. No males continued to work in total darkness, but when the tank lights were dimmed to the point that the fish could barely be observed, construction continued although at a reduced rate. Construction recommenced with the turning on of the lights and in several cases a spawning occurred before the nest reached the size of the previous day.

Age or past experience of the male in nest construction appeared to have little or no effect on size or method of construction. For example, male #I spawned 4 times during the study and constructed an equal number of nests. The first nest was 17 cm in diameter; ensuing sizes of nests in order of construction were 23, 13, and 18 cm. Male #II constructed 3 nests. In order of construction, the nests were 21, 25, and 18 cm in average diameter. The size of the fish in relation to nest size shows some correlations, and although the largest nests were constructed by the largest fish, the smallest of the nests was produced by one of the largest males. Two small males both constructed nests above average size (Table I).

## TABLE I

## FISH SIZE AND PREVIOUS NESTING EXPERIENCE IN RELATIONSHIP TO NEST SIZE

| Fish | Standard Length (mm) | Number Nests | Avg Diam of Nest at Spawning (mm) | Avg Diam (mm) |
|---|---|---|---|---|
| II | 112 | 3 | 21-25-18 | 21.3 |
| V | 110 | 1 | 16 | 16.0 |
| I | 106 | 4 | 17-23-13-18 | 17.8 |
| VII | 105 | 2 | 25-20 | 22.5 |
| VI | 100 | 1 | 16 | 16.0 |
| III | 95 | 2 | 24-16 | 20.0 |
| IV | 95 | 1 | 15 | 15.0 |
| VIII | 75 | 1 | 23 | 23.0 |

### Pre-Nest Construction and Site Selection

For several days prior to nest construction males exhibit apparently random pushing, tugging, and carrying of surface vegetation for up to several centimeters throughout the tank. In 10 out of 16 nest constructions such vegetation carrying was observed at least one day prior to construction and in only 3 cases were males not observed carrying vegetation prior to nest construction. On several occasions, however, males observed carrying vegetation failed to construct nests.

During the behavior described above, the females usually remained near the male despite frequent chases. On four occasions females were observed tugging vegetation while in close proximity to the male but no dragging or carrying of vegetation by the female was observed.

Once these behaviors had begun the future nest site could usually be determined since it was the location in which the male was spending the most time and from which intruders were aggressively chased.

The nest site appeared to be associated with several physical factors of the tank: location and intensity of light, degree of surface disturbance, and vegetation location and density.

With few exceptions nests were constructed away from the tank lights in a relatively dark location and away from disturbance by the tank filters and air stones. Nests were usually located near but not directly over rooted plants, and where no plants came within 15-25 cm of the bottom of the nest. Ends of trailing leaves of adjacent plants were often incorporated into the nest serving to anchor it firmly. Nests in tanks without rooted vegetation drifted over the surface and were followed by the attending males. Lack of vegetation beneath the nest allows space for spawning behavior to be executed. In some cases where rooted *Vallisneria* plants grew beneath the nests, circling and clasps were interrupted as the pair became entangled in the leaves. Only after repeated pushing and pulling by the male were these leaves removed, at which time spawning efficiency was usually improved.

## Material Selection and Manipulation

Carrying of vegetation to the previously defended site commenced in most instances in the late morning. Thirteen of the 15 nests observed were started between 3-6 hours after lights-on. After several pieces of vegetation had been conveyed to the nest site, air snapping and air release into the floating vegetation began. Floating vegetation is the first to be utilized and all portions of the tank are searched for loose pieces or those which are insecurely attached, and these are then carried to the nest. As loose plant material becomes depleted, fragments of rooted plants and small pieces of debris found on the bottom are used with increasing frequency.

## Procurement of Plant Fragments

Pieces of vegetation to be carried to the nest are often first pushed with closed mouth, perhaps to determine how solidly the piece is attached, and frequently several are shoved or bitten before an apparent attempt is made to carry them to the nest. After an object is secured in the mouth, the head is jerked sideward at the same instant that the fish swims away propelling itself by strong caudal beats with anterior end slightly elevated. If the object is not freed, the male seldom attempts to detach the same piece a second time but usually swims directly to the nest in a manner similar to that seen when he is carrying vegetation. In some instances he appears to place an imaginary piece into the nest. Perhaps during the tugging, minute pieces of stems or leaves become dislodged and come off in the mouth of the fish, and it is these small pieces which he is carrying to the nest. An alternate explanation is that once the act of retrieving is begun the sequence of behavior in placing the material in the nest must be continued to completion. Because of the lack of such inalterable stereotyped sequences of behavior in other phases of behavior, however, the former explanation seems more logical. There is no evidence that a fish sought vegetation of any particular size and on no occasion was vegetation dropped in order to retrieve a larger, smaller, or more readily available piece.

Small fish are not physically capable of freeing large pieces of attached vegetation and are limited to smaller, more available plant fragments. On several occasions, however, large males were observed pulling well rooted Vallisneria plants free from the substrate and conveying the entire plant to the nest site.

Strands of Ceratophyllum up to 20 to 30 cm in length often were carried to the nest. Fragments of this size were usually seized near one end, and as they were conveyed to the nest the drag produced by moving them through the water caused the male to swim somewhat sideways. In extreme cases the fish swam at an angle of 40 to 50 degrees with the trailing stem. Most materials carried back to the nest were moved rapidly at speeds comparable to those attained in aggressive chases.

Floating plant fragments a centimeter or so in length are often carried to the nest several at a time. When small, freely floating fragments are secured in the mouth, the head is not jerked and the fish often backs away smoothly from the surface without the head jerking common in freeing larger pieces. Backing is uncommon when securing a large fragment.

When a female leaves shelter to approach or follow the male as he returns to the nest with vegetation, she is often chased. If the male is carrying small fragments, the chase is usually accomplished without releasing them and when the female reaches shelter, the male goes directly to the nest and deposits the fragments as if no chase had occurred. If the vegetation is large, it is usually dropped during the chase. The male then returns to the location from which he is inspiring air and continues his nest building effort by blowing air bubbles into the nest.

## Placement of Plant Fragments

Methods of placement of matter into the nest varies according to the nature and size of the material being placed. When bringing a large piece of vegetation to the nest, the male usually passes beneath the nest, slows down, pauses, then pushes the end held in his jaws firmly into the nest as he darts upward at approximately a 45 degree angle, using strong caudal beats. After fastening one end of the fragment, air is inspired and released under the point of attachment. One to several trips are made to the nest bringing air for release under this point. If necessary, another point along the fragment several centimeters from the initial point of attachment may be grasped and pushed into the nest; bubbles are again released beneath this point in the same manner as before.

Even the longest pieces are rarely grasped and pushed upward in more than three places before additional materials are brought to the nest. Bubbles are either released freely from 1-4 cm beneath the fragment or they are released as the piece is pushed upward with the mouth. Pushes of this type are common and aid in consolidating the nest and resecuring loose fragments.

When small fragments are brought to the nest the fish usually takes up to several turns while assuming a head-up position at approximately a 45 degree angle with the surface. The fish then propels himself directly into the nest with strong caudal beats and releases the material as his gape enters the nest. Extremely fine material such as detritus or fecal plugs are often spit into the nest from as far as 2 cm below, and air is characteristically released below the point of each additional placement of material.

## Procurement and Placement of Bottom Debris

As construction continues, more time is spent searching for bottom material and almost any object capable of being placed into the nest is utilized. Several tanks were supplied with a variety of materials which settled to the bottom to determine if preference might exist. Excelsior and bits of paper appeared to be used as readily as plant fragments with larger pieces used first. Other material picked from the bottom included living snails, snail shells, and fine detritus. Although the use of bottom materials increased with decreased availability of surface material, the behavior occurred in all tanks, even in several in which floating fragments were continuously added to one corner of the tank. This suggests that as nest construction continues, a greater proportion of finer material is used regardless of availability of floating fragments. Bottom material, although used in great quantities by some males, never included sand or gravel which is occasionally spit into the nest by _T_. _leeri_ in considerable quantity.

The method of procurement of bottom debris for use in the nest depended on the size of the material. Materials picked from the bottom in greatest quantity were small plant fragments a centimeter or less in size. These usually accumulated in low places, especially in tanks in which peat moss was added, and formed layers up to 10 cm in depth. These accumulations were approached with head lowered so that the body axis was at an angle of 20 to 40 degrees to the substrate. The rate of pectoral beating was considerably more rapid than during feeding or searching the substrate in other phases of behavior and currents of water resulting from fin movement raised bottom materials several centimeters off the bottom. One to several of these floating pieces were secured crossways in the mouth and conveyed rapidly to the nest. Whether the increased rate of pectoral beats is deliberately used to raise bottom debris or is a result of maintaining position is questionable. Feeding and other activities on the bottom of the tank usually do not produce such results, however.

Large objects, too heavy to be lifted from the bottom by the current created by the fanning pectorals, were picked up from the substratum and handled in the same manner as loose surface vegetation. Most males incorporated snail shells and live snails into their nests. This behavior was extremely detrimental in two cases in which live snails were carried to the nest in such numbers that they destroyed the bubbles and eggs. One nest alone had over 70 live snails visible at its upper surface.

Exposed roots of _Vallisneria_ were used in large amounts by several males which severed them by grasping them in the mouth, jerking the head, and simultaneously propelling themselves away, using strong caudal beats.

## Use of Vegetation by Other Species of Trichogaster

Use of vegetation by _T. trichopterus_ is rare. Miller (1964) reported that clear attempts to incorporate plant fragments or bottom detritus into its nest by _T. trichopterus_ was not seen. _T. leeri_ on occasion adds plant fragments as well as detritus and sand but such materials are not a major part of the nest, at least in domesticated strains. As mentioned above, _T. pectoralis_ constructs a nest with large amounts of vegetation, perhaps similar to that of _T. microlepis_.

## Bubble Blowing

Although vegetation makes up the major portion of the nest, an equally important element of most T. microlepis nests appears to be air bubbles.

Four methods of adding air bubbles to the nest are used by the genus Trichogaster: surface inspiration with sub-nest release, surface inspiration and release, jetting, and opercular emission. Only surface inspiration with sub-nest release and jetting are used to any extent by T. microlepis.

### Surface Inspiration with Sub-Nest Release

This is the primary behavior responsible for the addition of bubbles to the nest and is present in all species of the genus. Air is usually inspired in open water nearest the nest. During inspiration the upper jaw is thrust above the water surface and the remainder of the body is held at approximately a 45 degree angle to the surface. The dorsal fin is usually partly erected and the anal fin, particularly the spiny-rayed anterior portion, is erected so the first 2 or 3 spines project in an anterior direction. Pectoral fins and the dorsal portion of the anal are used to maintain position. Pelvic fins are held out from the side of the body and are extended forward at varying degrees of abduction and appear to be used as stabilizers. Occasionally the pelvics pulsate back and forth for a centimeter or so as air is inspired.

Air is snapped as many as 40 or more times each trip. The frequency of snapping per trip, trip duration, and the number of trips per unit time vary according to the stage of nest development, time of day, availability of nesting materials, activities of other fish, and reproductive readiness of the fish. Quantitative aspects of air snapping are discussed in Chapters VII, VIII, and IX.

After air snapping, the fish drops several centimeters below the surface, turns and swims with fins partially erect directly beneath the nest. The inspired air is transformed within the mouth into small bubbles and coated by mucous secreted by unicellular glands in the oral cavity. After the nest is reached, the male circles slowly one or more turns with the head elevated approximately 20 to 45 degrees. Air is released from 1-4 cm beneath the nest and during active nest construction, the fish leaves immediately for additional air or vegetation.

All but one of the nests studied possessed approximately the same relative amounts of plant fragments and bubbles. One nest, however, was bubbleless and was constructed in a tank in which the Ceratophyllum was 10-15 cm in depth over the entire surface of the tank. In order for the fish to reach the surface to inspire or feed it was necessary to swim forcibly through to the surface and back down to open water. Nest construction was considerably different in this case since vegetation was dragged to the nest less frequently, almost no bubbles were added, and more trips were made to the bottom for nesting materials. Nest pushing was more frequent and consumed most of the male's time. The first indication of construction of this atypical nest was the dragging of vegetation to the nest site and the commencement of nest pushings. After pushing and conveyance of vegetation to the nest for approximately 8 hours a dome-shaped mat of vegetation was formed 2-3 cm above the surface. Since the nest was constructed in a corner, it was bounded laterally on two sides by glass and on the remaining sides to a distance of 10-15 cm below the surface by the unpacked vegetation covering the surface of the tank. Thus, a hollow, cup-shaped dome, 10-12 cm resulted. Other than the lack of using bubbles during construction, activity of the spawning series was similar to that of other series. Apparently use of bubbles in nest construction, at least in this case, was not necessary for spawning to occur. Although approximately 450 eggs were laid and 20-30 hatched, most eggs were destroyed by snails which were carried to the nest in great numbers by the male during construction.

### Jetting

Jetting is most evident between spawns after egg release and continues after the spawning series is complete. Following air snapping, the fish orients himself beneath the nest with body nearly perpendicular to the surface. He thrusts his nose deeply into the nest by strong caudal beats such as in nest pushing, and then a jet of water is forced from his mouth into the nest. Because of the extreme density of the nest at spawning time, the jet is often obscured and only when a loose portion of the nest is struck can the jet be viewed from above. The function of jetting during parental care is discussed further in Chapter VIII.

### Opercular Air Emission

Opercular emissions of air beneath the nest is common in both *T. trichopterus* and *T. leeri* but is rare in *T. microlepis*.

### Surface Inspiration with Surface Release

Surface inspiration and release common in _T. trichopterus_ and _T. leeri_ is absent in _T. microlepis_.

## Nest Pushing

Nest pushing is a prominent nest construction behavior in _T. microlepis_ but is not performed by _T. trichopterus_ or _T. leeri_. When executed it usually occurs from 1-3 seconds after air release and has a duration of approximately a second. Occasionally, nest pushing of longer duration occurs.

After air release, the fish ascends at an angle of 45 degrees or more by strong caudal beats and the snout is shoved against the nest as median fins are partly erected and the pelvics abducted. This behavior perhaps functions in the arrangement of vegetation or the dispersal of bubbles throughout the mass of plant materials. Miller (1964) suggested that the lack of this behavior in _T. trichopterus_ may be due to less extensive use of vegetation in nest construction.

Nest pushes usually follow air snaps of shorter duration than average. Twenty 10 minute periods of nest construction, taken at random, showed that while the average duration of an inspiration of air snap was 6.2 seconds, the duration of snaps immediately preceding a nest pushing was 4.1 seconds, and immediately following a push was 6.3 seconds. These figures show a tendency to cut short the period of air snapping immediately prior to a nest push.

The relative number of pushes compared to the number of air releases increases as nest construction continues. Quantitative aspects of nest pushing are treated in detail in Chapters VII, VIII, and IX.

## Possible Environmental Factors Affecting Nest Construction

Fifteen nests were observed during the study and all were begun within 8 days after some previous alteration of the physical properties of the tank had been made by the investigator. Alterations included changes in pH, temperature, turbidity, and water replacement.

In all but two cases nest building followed a lowering in pH of the water. The normal pH of tank water without treatment varied from 7.8 to 8.4. Two nests were constructed in tanks having pH of 8.1 and 8.2 and in which the water had been changed within 96 hours, the other 14 nest constructions occurred in water which had the pH lowered to from 7.5 to 5.3. The pH was lowered by use of sodium bisulphide in 3 of these cases and by addition of peat moss directly to the water in 11. One nest was constructed at pH of 7.4 and 2 at 6.8 using sodium bisulphide and 1 each at 5.3, 5.7, 6.1, 6.2, and 7.5 with 2 at 6.3 and 3 at 6.5 in tanks in which peat moss was added. Water in chemically treated tanks remained clear while that in which peat moss was added was temporarily so turbid that fish in the back of several of the tanks were obscured from vision. Water in all tanks to which peat moss was added cleared within 24 hours.

By addition of river silt turbidity was increased in three tanks with a high pH to about equal the turbidity produced by adding peat moss. The pH remained approximately the same and no increases in reproductive activity was observed.

As discussed previously the nest site was usually in a location of low light intensity and undisturbed water surface below which was adequate room to carry out spawning activities.

Lighting appeared to be influential not only in site selection, but also in orienting the fish to the nest. This was shown several times when lights were turned off during normally daylight hours over tanks where active nest construction was in progress. The room remained lighted because of illumination of other tanks but the direction of the major light source to the darkened tank was changed. Under such conditions fish experienced difficulty orienting under the nest, the ensuing trips back to the nest were less direct, and the time between inspiration and expiration under the nest increased. Air was frequently expelled short distances from the nest and vegetation was carried to areas not directly beneath it. There thus appeared to be general disorientation to the original nest site and in several cases where light remained changed for an hour or more the center of nest construction became displaced several centimeters from that existing before the light change.

The effect of females with distended abdomens on initiating male nest building could not be determined since all tanks having the water changed were supplied with at least one such female. In several tanks spawning occurred with the female with least enlargement of the abdomen, while the most gravid appearing female did not spawn. This, however, does not exclude the possibility that the nest constructing activity was influenced by the female with the full abdomen.

Although no quantitative data were taken, the abdomens of females appeared to increase rapidly (in 4-5 days) at the onset of nest construction by the male.

# CHAPTER V

# COURTSHIP

Courtship is an amalgamation of behaviors performed by both sexes and results in bringing the pair beneath the nest in order to spawn.

## Behaviors Bringing Pair Beneath Nest

### Early Courtship Chases and Displays

Chases during early courtship are usually extremely aggressive and often include damaging encounters in which the male attempts to drive the female from the area of the nest. Duration and severity of chasing increase with the initiation of nest construction and continue to do so as the nest is developed. With the increased aggressiveness of the male, the female increases her attentiveness to him and continues to return near to him after each chase. This behavior continues until male aggressiveness mounts to the point that she seeks cover to keep from becoming severely injured.

By the time the nest has been under construction for several hours, male chases become extremely severe (Type #3 chases). Pursuits by the male often include bites to the anal and caudal fin of fleeing fish and females are often followed and chased from shelters that ordinarily furnish safety from the harassing male.

Females not fleeing from aggressive males are sometimes viciously bitten even though they assume an appeasement posture which, under ordinary conditions, thwarts the attack. More often, however, the appeasing female is subjected to violent tail beats, and in more aggressive situations the pelvic fins are thrashed over her sides by the tail beating male. During tail beats and fin thrashing of this magnitude, the male often leans away from the female at an angle of approximately 45 degrees or more.

Thus as nest building proceeds, male aggression increases and chases and other behaviors become more severe and damaging to the female. Some quantitative aspects of the above behaviors will be discussed in Chapter VIII.

### Pre-Lead Butting and Associated Behavior

Response by the female to these attacks may be to avoid the harassing male or to counter the attacks and displays of the male by remaining and butting his side slightly below and behind the posterior insertion of his dorsal fin.

Pre-lead butting by the female may be initiated by the male or the female. Encounters in which the female is sought out by the male are considered male initiated, while situations in which the female seeks out the male are considered to be female initiated. Miller and Hall (1968) show that various behaviors of *T. leeri* vary greatly depending upon the sex which initiated them.

When *T. microlepis* males initiate the behavior they usually approach to within several centimeters of the female and after preliminary lateral spreads begin to tail beat. In the most aggressive displays, the male leans away from the female with fully erected medians while tail beating and pulsating forwardly outstretched pelvics toward or against the female who usually is in shelter in a head up position with median fins partially to fully erected and pectorals fanning. If the female does not respond by coming from shelter and butting him, he either continues harassing her until she flees, at which time an extensive and damaging chase ensues, or he attempts to lead her to the nest. If the female turns and butts the male, he swims to the nest and may be followed by her. Generally, the less aggressiveness shown by the female the more overt is behavior evidenced by the male.

Female initiated encounters generally elicit less overt behavior from the male than those initiated by him. They generally consist of a rapid female approach to the male which shows no apparent response, at least at the beginning of the approach. The male often turns to the female as she commences her approach and is butted by her. Usually both fish have fully to partially erected median fins during the approach. When butted, the male usually turns and swims directly to the nest and either is followed or preceded to it by the female.

Occasionally the male is reluctant to move when butted and displays to the female, who in turn butts with greater force. If the male does not swim nestward after several such attempts, the female flees and is severely chased. Quantitative data on male and female initiated encounters are discussed in Chapter VII.

## Leading to the Nest

These leads are commonly, but not exclusively, executed by the male apparently in an attempt to entice the female to follow. Varying degrees of median fin erection, tail beating, and ventral fin thrashing accompany such behavior.

The most common pattern observed throughout most of the spawning series is simple following of the male by the female, the frequency of which decreases as the spawning series continues. The probability that the female will follow appears to be enhanced when the male spends comparatively greater periods of time collecting vegetation and snapping air in the vicinity of the female. In many instances he also deviates from the most direct route to the nest and swims near the female. If the female leaves shelter, she may or may not butt the male, but whether he is transporting vegetation, bubbles, or neither, he increases speed and spreads his median fins as the female swims after him. He continues in most cases to carry the nesting material, but upon reaching the nest, he releases it.

Perhaps the most spectacular leading pattern occurs in the absence of female butting and when she is reluctant to follow. Leads of this type occur primarily at the beginning of the spawning series and after the male has sought out the hiding female. Lateral displays, tail beating, and sometimes ventral fin thrashing are executed by the male. When the female fails to approach, the male turns and commences swimming rapidly to the nest with median fins fully erected and pelvics held forward and pulsated. The body of the male is held with anterior end upward at approximately a 45 degree angle and assumes a sigmoid curve. As the fish swims nestward he may stop and turn somewhat sidewards to the female before resuming his progress to the nest. Such behavior of the male often elicits following from the female, and then the exaggerated hesitating zig-zag motion of the male develops into a more direct approach to the nest with reduced fin erection.

Most damaging chases occur during the female approaches to the nest just described. If the female does not direct strong butts to the male or fails to follow him closely to the nest, she is subjected to severely damaging aggressive behavior. At this time only strong butting of the female will thwart prolonged damaging attacks and chases.

### Approach to Nest Without Lead

After several spawns have been completed, independent approaches by the female without leads by the male become the rule. Once this occurs, it is usually continued throughout the remainder of the spawning series.

The female most commonly approaches the nest slowly along the bottom and under cover, when possible, until a place of shelter somewhere near the nest is reached. She usually waits until the male has left the nest to retrieve materials, or has just turned to bring the materials back before she makes her ascent to the nest. Upon seeing the female swimming rapidly to the nest the male swims to meet her with erected median fins. As they meet, bites or butts are exchanged to the side of the other fish. The male with few exceptions turns at this point and swims rapidly toward the nest, either followed or in some cases led closely (1-3 cm) by the female.

Occasionally, the female may reach the nest before the male reaches her or even before he sees her and as he enters beneath the nest, she butts him in the usual manner.

## Drive to the Nest

The female may also be brought beneath the nest during aggressive chases which frequently occur during each spawning series. Such behavior occurs most commonly near the beginning or end of the spawning series, during which time the behavior of the pair is less synchronized.

If the female stops beneath the nest during a chase the male invariably ceases his pursuit and begins the typical behavior elicited by a female beneath the nest. Spawnings at this point are seldom successful, and it is questionable whether the female seeks the nest on purpose to spawn. There is also doubt whether the male intentionally chases her there. However, the female appears to be aware that the nest is a unique location of safety because she does not stop under other dark areas with equally dense surface cover. When chased beneath the nest any fish in the tank appears to recognize it as a temporary sanctuary from pursuit by the male.

On one occasion during early spawning a male which had made numerous unsuccessful attempts to lead a female to his nest intercepted the female as she approached the nest. The female weakly butted the male, who commenced tail beating and thrashing his pelvics. She did not continue to butt, however, and started to swim away. As she was vigorously chased she turned to butt the male and a frenzied exchange ensued from which the male emerged dragging her to the nest by her pelvic fin. After 20-30 cm, the female succeeded in butting him and he released his hold immediately doing a lateral spread. The female immediately swam for cover with the male chasing. Although this incident of dragging a female nestward is unique, the pelvics of the female are often seized and pulled or even severed by nest building or spawning males apparently in attempts to remove females from areas near the nest.

# CHAPTER VI

# SPAWNING

## Sub-Nest Butting

Once the pair was located beneath the nest, behavior became more stereotyped and the female assumed a horizontal position a centimeter or so beneath the center of the structure as she commenced butting the male. Butting at this point was directed to the region posterior and ventral to the dorsal fin and as in other butting situations, appeared to function in the reduction of male aggression. If not butted immediately by the female, however, the male began to lateral display and tail beat. The longer the female refrained from butting, the stronger the tail beats of the male became as he leaned away from her. In extremely aggressive encounters the pelvics were thrashed alternately during tail beating and, although they were directed mainly forward, the fin nearest the female was often directed against her as he was tail beating and fin thrashing. He usually moved around the perimeter of the nest falling slowly away and down from it, often falling completely away from beneath the nest before dashing back under and resuming tail beating. As long as the male continued to swim sporadically around the female she continued to butt him intermittently below the posterior base of his dorsal fin. Usually, however, after the first or second butt, tail beating and fin thrashing ceased and he moved to within a centimeter or two from the female and commenced to circle about her maintaining a weak lateral display posture. If the female failed to remain oriented properly at the side of the male, violent tail beating was resumed which resulted in another butt from the female and the formerly described sequence of behavior was repeated. Violent tail beating and fin thrashing drove some females from beneath the nest and severe chases by the male ensued. If the female administered strong butts, she usually was not driven away and circling began.

Butting by the female on arrival beneath the nest appears to be a common characteristic of the genus, although areas butted vary from species to species. While *T. microlepis* butts slightly posterior and ventral to the dorsal fin, *T. trichopterus* and *T. leeri* butt at the dorsal part of the body and caudal peduncle (Miller 1964) and (Hall 1966). Butting also varies in frequency from approximately 2-6 per spawning encounter in *T. microlepis* to 40 or more in *T. leeri* with *T. trichopterus* intermediate.

Female butting of the male appears to function in reducing male aggression toward the female. When butting occurs either beneath or away from the nest, it usually is followed by rapid loss of male aggression and in most cases approach to the nest by both fish (if the pair is not already there) and the commencement of circling. Also when butting occurs during tail beating beneath the nest, tail beating stops and circling usually begins. Butting thus not only reduces male aggression but also encourages spawning behavior in both sexes. Miller and Hall (1968) suggest that in *T. leeri* butting by the female is an indication of her sexual motivation whereas the same behavior by the male is closely related to aggressiveness.

Seldom are more than a few butts delivered in any one sequence. For example, butting preceding circling seldom exceeds three or four and when butting occurs out from beneath the nest the number is lower.

Butting is not observed except in reproductive situations but neither are the aggressive situations which would elicit such behaviors.

## Circling

Circling occurs several centimeters beneath the center of the nest. The male swims a tight circle around the female as she orients with her snout or chin at the posterior margin of his dorsal fin and with her ventrum turned slightly toward him. Their anterior ends are elevated so that the axis of their bodies is at an angle of 25 to 45 degrees to the substrate.

As they begin to circle, the fins of both fish are partly to fully erected, those of the male to a greater degree than those of the female. The male retains a slight sigmoid position with head turned away from the orienting female. Forward motion and orientation of the pair is accomplished by pectoral fin beats and undulating of the dorsal portion of the caudal fin. Throughout the period of circling the pair maintains a position perpendicular to and approximately 1-3 cm from one another, the "X" position. The snout of the female protrudes to the level of the eye above the posterior margin of the dorsal fin of the male.

If disorientation occurs during circling, male tail beating usually follows and the pre-circling behavior, butting, and tail beating is repeated. The most apparent reason for disorientation during circling is failure of the female to maintain orientation to the male and her failure to butt if he starts falling away. After circling around the female from 1-8 times the male loses his sigmoid posture and the pair cease circling and remain stationary approximately 1 cm beneath the nest in the "X" position.

Circling appears to orient the pair beneath the nest and perhaps also to synchronize activities of the pair in order to facilitate a successful spawn. Some quantitative relationships between circling duration, frequency, and spawning success is noted in Chapter VII.

## Post-Circling Pause

Circling is followed by a pause, the post-circling pause, which is not present in other Trichogaster and varies in duration from 1-80 seconds with an average of 11.4 seconds. The pair remains oriented during the pause as they were during late circling, in the "X" position approximately 1-3 cm apart, maintaining their positions by undulations of the dorsal portion of the caudal as well as the pectoral fins.

As the pause continues the pair sometimes begins to drift apart, at which time the female usually follows the male maintaining the same relative position to him. If the male drifts rapidly, the female butts near his dorsal fin eliciting male median fin display and reorientation of the pair and circling commences again. On rare occasions, however, a lightly butted male stops drifting and the pair remain in a stationary position without circling.

During the pause, fins of both fish are relaxed and are raised only if reorientation and/or circling commence. About halfway through the pause the two fish begin to curve slightly toward one another. After curving continues for several seconds it is terminated by the clasp of the male.

Although on occasion disorientation by the male away from the female elicits behavior by her (usually in the form of butting) to maintain their relative positions, poor orientation by the female to the male is more common. Three types of such faulty orientation are common during the pause: orienting too high to the dorsal fin of the male, nest-nipping, and drifting away while the male curves into the clasp. The above three are not observed in every spawning series and some females are more prone to one type than to another. They are most common in early and late spawns.

Orienting too high to the dorsal fin of the male, if occurring, usually begins immediately after circling stops. At this time the female fails to orient to the male's dorsal fin and rises above the male. Generally the male responds by tail beating, and the female usually comes back down and butts the male. However, if the female raises only several millimeters above the normal position, the pause may continue to the clasp but the resulting clasp is often closed improperly and is of short duration. As the male recovers from such a clasp he usually tail beats and is butted by the female.

Rising of the female above the dorsum of the male often brought the female in contact with the lower portions of the nest. In most cases the mouth of the female was thrust into the structure and a behavior like surface feeding occurred. Egg eating took place several times but the behavior occurred commonly in nests without eggs. It elicited violent tail beating by the male and eventual butting, reorientation or flight by the female. Egg eating by females at such times will be discussed later. Severe attacks on the female by the male at this time were rare.

Drifting of the female away from the male commonly occurs late in the pause immediately before or during the start of male curving. The female makes no overt movement from the male but usually drifts outward and upward from him. Such behavior usually precedes an unsuccessful clasp. The effect of such disorientation on the clasp will be discussed in the section on curving and clasping.

The post-circling pause, the second longest element of the spawn, may promote an increase in spawning motivation and synchronization and also serve to orient the pair to one another. The behavior is probably more related to synchronization than to orientation since the latter occurs before the pause and relative positions of the pair change little after the pause begins.

A pause of this type has not been reported by Miller (1964) for *T. trichopterus* or by Hall and Miller (1968) for *T. leeri*. However, both species have behaviors which prolong pre-clasp time. *T. trichopterus* circles for only an average of 5-6 seconds but executes a rubbing behavior, absent in the other species, for an average of 70 seconds. *T. leeri*, while not rubbing, spends an average of 15 seconds in lateral spreads and an average of 30 seconds circling (twice as long as *T. microlepis* and 5 times that of *T. trichopterus*). Extension of pre-clasp time, although accomplished differently in each species, may function in allowing the pair to synchronize their reproductive behavior before the clasp.

## Curving

Toward the end of the pause the already slightly curved body of the male slowly accelerates in its curving as the peduncle is brought under the venter of the female and appears to pull the male toward the female. The female usually remains stationary in the water or moves slightly away as the male closes the clasp. Only on rare occasions does the female move toward the male, as is the case of _T_. _trichopterus_ (Miller 1964) and _T_. _leeri_ (Hall 1968). As the male closes around the female she is pushed from the position maintained in the pause to an almost vertical one and the male becomes horizontally oriented.

## Clasping

The body of the clasping male assumes a U-shaped curve around the anterior portion of the female. As well as synchronizing release of sex products, the clasp brings the genital orifices of the pair close together and thus increases fertilization efficiency. The female leans slightly into the closed end of the clasp with her peduncle somewhat toward the open portion of the clasp of the male. The eye is barely visible at the anterior base of the dorsal fins and the distal half of the pectoral fin is exposed beneath the belly of the male. The anterior and posterior extremities of the anal fin of the male are pressed tightly to the sides of the female while the remaining portion adjacent to her belly is flared outward (Figure 1).

The pair apparently maintains its position under the nest during the clasp by use of the anal fin of the female and the free outside pectoral fin of the male which is fanned rapidly. If the pectorals of the female were free to move and were not restricted by the clasping

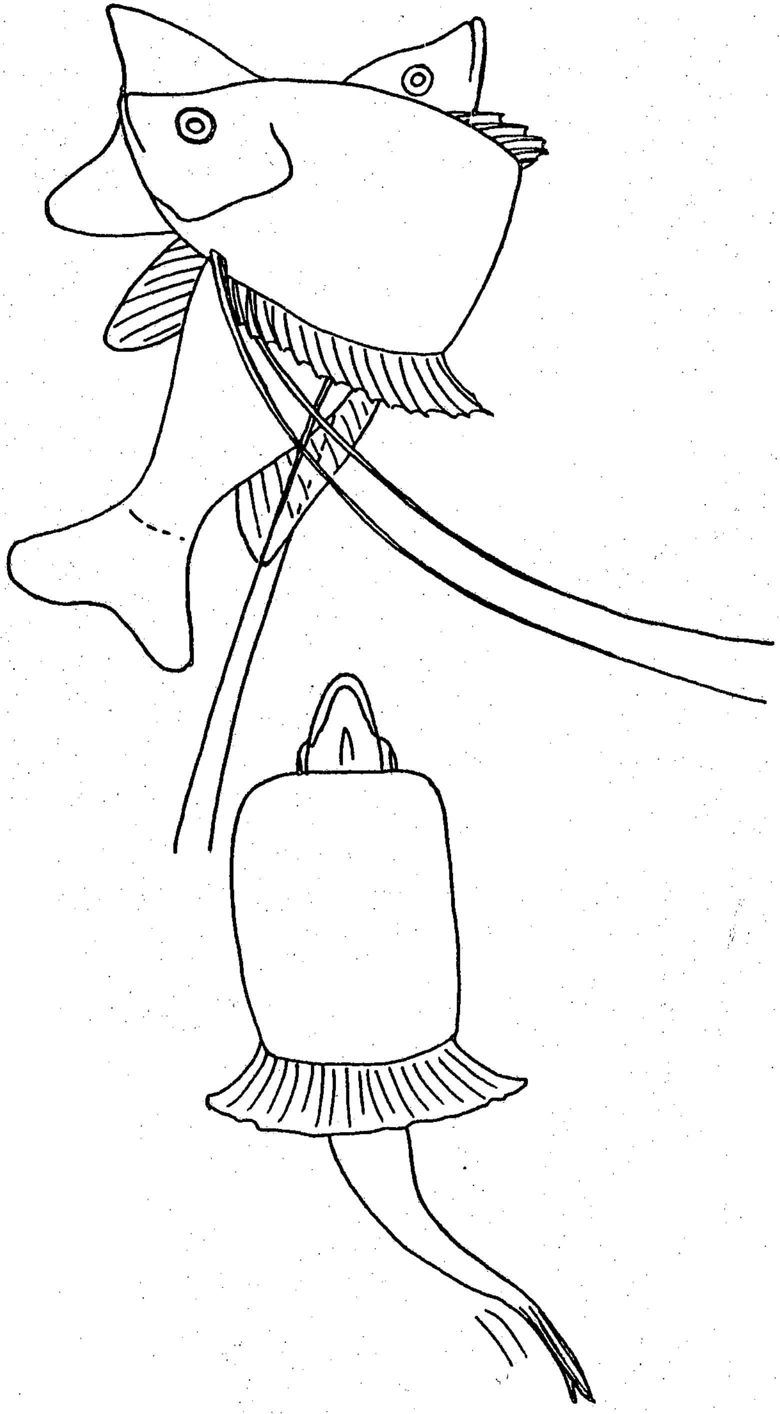

Figure 1. Male Clasping Female (Above) and Pair Beginning to Roll Over (Below).

male, as was occasionally the case, they also pulsated. After the clasp began the caudal peduncle of the female began to curve upward. Once the clasp was closed the pair seldom lost orientation before rolling. If, however, the female slipped from the clasp or some other factor caused disorientation, there was seldom resumption of the clasp without going through butting, circling, and a post-circling pause. These behaviors, however, were usually briefer in duration than similar behavior in the preceding attempt.

Clasp duration varies less than any other element in the spawning bout. It ranged from 1-15 seconds with an average of 8.2 seconds. Average duration in successful bouts was 9.3 seconds while it was only 3.4 seconds in unsuccessful bouts. In successful, one circle bouts relatively few clasps were of short duration and of 178 only 11 were less than 7 seconds and none were longer than 14 seconds.

## Rolling Over

After several seconds in the clasp the caudal peduncle and median fins of the female commence vibrating and the peduncle begins to curve sharply just below the body of the male toward his tail. At approximately the same time that quivering commences in the female or an instant afterward the body of the male and particularly the anal fin may also start to vibrate. As the peduncle of the female assumes an angle of approximately 90 degrees, the pair begins to roll over, away from the female's tail and towards the head of the male, twisting slightly so that the open end of the clasp and head are downward (Figure 1).

During the roll quivering stops and the female remains tightly clasped by the male and remains so until his head and caudal peduncle are down and the female is horizontal to the substratum with venter up. In most cases release from the clasp at the end of the roll and the beginning of swimming inhibition is marked by a definite relaxation by the male. In perhaps 30 per cent of the clasp releases there was no sudden relaxation and the clasp was terminated less abruptly as the female slipped from the clasp. Subsequently, the fish drifted in a state of swimming inhibition.

The clasp aids in synchronization of gamete release although it is questionable as to whether actual mechanical pressure exerted on the female by the clasping male is a contributing factor in expelling eggs. On several occasions eggs were observed to be released by pairs clasping so loosely that it was difficult to conceive the presence of pressure sufficient to aid egg deposition mechanically. Also, in one spawning preceded by 13 and followed by 16 spawns, the female released 20 to 30 eggs after a clasp that was only partially closed as rolling started and the fish separated. Egg release occurred after the pair had completely separated. This was the only spawn observed in which eggs were released without a complete clasp and before the pair rolled over.

Miller (1964) reported that in T. trichopterus the anal fins of both sexes as well as the caudal of the female vibrated during the clasp, and both sexes trembled violently as the sex products were released. Hall and Miller (1968), in describing T. leeri, referred to quivering after the clasp which continued as the sex products were released but, although they never specifically state vibrating by the male, there is implication of such. Quivering in *T. microlepis* occurs primarily in the female as the peduncle starts up and continues until egg release, at which time it ceases. The male may or may not quiver during this time.

Hall and Miller (1968) describe a terminal squeeze in *T. leeri* in which the male, near the end of each spawn, momentarily releases his clasp following it immediately by a convulsive tightening of his body on the female. If this convulsive tightening is a mechanical aid to sperm ejaculation or egg release, it appears to be unnecessary in other species of *Trichogaster* since they possess no such behavior.

## Swimming Inhibition

As the pair drift apart swimming inhibition, which lasts up to 6 seconds, occurs in the majority of spawns. In this state little or no fin movement is observed and the fish settle to the bottom.

The position of both fish as they drift downward is similar to that when release of the clasp occurs. The female is head down in a vertical position and the male floats on his back or side in a nearly horizontal position. They drift downward until they come to rest upon the substrate. The female usually recovers first and in most cases swims from beneath the nest before the male recovers, at which time he usually begins to tail beat even before he assumes the normal swimming position. If the female is still beneath the nest, she is chased aggressively but if she has departed and eggs are present, he often begins retrieval before recovering complete equilibrium, while still lying partially on his side attempting to regain normal position in the water.

Departure of the female before being chased appears to be an advantage because the male need not leave the nest before beginning egg retrieval, thus reducing the chance of egg loss.

Following swimming inhibition the female usually seeks shelter and remains there for a variable period of time under constant threat of attack by the male before another approach to the nest. The male after a possible chase of the female collects and cares for the eggs, if present, and/or continues to maintain the nest.

## Atypical Attempts of the Male to Spawn Successively

On five occasions, early in the spawning sequence after successful spawns had been accomplished, the female after recovery from swimming inhibition responded to attack by butting rather than fleeing. When butted, the male in every case started to tail beat. In two cases the female fled and in three the pair reoriented beneath the nest. All three attempts broke up during circling when the female continually drifted away from the male after several circles. Although the above data are meager, it suggests that the male is capable of commencing a second bout immediately after the completion of the first. Since the female appeared to orient improperly it may be assumed also that she was incapable of a second immediate spawn because of insufficient spawning motivation, physical exhaustion, or physiological incapabilities. Butts by the female could have been normal defensive butts, discussed earlier.

A second situation observed 10-15 times, tending to substantiate the above suggestion, occurred when a second female entered beneath the nest immediately after a successful spawning female had departed.

In such cases all second females appeared to be treated by the male in the same manner as the first female. Although the per cent of success of these attempts was lower than with the primary spawning female, several successful spawns occurred. This lowered success may be due to lack of enough aggressiveness to enable the female to remain oriented throughout the bout. As shown below, spawns become more efficient with larger degrees of success as the series continues. Thus the female intruding into the normal sequence of the spawning series probably is not as reproductively ready or synchronized with the male and is thus undoubtedly incapable of spawning with the same success as the primary female.

# CHAPTER VII

# SOME QUANTITATIVE ASPECTS OF SPAWNING BEHAVIOR

## Circling Periods

The duration of individual circling periods and the frequency with which they occurred in each bout were both interdependent and dependent upon several additional characteristics of the bout such as the relative position of the circling period in relation to the duration and frequency of other circling periods in the bout, the duration of the bout itself, the location of the bout in the spawning series, and the success of the bout. To facilitate discussion, bouts have been considered primarily in regard to duration and frequency of circling periods.

The duration of circling periods in 427 bouts analyzed varied from 1-40 seconds and had an average of 13.7 seconds.

### Duration of Successive Circling Periods

In most multicircle bouts the duration of each successive circling period became shorter than that of the previous period (Table II). For example, in 23 successful bouts with 3 circling periods the first period of circling had an average duration of 10.8 seconds, the second circling period an average of 5.1 seconds, and the third 4.0 seconds, or in 21 unsuccessful 3-circle bouts the average duration of the first, second, and third circling periods were 12.8 seconds, 6.4 seconds, and 4.9 seconds, respectively.

The average duration of the first circling period in multicircle bouts was 84.3 per cent longer than the second circling period in successful bouts and 137.47 per cent in unsuccessful bouts. In 88 successful bouts the average duration was 10.5 seconds in the first circling period and 5.7 seconds in the second circling period; in 79 unsuccessful bouts the average of the first circle duration was 12.1 and the second was 5.1 seconds.

The average duration of the second circling period was 27.1 per cent longer than the third period in successful and 30.6 per cent longer in unsuccessful bouts.

The average duration of the third circling period was 12 per cent longer than the fourth period in successful and 8.3 per cent longer in unsuccessful bouts. In 3 successful 4-circle bouts the duration of the third circling period was 5.6 seconds and the duration of the fourth was 5.0 seconds. In 9 unsuccessful bouts the average duration of the third was 5.2 and the fourth was 4.8 seconds.

The above data suggest that although synchronization of behavior may not be sufficient to bring about a successful spawn after one circling period and since successive circling periods become progressively shorter there is some degree of holdover in the effect of the preceding circling period and associated behavior. The possibility of an effective spawn after a successive circling period is thus enhanced.

Multicircle bouts and the ability to reorient without leaving the nest appear to function in enabling a poorly synchronized pair to

# TABLE II

## MAXIMUM, MINIMUM, AND AVERAGE DURATION OF SUCCESSIVE CIRCLING PERIODS IN SUCCESSFUL AND UNSUCCESSFUL BOUTS CONTAINING 1, 2, 3, AND 4 OR MORE CIRCLING PERIODS IN 9 SPAWNING SERIES

| | | Successful Bouts | | | | Unsuccessful Bouts | | | |
|---|---|---|---|---|---|---|---|---|---|
| Circle Period | | 1st | 2nd | 3rd | 4th | 1st | 2nd | 3rd | 4th |
| 1-Circle Bouts N = 260 | Max | 26.0 | | | | 27 | | | |
| | Min | 2.0 | | | | 1 | | | |
| | Avg | 11.2 | | | | 10.2 | | | |
| 2-Circle Bouts N = 111 | Max | 18 | 13 | | | 26 | 16 | | |
| | Min | 1 | 1 | | | 1 | 1 | | |
| | Avg | 10.4 | 5.9 | | | 11.6 | 4.7 | | |
| 3-Circle Bouts N = 44 | Max | 33 | 13 | 9 | | 40 | 12 | 14 | |
| | Min | 1 | 1 | 1 | | 1 | 3 | 2 | |
| | Avg | 10.8 | 5.1 | 4.0 | | 12.8 | 6.4 | 4.9 | |
| 4-Circle$^{+}$Bouts N = 12 | Max | 15 | 6 | 9 | 8 | 25 | 9 | 8 | 9 |
| | Min | 4 | 3 | 3 | 3 | 1 | 1 | 3 | 1 |
| | Avg | 9 | 5 | 5.6 | 5 | 13.6 | 4.6 | 5.2 | 4.8 |

eventually accomplish a spawn and decrease the relative number of spawning bouts and total time necessary to complete the spawning series.

## Duration of Circling Period Throughout Spawning Series

When 9 spawning series were averaged together and temporally analyzed by tenths of the series, it was found that throughout the first half of the series the average duration of circling periods in 178 successful spawning bouts with one period of circling became progressively shorter, decreasing from 12.1 seconds during the first tenth of the series to 10.3 in the fifth and sixth tenths. The duration increased gradually from the seventh tenth to an average of 11.5 in the final tenth (Figure 2).

Circling period duration in 82 unsuccessful bouts, with exceptions, showed the opposite trend to that observed in successful bouts and increased from 9.2 seconds during the first tenth to 14.0 seconds during the sixth tenth. From this point the duration dropped to 9.8 seconds in the seventh tenth and continued to decline with exception of the ninth tenth during the remainder of the series to a low of 6.1 in the last tenth (Figure 2). The duration of the ninth tenth, which rose to 15 seconds, was probably due to a relatively low number of occurrences (5) in which the duration of 2 periods were 20 and 19 seconds.

From the above analysis of circling period duration throughout the spawning series, it appears that since successful circle length is shortest during mid-series there is a continued increase in efficiency through the first half of the series reaching a maximum during the

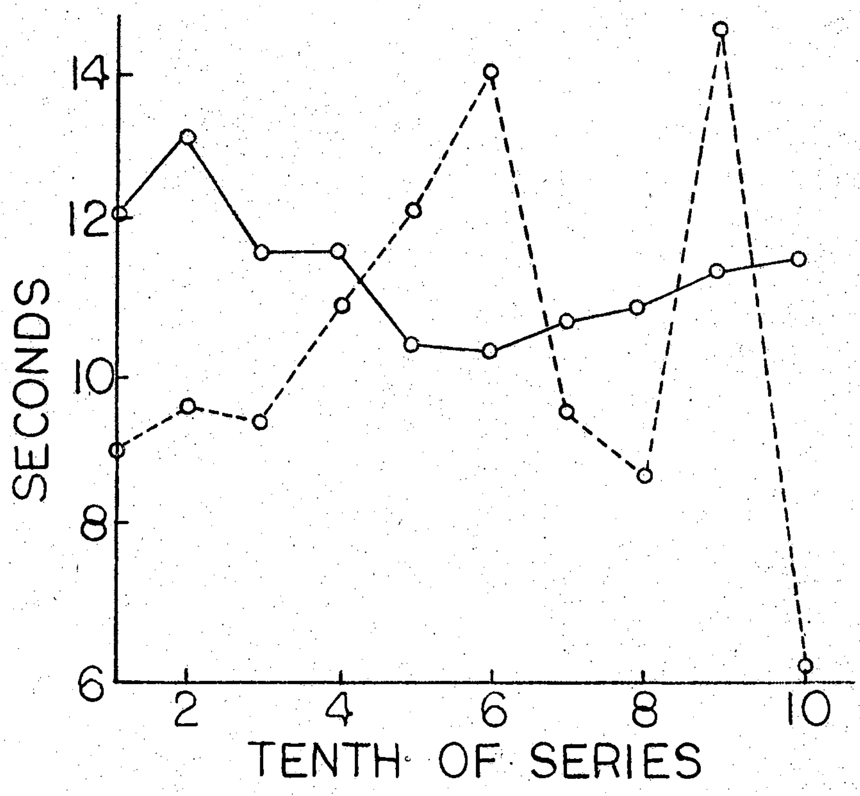

Figure 2. Average Duration of Circling Periods in Successful (Solid Line) and Unsuccessful (Broken Line) 1-Circle Bouts in 9 Spawning Series.

middle fifth of the series. During the remaining two-fifth efficiency becomes lower but not to the level of inefficiency possessed during the first portion of the series.

The second circling period of successful 2-circle bouts showed much the same trend as did the successful 1-circle bouts decreasing from a duration of 10.0 seconds in the first tenth to 7.0 seconds in the seventh tenth (Figure 3). Also, an increase during tenths 8 and 9 to a duration of 7.8 in the final tenth occurred. Unsuccessful bouts were more variable but during most later tenths of the series they were of greater duration than in the successful ones.

Successful 3-circle bouts (Figure 4) assumed much the opposite curve. It is difficult to assign such a configuration to chance or to the small sample (N-21). Perhaps with the increased motivation to spawn which appears to be typical of mid-series spawns, circling for longer and more numerous periods occurs thus increasing spawning success.

## Frequency of Circling Periods in Each Bout

Circling bouts included from 1-11 periods of circling. Most bouts contained 3 or less, only 12 of 427 having more than 3.

Spawning appears to be quite efficient in *T. microlepis* since the majority of circling bouts possess only one period of circling (Figure 5). Of 427 circling bouts 260 (60.8 per cent) possessed only one circling period, 111 (25.9 per cent) possessed 2, 44 (10.3 per cent) possessed 3, and 12 (2.8 per cent) possessed 4 or more circling periods.

Successful bouts had a greater number of 1, 2, and 3-circle bouts than did unsuccessful bouts (Figure 5 and Table II). Of 427 circling

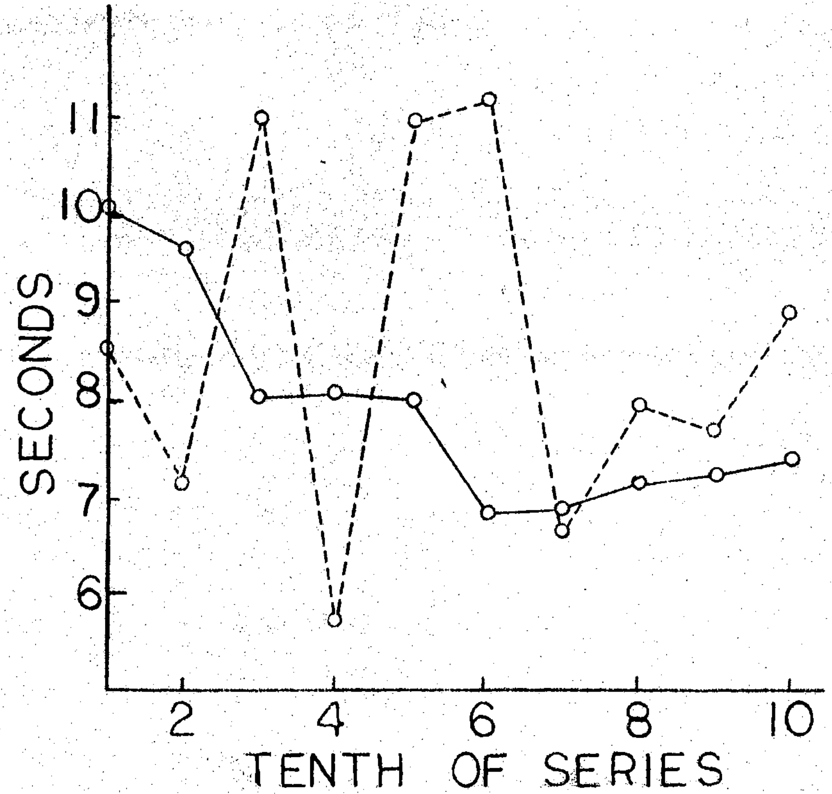

Figure 3. Average Duration of Circling Periods in Successful (Solid Line) and Unsuccessful (Broken Line) 2-Circle Bouts in 9 Spawning Series.

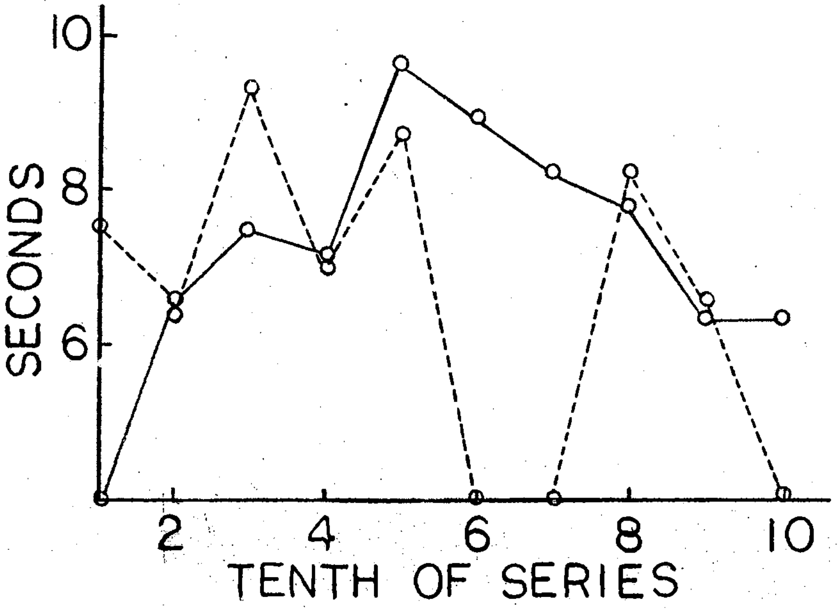

Figure 4. Average Duration of Circling Period in Successful (Solid Line) and Unsuccessful (Broken Line) 3-Circle Bouts in 9 Spawning Series.

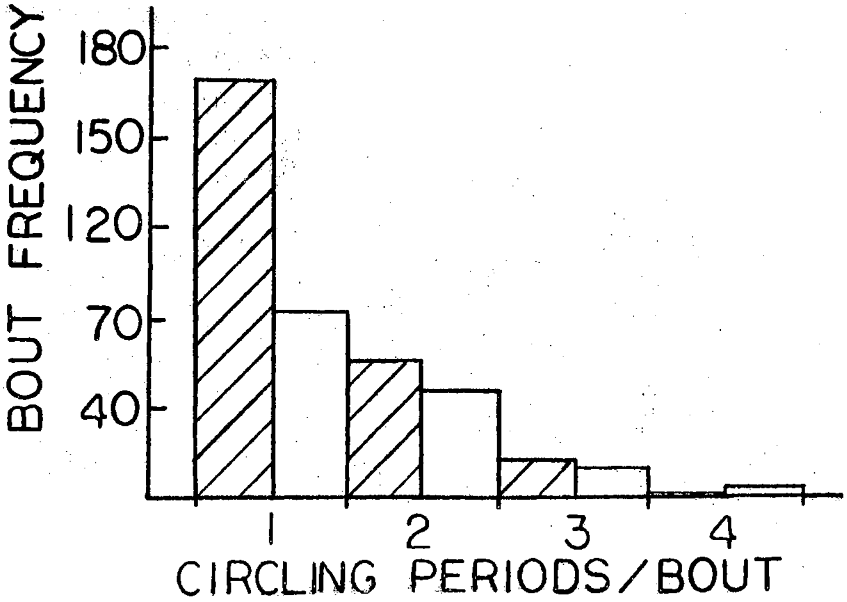

Figure 5. Frequency of Successful (Hatched Bar) and Unsuccessful (Unhatched Bar) Bouts with 1, 2, 3, and 4 or More Circling Periods in 9 Spawning Series.

bouts, 178 (41.9 per cent) successful bouts had one circling period, while only 82 (19.2 per cent) unsuccessful bouts had one circling. Sixty-two (14.5 per cent) successful bouts contained 2 circling periods while 49 (11.5 per cent) unsuccessful had 2. Twenty-three (5.4 per cent) successful bouts had 3 periods of circling while 21 (4.9 per cent) unsuccessful bouts had 3. Bouts with 4 or more circle periods were the exception in that there were more unsuccessful than successful bouts, 9 (2.1 per cent) and 3 (0.01 per cent), respectively.

The above data indicate that successful bouts are more numerous than unsuccessful ones and, as the number of circling periods in each bout increases, fewer successful bouts occur relative to unsuccessful ones. There is thus a decrease in efficiency of the pair as the frequency of circling periods per bout increases and in extreme cases in which 4 or more periods exist, the unsuccessful bouts are most frequent. Therefore, the greater the number of circling periods in each bout the less chance the bout has of being successful. Miller and Hall (1968) established that in _T. leeri_ unsuccessful bouts have a longer circling duration and state that bouts with shorter circling are typical of pairs that show a readiness to spawn.

Successful bouts had a greater per cent of 1-circle bouts than did unsuccessful ones, since 66.9 per cent of 266 successful bouts possessed only one circling period while only 50.9 per cent of 161 unsuccessful bouts had but 1 circle. In bouts with 2, 3, and 4 circling periods, however, successful bouts composed a smaller percentage than did unsuccessful ones and had a percentage in successful of 23.3, 8.6, and 1.0 and in unsuccessful of 30.4, 13.0, and 5.5, respectively (Figure 6).

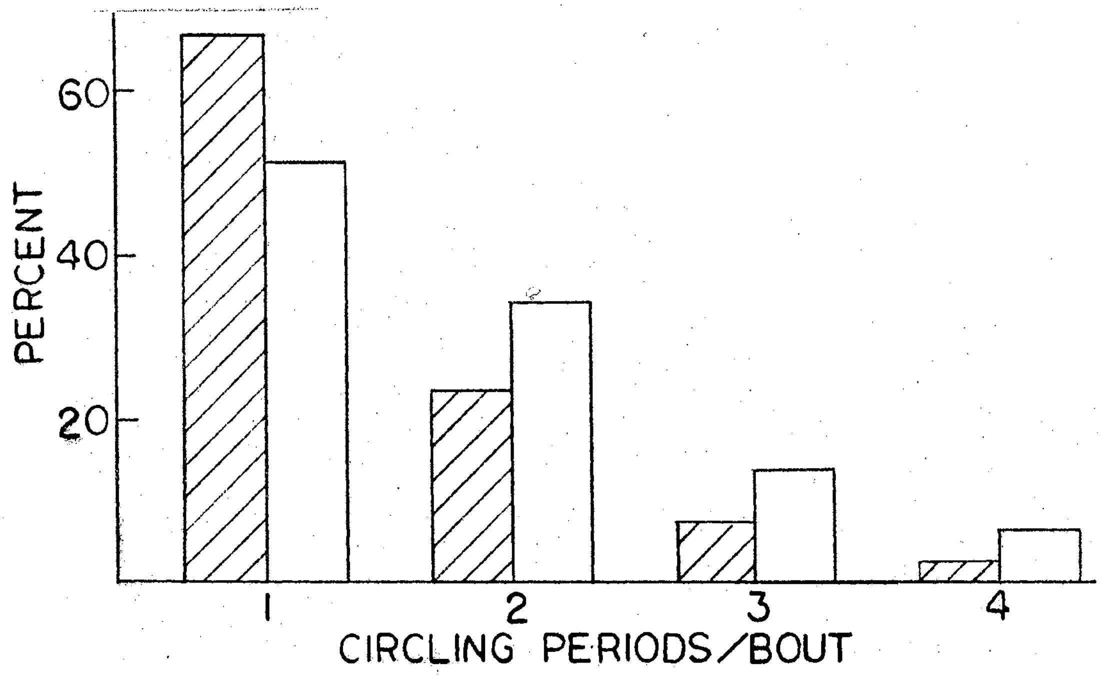

Figure 6. Percent of Successful (Hatched Bar) and Unsuccessful (Unhatched Bar) Bouts Possessing 1, 2, 3, and 4 or More Circling Periods in 9 Spawning Series.

The greater percentage of unsuccessful multicircle bouts emphasizes the poor synchronization of the pair and the increased attempts to reorient and spawn after disorientation.

The possibility of a circling period continuing to a successful spawn decreased 16.1 per cent as the number of circling periods increased from 1-3. Since 68.4 per cent of bouts with 1 circling period, 55.8 per cent with 2, and 52.3 per cent with 3 were successful. As the number of circling periods exceeded 3, the probability of successful spawning dropped to 25.0 per cent.

## Frequency and Duration of Circling Periods and Bouts

Successful bouts were usually longer than unsuccessful bouts with the same number of circling periods. For example, successful bouts with 1, 2, 3, and 4 circling periods had average durations of 44.2 seconds, 55.8 seconds, 58.2 seconds, and 73.0 seconds, respectively, while similar data for unsuccessful bouts were 29.3 seconds, 38.8 seconds, 49.3 seconds, and 77.5 seconds. Successful bouts with 1, 2, and 3 circling periods were thus 33.7 per cent, 30.4 per cent, and 15.2 per cent longer, respectively, than unsuccessful bouts (Table III). The longer duration of successful bouts suggests a need for the bouts to be sufficiently long to properly synchronize the activity of the pair and may be an attempt to reorient for spawning.

In accord with an increase in bout duration came an increase in the total time spent circling in both successful and unsuccessful bouts. In 266 successful bouts containing 1, 2, 3, and 4 or more circling periods the total time spent circling was 11.2, 16.3, 19.9, and 24.6 seconds, respectively, while similar data for 161 unsuccessful bouts was 10.2, 16.3, 24.1, and 28.2 seconds, respectively (Table II). Circling in successful bouts comprised from 33.9 to 51.2 per cent of the total bout time and in unsuccessful bouts from 53.4 to 95.3 per cent of the total duration of the bout.

TABLE III

MAXIMUM, MINIMUM, AND AVERAGE DURATION AND FREQUENCY OF SUCCESSFUL AND UNSUCCESSFUL SPAWNING BOUTS POSSESSING 1, 2, 3, AND 4 OR MORE CIRCLING PERIODS IN 9 SPAWNING SERIES

| | Successful Bouts | | | | Unsuccessful Bouts | | | |
|---|---|---|---|---|---|---|---|---|
| Circle Periods | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Max. Duration | 77 | 92 | 70 | 98 | 91 | 118 | 82 | 199 |
| Min Duration | 16 | 27 | 44 | 48 | 4 | 14 | 21 | 48 |
| Avg Duration | 44.2 | 55.8 | 58.2 | 73.0 | 29.3 | 38.8 | 49.3 | 77.5 |
| Total Freq of Bouts | 178 | 62 | 23 | 3 | 82 | 49 | 21 | 9 |
| % of Succ or Unsucc Bouts | 66.9 | 23.3 | 8.6 | 1.1 | 50.9 | 30.4 | 13.0 | 5.5 |
| % Total Bouts | 41.6 | 14.5 | 5.3 | 0.7 | 19.2 | 11.4 | 4.9 | 2.1 |

Miller and Hall (1968) found that in T. leeri unsuccessful bouts have longer circling times and that longer time spent circling in unsuccessful than successful bouts appears to be due to failure of the pair to become properly oriented to one another and is an indication that the pair is not ready to spawn. They also stated that if sexual systems are acting at optimum during spawning then it would seem proper to assume that circling possesses a positive correlation with aggressive systems and a negative one with spawning.

### Frequency of Circling Period Throughout Spawning Series

The number of circling periods in each bout varied from 1-11 and averaged from 1.8 to 1.4 depending on the location of the bout in the spawning series.

Nine spawning series averaged together and temporally analyzed by division into tenths had the greatest number of circling periods occurring in each bout during tenths 1, 9, and 10 at which time there were 1.7, 1.8, and 1.7 circling periods per bout, respectively. The smallest average number of circling periods was 1.4 per bout occurring during tenths 6 and 7 (Figure 7). From the first to the sixth tenth there was a continual decrease in circling frequency (1.7 to 1.4) and from the seventh to the termination of the series the frequency increased (to 1.8). This trend may be explained by increases in synchronization and efficiency as the series proceeds with longer periods at either end during periods of less efficiency.

### Frequency of Circling Periods in Successful and Unsuccessful Bouts

If the above data are considered according to successful or unsuccessful circling bouts, a remarkably consistent average circling period frequency is obtained for the successful bouts which was 1.4 through most of the series (Figure 8). With exception of the final tenth of the spawning series unsuccessful bouts had more circling periods than did successful bouts, exceeding most during the first half of the spawning series and least during tenths 6 and 7. During the final tenth, unsuccessful bout circling periods averaged 0.5 less than successful ones (Figure 8). Unsuccessful bouts showed greatest numbers

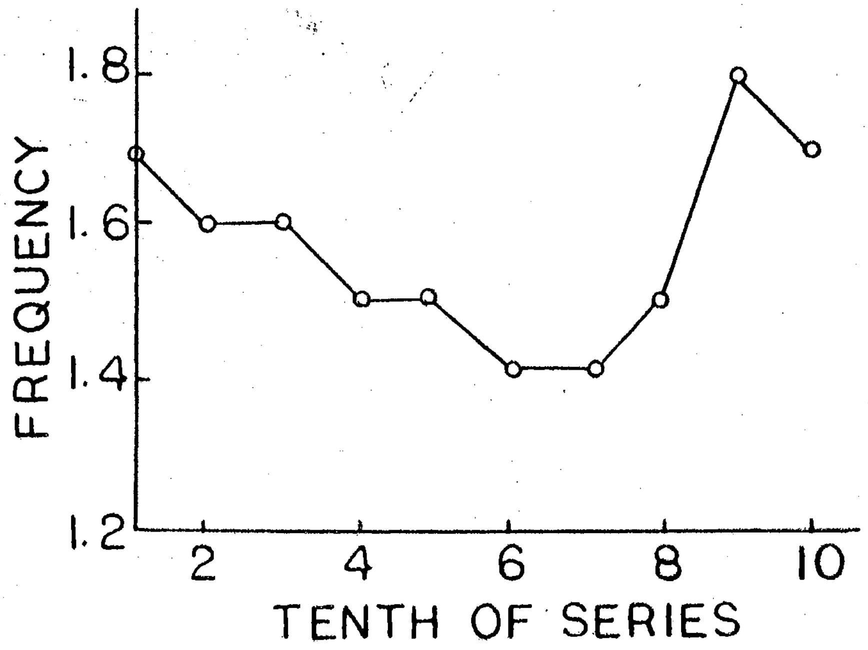

Figure 7. Average Number of Circling Periods Per Bout in Each Tenth of 9 Spawning Series.

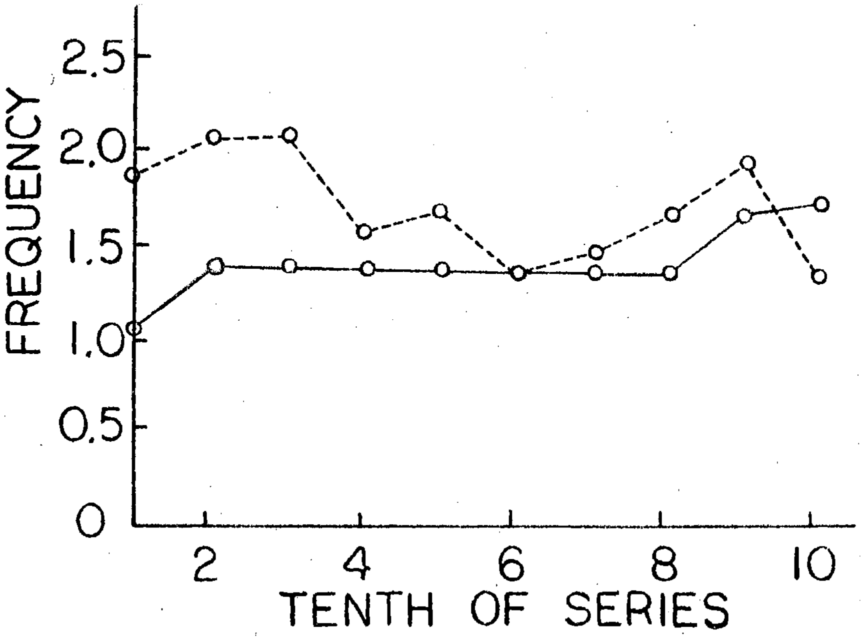

Figure 8. Average Number of Circling Periods Per Bout in Successful (Solid Line) and Unsuccessful (Broken Line) Bouts in Each Tenth of 9 Spawning Series.

of circling periods early in the series at which time tenths 1, 2, and 3 possessed 1.9, 2.1, and 2.1 circling periods, respectively, an average of 0.1 periods more per bout than successful bouts. During the remainder of the series with exception of the final tenth of the series, they possessed up to 0.3 circle periods more than successful bouts.

Such a relationship points again to a gradual increase in efficiency with most efficient spawning during mid-series and less efficiency late in the series. The decrease in frequency of circling periods in unsuccessful bouts during the final tenth to 1.4 may reflect the increase in aggressiveness of the male at the termination of the series which tends to discourage poorly motivated females from spawning activity.

## Previous Experience and Number of Circling Bouts

Since 1-circle bouts are more efficient than multicircle bouts it might be expected that fish with previous spawning experience should become more efficient and fewer multicircle bouts would result. During the study only one pair performed more than a single spawning series, and there was no indication that experience enhanced efficiency of the series. During the first spawning series 66 per cent of the successful bouts possessed only 1-circling period. While the second series, 3 weeks later, contained 63 per cent 1-circle bouts.

## Post-Circling Pause

### Post-Circling Pause Duration

The duration of post-circling pauses varied from 1-80 seconds with an average of 11.4 seconds.

With exception of the bouts with 4-pause periods, an increase in the number of pauses in a bout produced pauses of a shorter average duration. For example, successful bouts with 1 pause had an average pause duration of 13.7 and bouts with 2 pauses had an average of 9.5 and those with 3 pauses had an average of 6.36 seconds. Average pause duration for unsuccessful bouts with 1, 2, and 3 pauses were 13.5, 7.9, and 5.9 seconds, respectively. Average pause duration in 4-pause bouts were longer than those in 3-pause bouts with 6.5 seconds for successful and 7.4 seconds for unsuccessful bouts.

With few exceptions bouts terminated during the post-circling pause rather than the circling period. This can be pointed out by the comparison of circling period and pause period frequency in a bout. Of 178 successful 1-circle bouts in every case there was 1 period of post-circling pause immediately following the period of circling. Successful 2-circle bouts possessed 124 circling periods and the same number of pauses. Successful 3-circle bouts possessed 65 pauses while 69 circling periods were carried out. In 3 successful 4-circle bouts there were 12 circling periods and 1 less pause; thus, only 5 out of 266 or 1.9 per cent of all successful bouts went directly from the circling period to the clasp without a post-circling pause. In unsuccessful bouts a similar trend exists. Circling terminated in the clasp or break up of the pair in 8 of 161 bouts or 5 per cent.

The average duration of pauses became shorter as the number of pauses in the bout increased. Thus in successful bouts the average duration of the first, second, third, and fourth pause was 11.9, 8.9, 5.7, and 6.3 seconds, respectively. In unsuccessful bouts, durations were 10.7, 6.3, 3.8, and 3.9 seconds for the first to fourth pauses, respectively.

## Duration of Successive Post-Circle Pause Periods

Unlike circling periods which became shorter with successive reorientations, the second pause became longer than the first (Table IV). For example, in 62 successful 2-pause bouts the average duration of the first pause was 9.2 seconds and the second 9.8 seconds. Similar data for unsuccessful bouts showed the first and second pause to be 7.2 and 8.5 seconds, respectively.

The first 2 pauses of 3-pause bouts increased in duration in both successful and unsuccessful from 6.1 to 7.3 and from 6.3 to 7.6, respectively, but the third pauses in both successful and unsuccessful bouts were 5.7 and 3.7 seconds, respectively.

Successful 4-pause bouts showed a similar trend to the 3-pause bouts with successive pause duration of 8.7, 4.7, 6.3, and 6.3 seconds.

The successive increase in the first 2-pause durations may result because of the shorter successive circling periods preceding them which brings about a necessity to hold the pair in adjacent positions sufficiently long before they are physiologically capable of entering the clasp. The decrease in pause duration following the third and fourth circling periods may indicate a cumulative effect of the circling

## TABLE IV

## MAXIMUM, MINIMUM, AND AVERAGE DURATION OF SUCCESSIVE POST-CIRCLING PAUSES IN SUCCESSFUL AND UNSUCCESSFUL BOUTS CONTAINING 1, 2, 3, AND 4 OR MORE PAUSE PERIODS IN 9 SPAWNING SERIES

| | | Successful Bouts | | | | Unsuccessful Bouts | | | |
|---|---|---|---|---|---|---|---|---|---|
| Pause Period | | 1st | 2nd | 3rd | 4th | 1st | 2nd | 3rd | 4th |
| 1-Pause Bout N = 260 | Max | 46 | | | | 76 | | | |
| | Min | 1 | | | | 1 | | | |
| | Avg | 13.7 | | | | 13.5 | | | |
| 2-Pause Bout N = 111 | Max | 32 | 28 | | | 52 | 80 | | |
| | Min | 1 | 1 | | | 1 | 1 | | |
| | Avg | 9.2 | 9.8 | | | 7.2 | 8.5 | | |
| 3-Pause Bout N = 44 | Max | 20 | 24 | 15 | | 31 | 18 | 15 | |
| | Min | 1 | 1 | 1 | | 1 | 1 | 1 | |
| | Avg | 6.1 | 7.3 | 5.7 | | 6.3 | 7.6 | 3.7 | |
| 4-Pause+Bout N = 11 | Max | 25 | 11 | 8 | 10 | 44 | 18 | 11 | 12 |
| | Min | 1 | 1 | 3 | 4 | 1 | 1 | 1 | 1 |
| | Avg | 8.7 | 4.7 | 6.3 | 6.3 | 11.6 | 4.6 | 3.9 | 3.0 |

periods and pauses in each bout resulting either in a clasp or disorientation after a relatively short pause.

## Duration of Pause Compared to Preceding Circle-Period Length

In general the most efficient spawning bouts (1-circle bouts) had relatively long pausing periods; of 178 successful 1-circle bouts 80 had circling periods of 10-12 seconds and 40 had periods of 7-9 seconds. The average pause following these circling periods was 15.0 and 14.9 seconds, respectively (Figure 9).

One-Circle Bout. In general as the circling periods increased from 4 seconds to 12 seconds, the pause period increased accordingly from 13.7 to 15.0 seconds. From this point as the circling period became longer, the average pause duration decreased (Figure 9).

This suggests again that to a certain extent time spent circling may substitute for the pause in synchronizing the pair. For example, a pair executing a successful 1-circle bout, circling from 10-12 seconds had an average pause duration of 15.0 seconds while a pair circling for 22-24 seconds had an average pause duration of 6.3 seconds.

Pause and circle duration in unsuccessful 1-circle bouts was erratic but generally was similar to that of successful bouts except that pause durations were usually relatively greater. For example (see previous paragraph) bouts with circling periods from 10-12 seconds long had pauses of 17.8 seconds, while circling periods of 22-24 seconds were followed by average pause duration of 13 seconds.

Two-Circle Bouts. The first circling period in 2-circle bouts differs in several ways from that of 1-circle bouts (Figure 10). Of the 62 successful 2-circle bouts few pauses reached the average

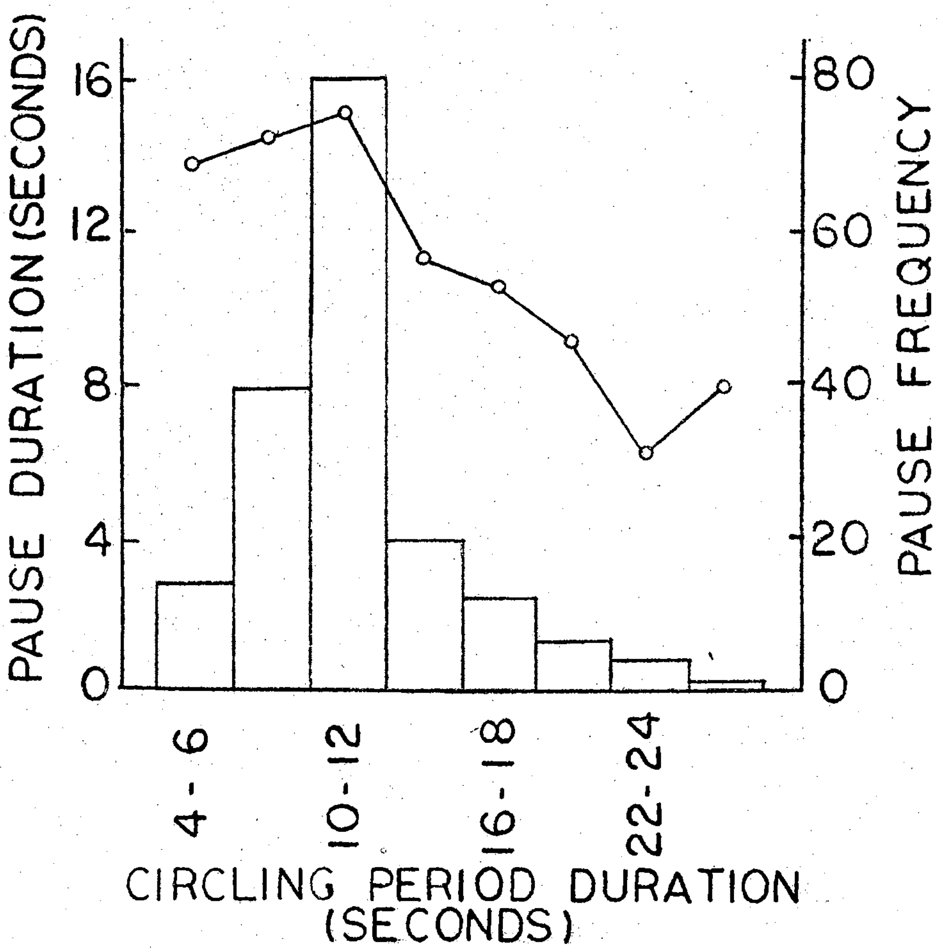

Figure 9. Average Post-Circling Pause Duration (Line) and Frequency (Bar) Following Circling Periods of Various Durations in Successful 1-Pause Bouts in 9 Spawning Series.

duration possessed by successful 1-circle bouts. Twenty-one bouts following circles of 10-12 seconds reached an average pause duration of 13.3 seconds and following circling periods of 1-3, 4-6, and 7-9 seconds had pause averages of only 5.8, 6.0, and 7.9 seconds, respectively. These short pause durations reflect the inability of the pair to remain oriented sufficiently long during the initial pause or circling period to achieve a successful spawn. Pause duration decreased from 13.3 seconds following circling periods of 10-12 seconds to 4.7 seconds following periods of 13-15 seconds. Thus if orientation and synchronization were not achieved by the end of a 10-12 second circling period, the pause was greatly reduced and butting and circling again resumed (Figure 10).

Pauses following the second circling period of 2-circle bouts showed the same trends as did those following the first circling period except that pause duration reached a maximum after shorter circling periods. Pauses following circling durations of 7-9 seconds had average durations of 13.1 seconds while those following circling periods of 10-12 seconds dropped to an average duration of 7.5 seconds.

Three-Circle Bouts. First and second pauses in 3-circle bouts are on the average shorter than first and second pauses in 1 or 2-circle bouts. For example, in successful 2-circle bouts the average pause duration of the first and second pause was 9.2 and 9.8 seconds, respectively and in 3-circle bouts corresponding durations were 6.1 and 7.3 seconds (Table IV).

As was the case in 1 and 2-circle bouts, successive pause periods of a 3-pause bout followed circling periods which became progressively shorter. For example, most first pauses followed circling periods of

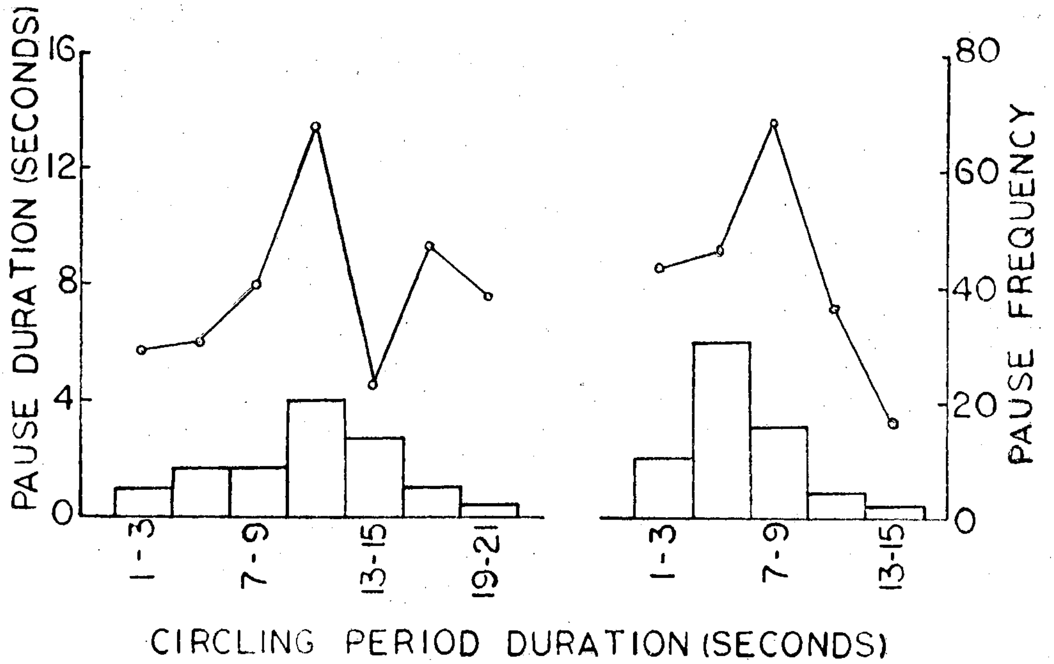

Figure 10. Average Post-Circling Pause Duration (Line) and Frequency (Bar) Following Circling Periods of Various Durations in Successful 2-Pause Bouts (First Pause Left, Second Pause Right) in 9 Spawning Series.

from 10-12 seconds, most second pauses followed periods of 1-6 seconds and most third pauses followed circling periods of 1-3 seconds (Figure 11). This suggests that with each additional period of circling in a bout there is retention of the effect of the previous circling period and/or pause.

As in 1-circle bouts, after the first circling period of 2 and 3-circle bouts the longest post-circle pauses followed circles of from 10-12 seconds duration. Also, in each case there was an evident decrease in the duration of the pause following circles of 13-15 seconds duration.

## Duration of the Post-Circle Pause Throughout the Spawning Series

Average duration of successful and unsuccessful post-circling pauses throughout the spawning series shows a general increase in duration from 8.2 seconds in the first tenth to 10.4 in the fifth tenth and 14.1 in the final tenth. Most pause periods, whether 1, 2, or 3, successful or unsuccessful, show the same trend and increase in duration throughout the series (Figures 12 and 13). Pause duration in successful 1-circle bouts, which are undoubtedly most efficient, varied from 11.1 seconds in the first tenth to 16.8 seconds in the final tenth, showing a gradual increase throughout the series with greatest increase between tenths 1 and 4 and tenths 9 and 10 at which time the duration increased from 11.1 to 14.3 and 14.0 to 16.8, respectively (Figure 13).

This increase in pause duration throughout much of the series is opposite to that occurring in the circling duration (Figure 14). Thus as the circling duration decreases the pause length increases. If an

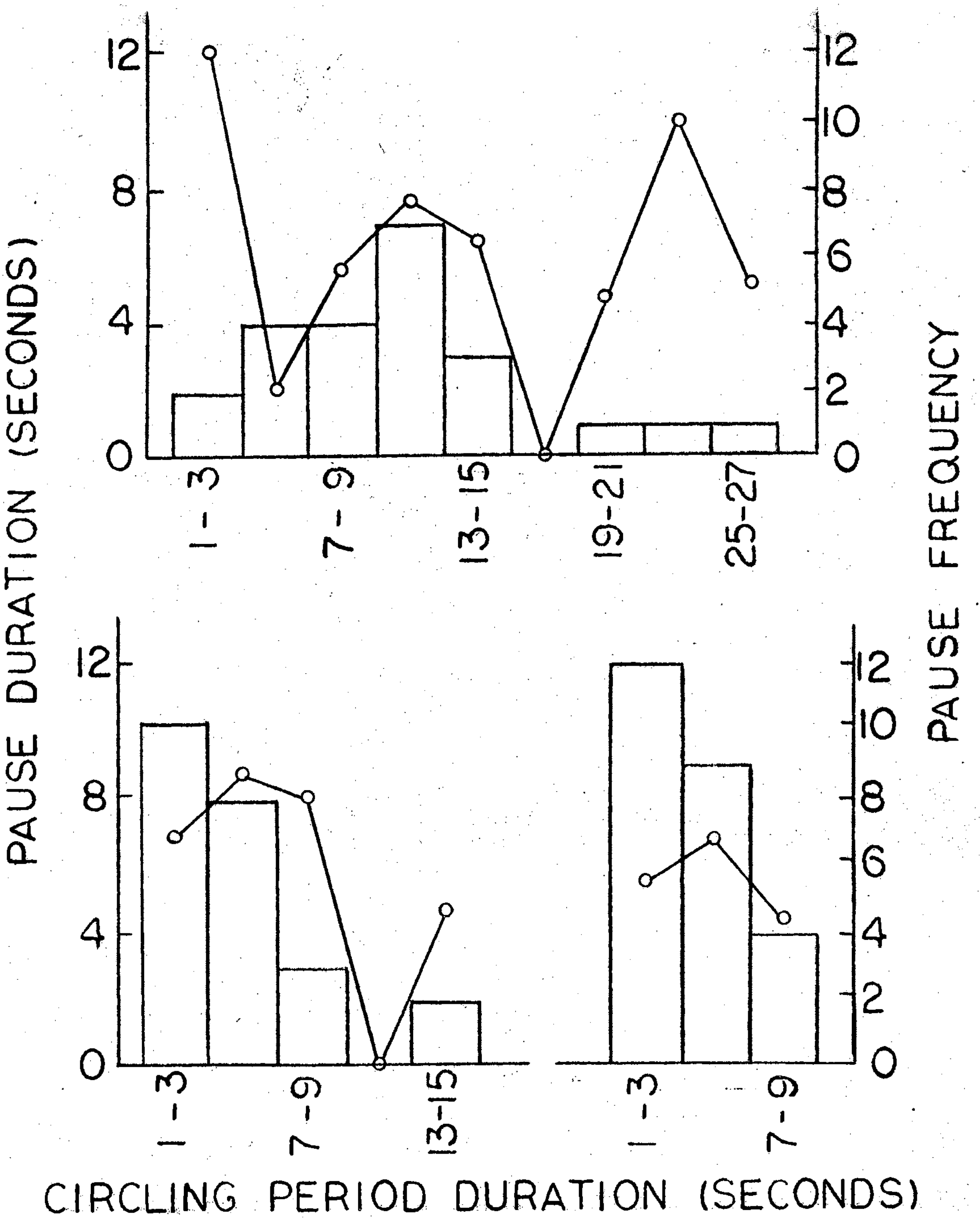

Figure 11. Average Post-Circling Pause Duration (Line) and Frequency (Bar) Following Circling Periods of Various Durations in Successful 3-Pause Bouts (First Pause Above Second Left, Third Right) in 9 Spawning Series.

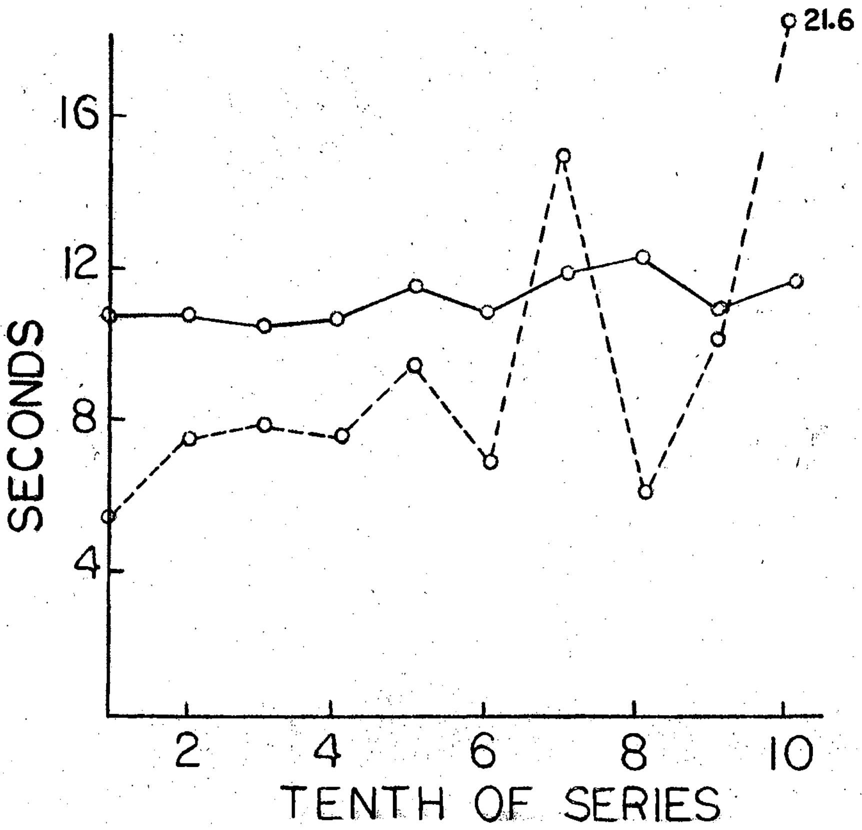

Figure 12. Average Duration of Post-Circling Pause in Successful (Solid Line) and Unsuccessful Bouts (Broken Line) in Each Tenth of 9 Spawning Series.

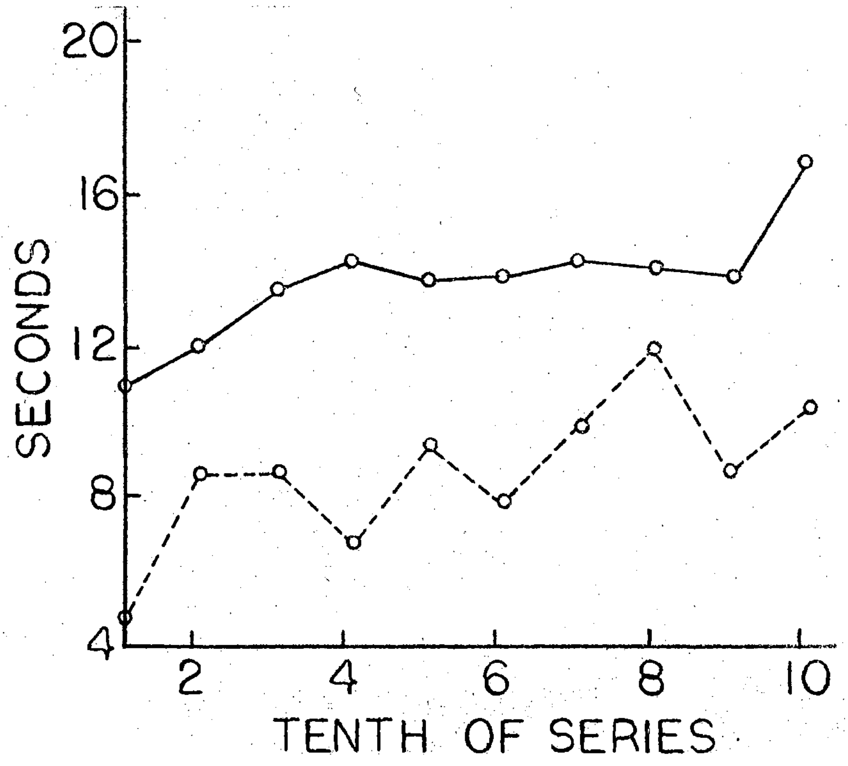

Figure 13. Average Duration of Post-Circling Pause in Successful (Solid Line) and Unsuccessful (Broken Line) 1-Circle Bouts in Each Tenth of 9 Spawning Series.

optimum pre-clasp time exists, perhaps then, as the pair becomes oriented more readily, thus needing a shorter circling period, there is a need for lengthening the pause to sum to a duration needed for synchronization in spawning behavior. Also, the above line of reasoning may explain the increased pause duration at the end of the series, when a longer pre-clasp duration is needed to achieve clasping. The increase in circling duration late in the series was approximately 1 second while the pause duration increased approximately 2 seconds. Furthermore, if the circling period is mainly an orienting behavior, there might be some learning occurring which would explain the lesser increase in circling duration. If the pause is mainly a means of synchronization of behavior and a stimulus to raise the spawning motivation level, an increase in pause duration would be expected toward the end of the series as the intensity of motivation to spawn begins to wane.

## Clasping

### Clasp Duration

Clasp duration appeared to depend mainly on whether the bout was successful or not, the number of circling periods and temporal location in the bout, but depended very little on the location of the bout in the spawning series.

As may be seen in Figure 15, the average clasp duration in each tenth of the spawning series in successful 1-circle bouts varied from 9.0 to 10.9 seconds. There was a slight increase in duration toward the middle of the spawning series.

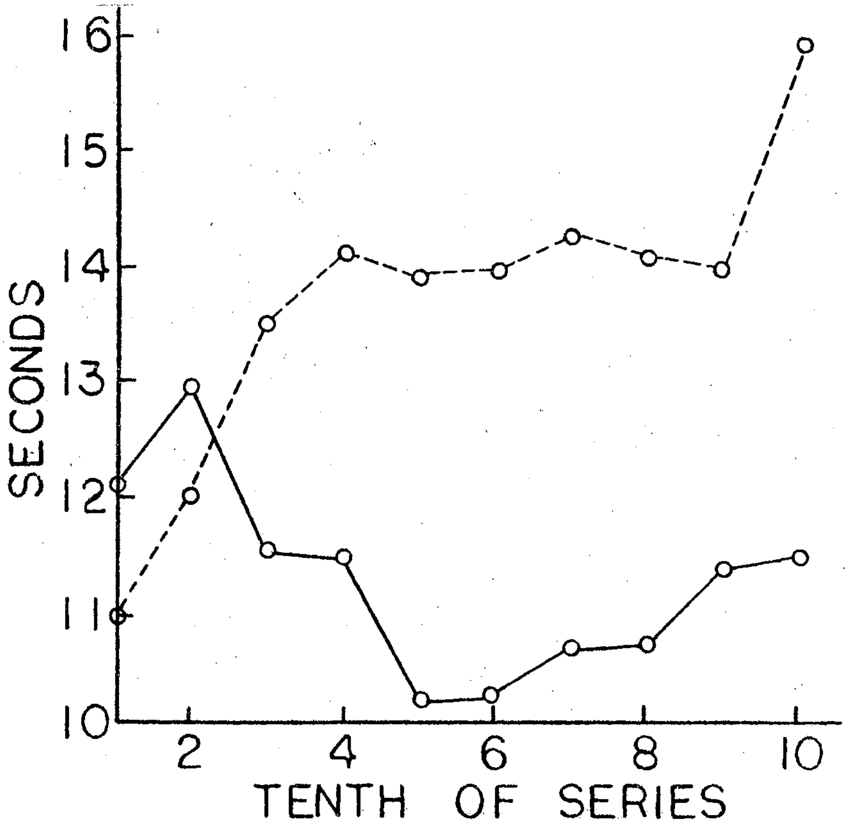

Figure 14. Average Duration of Circling (Solid Line) and Pause (Broken Line) Periods in Successful 1-Circle Bouts in Each Tenth of 9 Spawning Series.

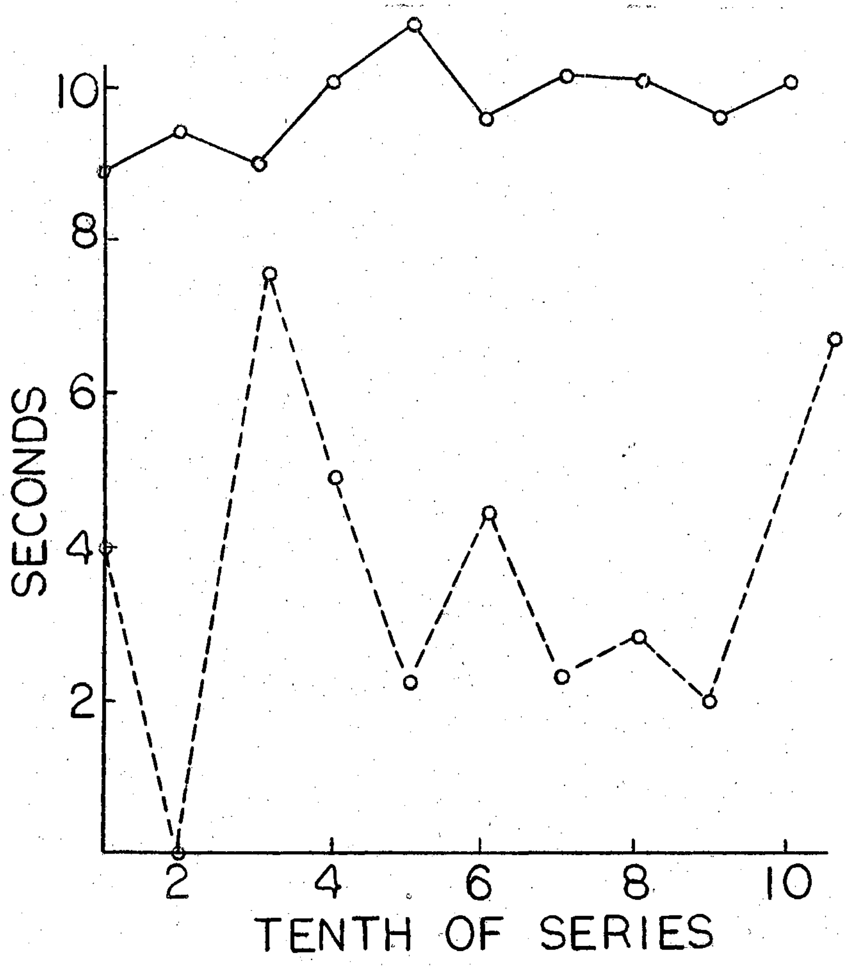

Figure 15. Average Duration of Clasp in Successful (Solid Line) and Unsuccessful (Broken Line) Bouts in Each Tenth of 9 Spawning Series.

Unsuccessful 1-circle bouts had average clasp durations varying from zero to 7.5 seconds throughout the series. They were also extremely variable throughout the series primarily because only 26 clasps were attempted in the 81 unsuccessful 1-circle bouts.

Once the clasp was reached there was an excellent chance for the bout to be successful since only 27 1-circle bouts achieving the clasp were unsuccessful while 178 were successful. In 62 successful 2-circle bouts, only 12 proceeded to a clasp following the first pause period. In 23 successful 3-circle bouts the clasp was reached only 6 times prior to the third pause; 3 following a first and 3 following a second period of circling. Thus in 266 successful spawnings only 19 attempted a partial clasp prior to the final clasp (Table V).

In unsuccessful as well as successful bouts most clasps were attempted after the final pause. Only 12 clasps were attempted before the final pause and 57 of the 161 unsuccessful circling bouts proceeded to a clasp. Thus of the 427 circling bouts possessing 672 post-circling pauses only 88 clasps were attempted that did not progress to a spawn, while 266 clasps were successful.

The average clasp duration in the final period of reorientation of each successful bout is greater in every case than averages of clasp attempts following preterminal pauses. For example, an average of 12 clasps attempted after the first circling period in 2-circle bouts had an average of 5.4 seconds while the final clasp average of these same bouts was 9.5. Clasps occurring before the final pause in successful bouts with 3 post-circling pauses had an average of 3 seconds while the average of the final clasp in 23 3-pause bouts averaged 9.2 seconds. Thus, it appears that if the clasp can be maintained for a sufficient

# TABLE V

## AVERAGE DURATION AND FREQUENCY OF CLASP FOLLOWING 1, 2, 3, AND 4 OR MORE CIRCLING PERIODS IN SUCCESSFUL AND UNSUCCESSFUL BOUTS IN 9 SPAWNING SERIES

| | | Successful Bouts | | | | Unsuccessful Bouts | | | |
|---|---|---|---|---|---|---|---|---|---|
| Clasp | | 1st | 2nd | 3rd | 4th | 1st | 2nd | 3rd | 4th |
| 1-Circle Bout | Avg | 9.8 | | | | 3.6 | | | |
| | Max | 14 | | | | 13 | | | |
| | Min | 1 | | | | 1 | | | |
| | Freq | 178 | | | | 27 | | | |
| 2-Circle Bout | Avg | 5.4 | 9.5 | | | 1 | 4.1 | | |
| | Max | 13 | 15 | | | 1 | 10 | | |
| | Min | 1 | 5 | | | 1 | 1 | | |
| | Freq | 12 | 62 | | | 2 | 16 | | |
| 3-Circle Bout | Avg | 3.0 | 3.0 | 9.2 | | 2.5 | 2.4 | 3.6 | |
| | Max | 5 | 4 | 12 | | 4 | 4 | 11 | |
| | Min | 2 | 1 | 2 | | 1 | 1 | 1 | |
| | Freq | 3 | 3 | 23 | | 2 | 5 | 8 | |
| 4-Circle+Bout | Avg | - | - | 2 | 9.0 | - | 1 | 2.5 | 3.2 |
| | Max | - | - | 2 | 10 | - | 1 | 3 | 9 |
| | Min | - | - | 2 | 7 | - | 1 | 2 | 1 |
| | Freq | - | - | 1 | 3 | - | 1 | 2 | 6 |

period of time a successful spawn may be accomplished. In only 8 cases did the clasp exceed 10 seconds with no sign of eggs and/or rolling over.

## Clasp Duration in Relation to Pause Length

There is some evidence that with increased pause length the duration of the clasp becomes somewhat shorter, and as the number of pauses increase, they are followed by a relatively short clasp, 9.8, 9.5, 9.2, and 9.0 seconds after 1, 2, 3, and 4-pause periods.

Comparison of clasp lengths following post-circling pauses in successful 1-pause bouts, however, indicates little or no correlation between the two, since a variation of clasp length less than 0.5 seconds occurs after pauses of from 5-20 seconds (Figure 16).

First clasp length in 2-circle bouts was quite variable, ranging from 2-9 seconds. The clasps in the second period of reorientation varied from 9.2 to 10.2 seconds following pause periods of from 1-24 seconds showing a rather constant clasp length regardless of the duration of the previous pause (Figure 17).

Clasps following the third circling periods in 3-circle bouts also showed some consistency and in 19 clasps following pauses of 1-8 seconds had an average of 8.75 seconds and varied from 8.2 to 9.5.

It, therefore, appears that the length of the final clasp in successful bouts is relatively constant and depends very little upon preceding events in the bout.

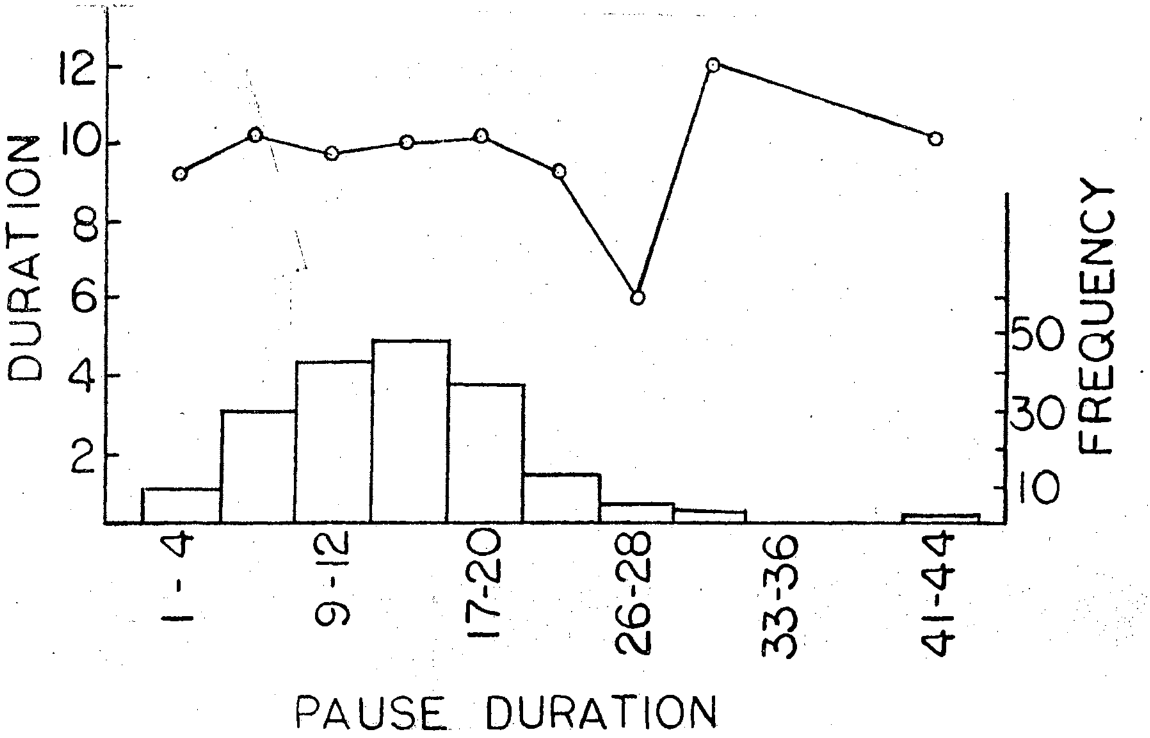

Figure 16. Average Duration (Line) and Frequency (Bar) of Clasps Following Pauses of Various Duration in Successful 1-Circle Bouts in 9 Spawning Series.

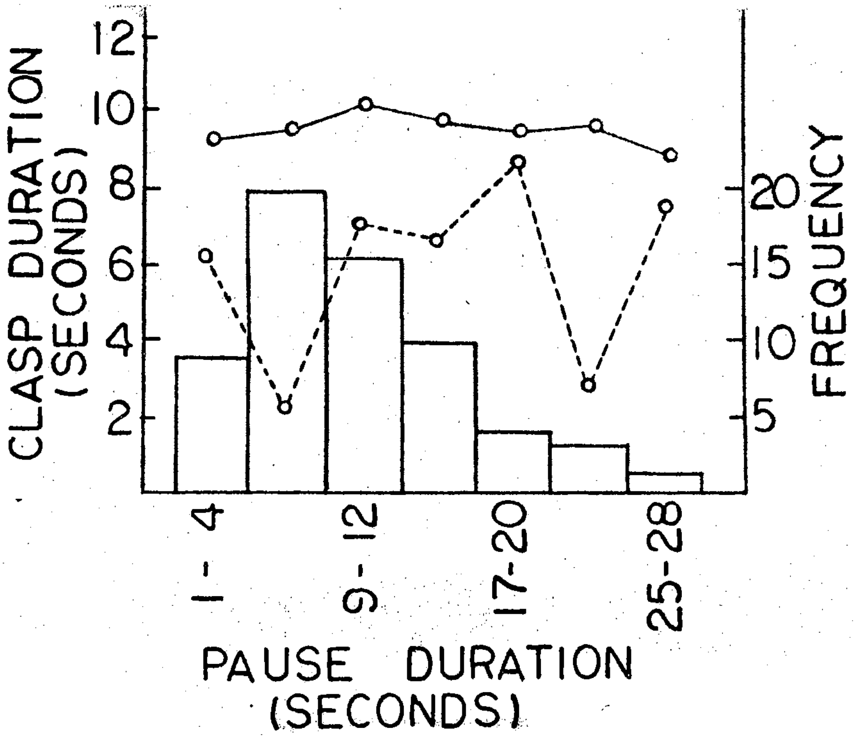

Figure 17. Average Duration (Lines) and Frequency (Bars) of Clasps Following the First (Broken Line) and Second (Solid Line) Pause Periods of Various Durations in Successful 2-Circle Bouts in 9 Spawning Series (Frequency of Second Clasp Only).

## Rolling Over

Figure 18 shows that rolls increased in average duration as the clasp preceding them increased to 9 seconds. Maximum roll duration followed clasps of 9 seconds and became shorter thereafter. Fifty-three of 178, or 30 per cent of the rolls, followed clasps of 10 seconds, 3 followed clasps of less than 5 seconds, and none followed clasps longer in duration than 14 seconds.

Rolls also increased in duration as the bout duration increased (Figure 19). Rolls in bouts of 26-30 seconds long had an average duration of 2.50 seconds. A general increase in roll duration continued as the bout duration increased reaching a maximum of 3.90 seconds after bouts of 51-55 seconds. In bouts of 36-45 seconds 113 or approximately 63 per cent of the clasps occurred, 3 rolls occurred in bouts shorter than 26 seconds, and 2 occurred in bouts longer than 55 seconds.

## Swimming Inhibition

Temporal data concerning the period of swimming inhibition was difficult to measure and, therefore, was often inaccurate. After apparently regaining stability, fish would often remain stationary in the water for up to 10-20 seconds before making an attempt to chase, flee, collect eggs, or perform any other movement. Females often remained stationary on the bottom until chased by the male. Tail beating by males which had not yet regained equilibrium made the point of recovery from swimming inhibition impossible to determine. Some fish of both sexes showed little or no inhibition while others showed much. Swimming inhibition is thus undoubtedly the most variable component of the spawn and little generalization is possible.

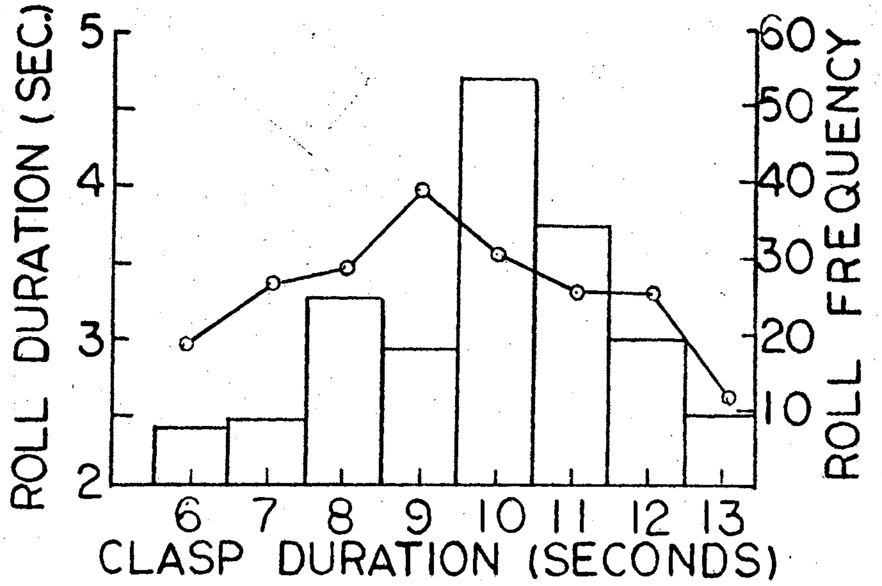

Figure 18. Average Duration (Line) and Frequency (Bar) of Rolls Following Clasps of Various Duration in Spawning Series.

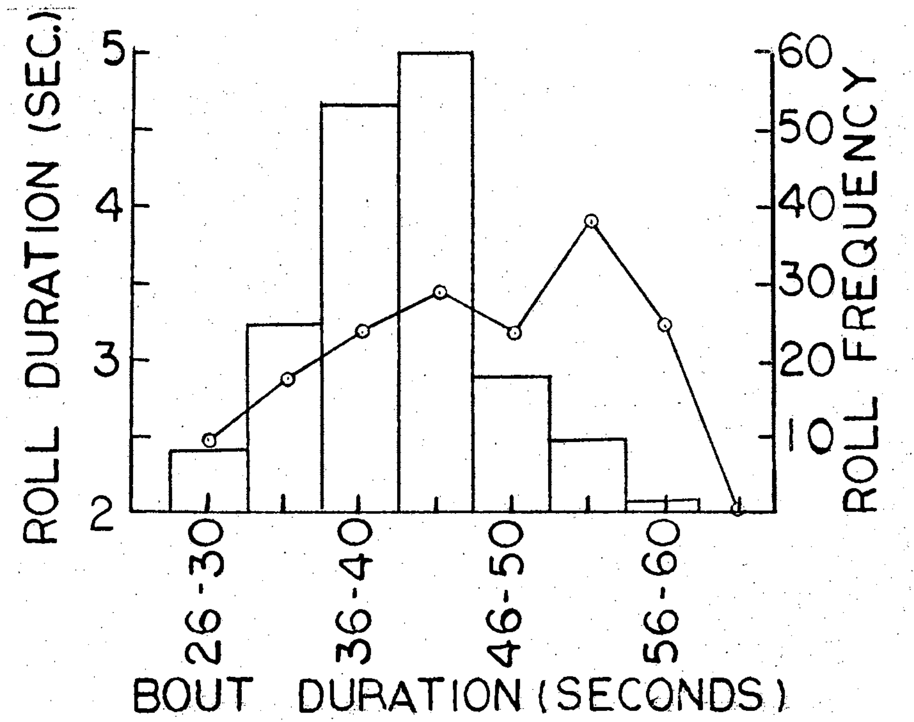

Figure 19. Average Duration (Line) and Frequency (Bar) of Rolls During Bouts of Various Durations in 9 Spawning Series.

# CHAPTER VIII

# PARENTAL CARE

Parental care includes the care and protection given the eggs, larvae, or fry by the male. Care commences with collection of eggs following the first spawn and usually continues several days following completion of the spawning series, at which time the fry and nest are deserted.

## Egg Care During Spawning

### Egg Retrieval

After swimming inhibition the fish usually have settled near the bottom of the tank. The male is in a head up position within a centimeter or two of the female, with median fin partially to fully erected. Although eggs are bouyant, they fall initially due to the current caused by the falling fish.

Method of retrieval depends on the number of eggs released (5-100). In bouts in which eggs are numerous, the male often commences egg retrieval before completely recovering from swimming inhibition, while still attempting to right himself. Although females are usually chased from beneath the nest they often escape by moving away while the male is collecting eggs or is still in swimming inhibition. The duration of inhibition varies among females and while some are chased from beneath the nest after almost every spawn, others recover quickly and leave the nest before the male recovers. When numerous eggs are present, the male's median fins are usually erected and a sigmoid posture and/or tail beating occurs, if the female is near when he recovers from inhibition. Simultaneously, his gape opens widely, as in a yawn, drawing water through his mouth. In turbid water, strong currents may be observed being expelled from opercles. Males appear to make no attempt at first to retrieve individual eggs but take several into the mouth with each inspiration. They may swim back and forth beneath the nest for as long as 2 minutes collecting eggs before taking them to the nest.

When only a few eggs are released chases are common before egg collection. After returning from the chase, eggs are usually collected individually and the gape is not continuously distended as when eggs are numerous. Eggs are collected much like individual food particles, and after several are taken into the mouth they are deposited in the nest. Eggs drifting away from the nest are usually picked up by the male, who often wanders 100 cm or more from the nest.

## Egg Placement and Collection

After a number of eggs are collected the male swims beneath the nest and generally thrusts his mouth into its lower portions. After nudging slightly, he releases the eggs, backs away, and leaves the nest.

Occasionally egg release results in the production of a jet of water through the nest. It is impossible to establish the frequency with which such jetting occurs since the thick nest often prevents the spurting water from penetrating it. Only when executed beneath a thin portion may a jet be observed. It is not uncommon for jets to go 4 cm beyond the upper surface of the nest and strike the tank glass cover. Droplets of water hanging from the glass above the nest commonly had up to 15 eggs per droplet. Eggs in these droplets matured into fry in 95 out of the 123 cases observed. Most eggs failing to hatch resulted from the droplets moving and leaving the eggs behind to dry.

It is interesting to speculate as to the survival value of a behavior of this type. Eggs jetted on the underside of a plant leaf above the water would have an abundance of oxygen and would also be free of aquatic nest marauders. Insects and dessication, however, would probably be an increased danger. Jetting probably aids in depositing the eggs in the upper aerated regions of the nest and probably helps keep the upper part of the nest moist.

In most cases after the eggs are deposited into the nest, bubbles are released beneath the nest either several centimeters below or by pushing the snout into the nest before release. In a few cases, however, air is snapped after eggs are picked up and the air is released into the nest with the eggs. When air and eggs were placed into the nest simultaneously, the snout was placed in the nest and no sub-nest release was observed.

Once eggs are placed in the nest they usually adhere to the vegetation. Some eggs, however, do not adhere and float freely at the surface in vacuities of the nest. These and other uncollected ones which rise to the surface outside the periphery of the nest are collected by surface snapping which is accomplished in much the same manner as air snapping for construction purposes. Unattached eggs are carried along the surface to the mouth of the male by the stream of water created by his inspiration. Eggs not catching on vegetation are then redeposited in denser areas of the nest and are usually propelled by jetting or pushes into higher areas of the nest. Eggs are commonly observed in moist nest materials up to 2 cm above the surface of the water.

## Nest Care During Spawning

Nest care varies as the spawning series continues and as the number of eggs collected increases. The most notable changes are in the frequency of air snapping trips, the frequency and duration of snaps per trip, the frequency of nest pushes, vegetation collection, and utilization of bottom debris.

### Air Snapping

The frequency of air snapping trips usually is at its maximum near commencement of the spawning series. Figure 20 shows the typical high frequency of air snapping trips executed one day prior to spawning, reading greatest frequency immediately prior to the spawning series at 28 trips every 10 minutes. Figure 21 shows the spawning series of Figure 20 in greater detail. Throughout the first two-thirds of this spawning series there was a continual decrease in the frequency of air snapping trips until only 4 trips every 10 minutes were executed. During the final hour the number of trips again increased, but not to the frequency occurring during the early part of the spawning series (16 trips per 10 minutes).

This trend can be explained partly by the necessity of the male to spend increasingly more time collecting and transporting eggs to the

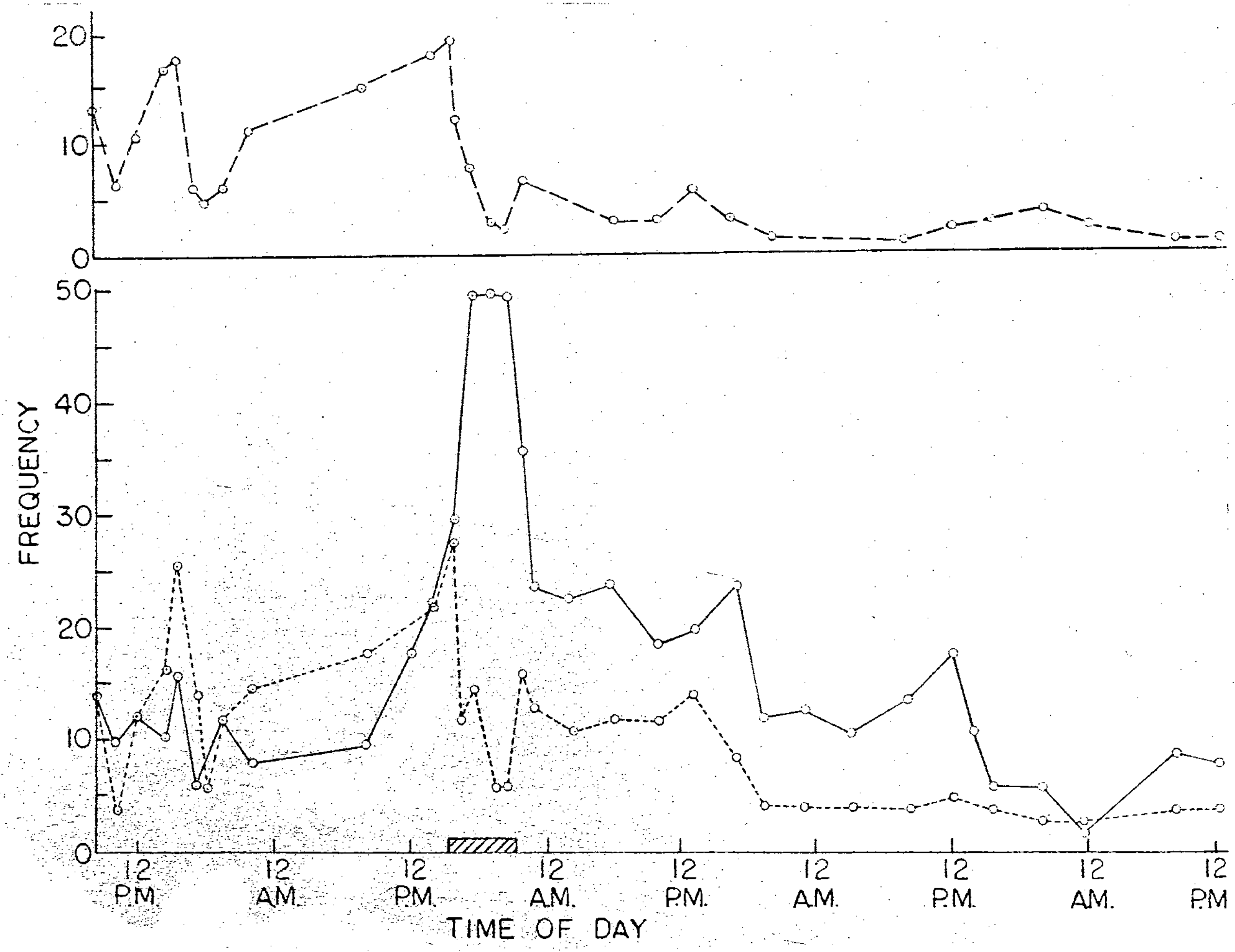

Figure 20. Frequency of Nest Pushes (Solid Line), Air Snapping Trips (Short Dashes), and Air Snaps per Trip (Long Dashes) per 10 Minute Period from 30 Hours Prior to 60 Hours Following a Single Spawning Series (Hatched Bar).

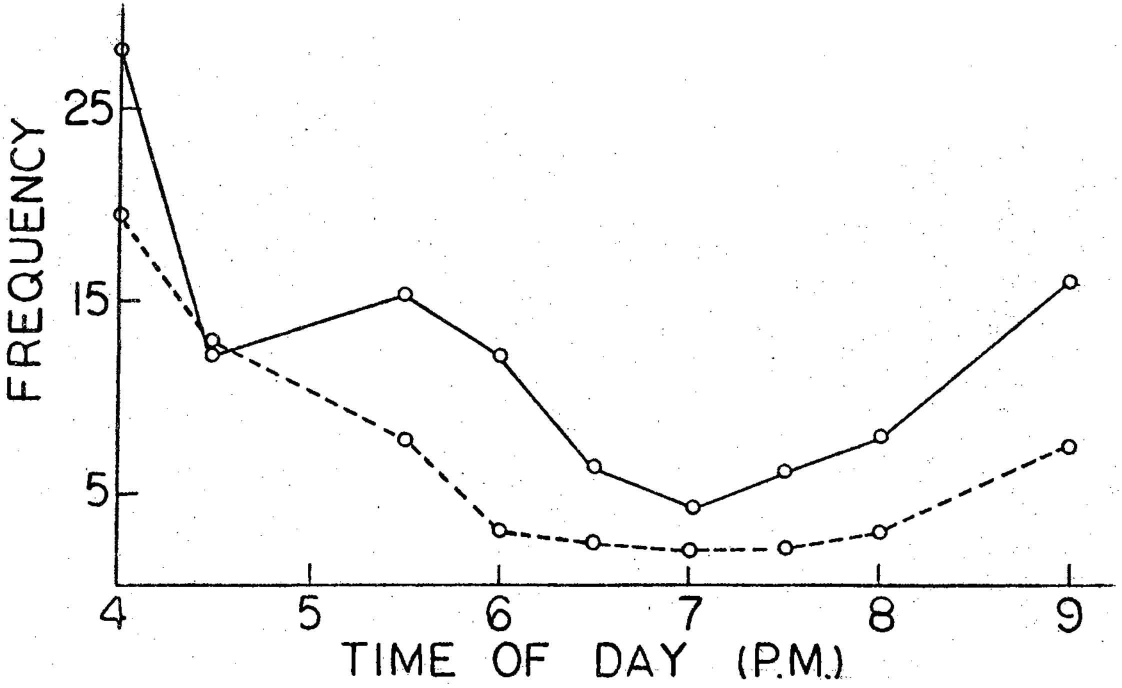

Figure 21. Frequency of Trips to Nest with Air (Solid Line) and Air Snaps per Trip (Broken Line) Throughout Spawning Series in Figure 20.

nest throughout much of the series. At the end of the series, with most eggs already in the nest and with spawning concluded, the number of trips back to the nest with air could be increased. Thus from a low frequency of 4-6 trips every 10 minutes during tenths 7 and 8, the frequency increased to 16 trips by cessation of the series. This increased level then continued through approximately the next 20 hours (Figures 20 and 21).

Along with a decrease in the number of air snapping trips throughout most of the series, a similar trend occurred in the number of individual snaps during each trip. A frequency of 19.8 individual snaps occurred early in the series and dropped to a low of 2 or 3 snaps per trip during most of the second half. An increase to 7.4 snaps occurred at the end of the spawning series and continued between this rate and about 3 snaps throughout the following 20 hours (Figures 20 and 21).

As might be expected a similar trend occurred in the duration of air snapping periods. Figure 22 shows a decrease in the duration of air snapping periods in two typical spawning series through most of the series, with a slight increase at the end. Not included in the figure is a substantial increase of several seconds in snapping duration immediately following the termination of spawning.

In T. microlepis bubbles probably do not play a major part in furnishing eggs with additional surface for respiration during maturation, since in most cases few bubbles remained more than a few hours after spawning. Thus, while T. trichopterus and T. leeri in all likelihood depend on air bubbles to support the egg mass and increase the common surface between egg and air they are not necessary in T. microlepis for this purpose since its eggs are held in moist

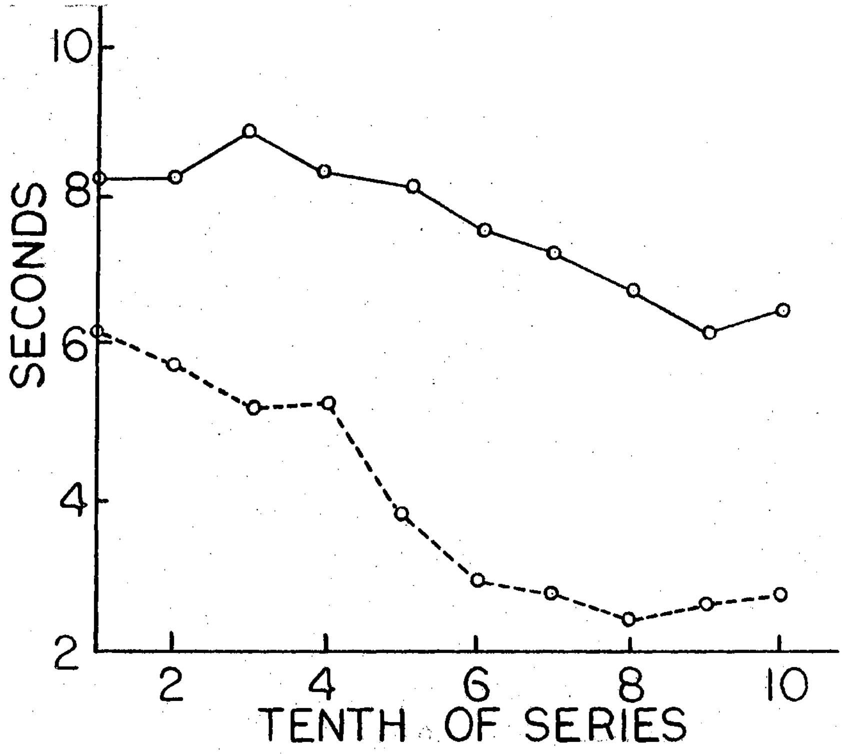

Figure 22. Average Duration of Air Snapping Periods in Each Tenth of 2 Spawning Series. Each Series Represented by Separate Line.

vegetation in contact with the air. However, bubbles appear to be quite useful in floating the massive nest while fragments are intertwined together and also in making the dense structure more permeable to eggs which are pushed up or jetted through it.

As mentioned above, in one case where there was a dense mat of vegetation already on the surface of the water, no bubbles were used and the eggs and fry developed as readily as in nests in which bubbles were present. Since the major construction material was *Ceratophyllum*, which is a floating plant, it is probable that the function of bubbles during later stages of construction would be more important if the materials used were heavier than water.

## Nest Pushing

With a decrease in the frequencies and duration of air-snapping, nest pushing became more frequent (Figures 20, 23, and 25). As is evident in Figure 25 (average of 3 spawning series) the frequency of nest pushing increased throughout most of the spawning series from an average of 10.5 seconds every 10 minutes during the third tenth to 40.0 seconds at the end of the series. The greater frequency of nest pushing during the first and second tenth (18.1 and 16.9, respectively) is due in part to a greater frequency of adding vegetation than later in the series and appears to aid in bonding the individual fragments together.

As is evidenced in Figures 20, 23, and 24 nest pushing increased during the second half of the series and reached a maximum rate late in the series increasing from about 18-50, 10-30, and 5-45 pushes per 10 minutes, respectively.

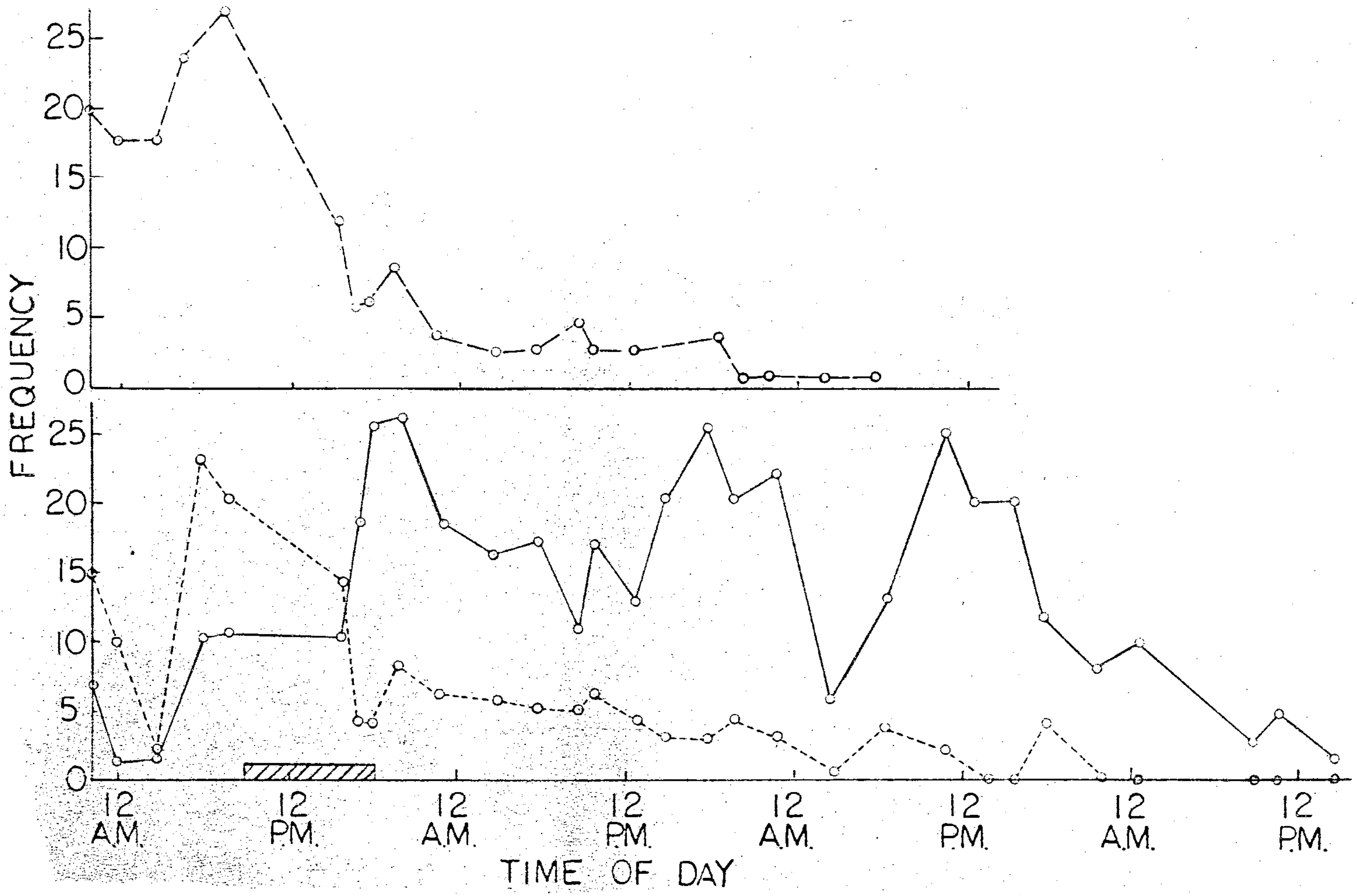

Figure 23. Frequency of Nest Pushes (Solid Line), Air Snapping Trips (Short Dashes), and Air Snaps per Trip (Long Dashes) per 10 Minute Period from 12 Hours Prior to 60 Hours Following a Single Spawning Series (Hatched Bar).

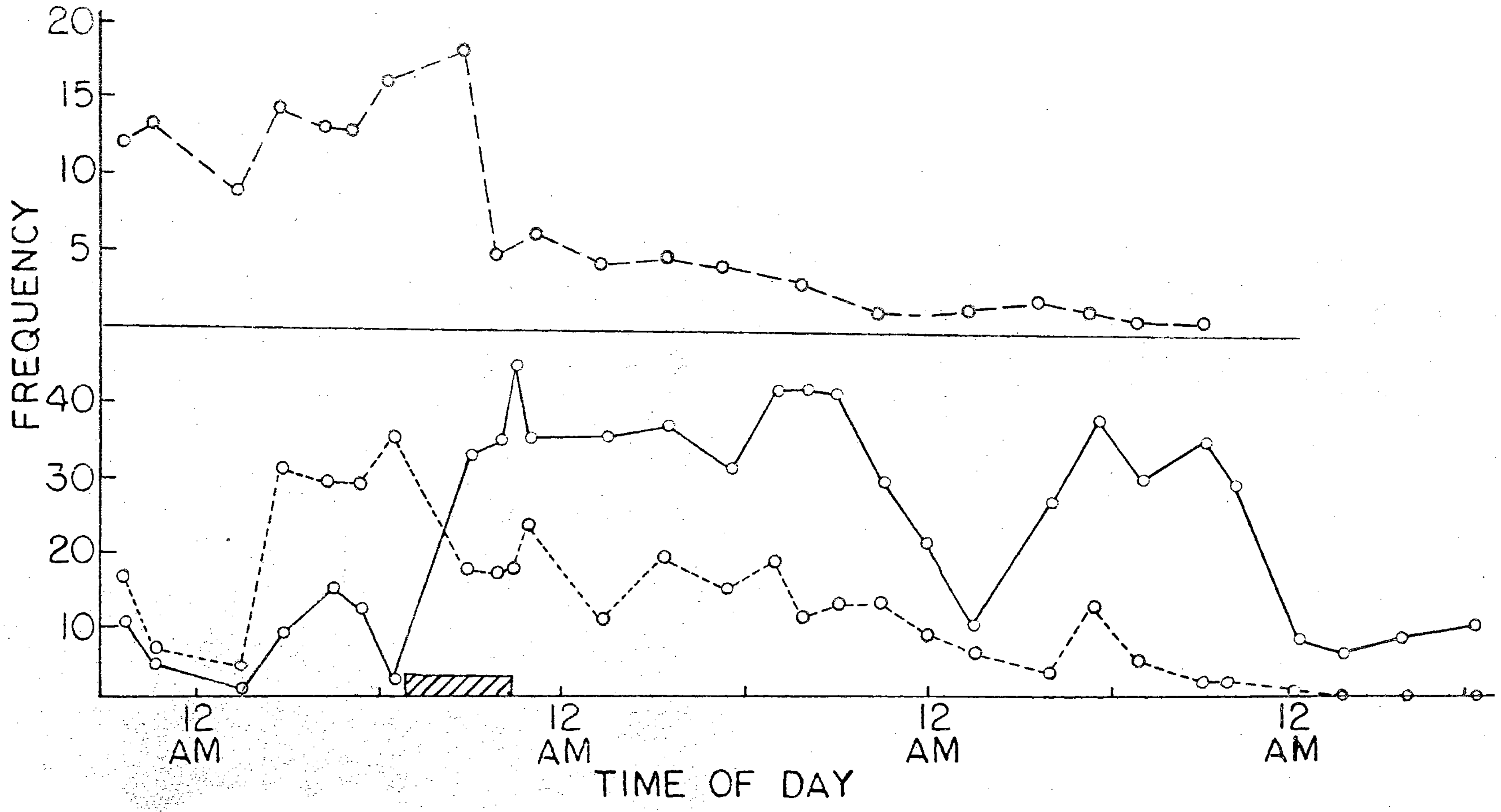

Figure 24. Frequency of Nest Pushes (Solid Line), Air Snapping Trips (Short Dashes), and Air Snaps per Trip (Long Dashes) per 10 Minute Period from 20 Hours Prior to 60 Hours Following a Single Spawning Series (Hatched Bar).

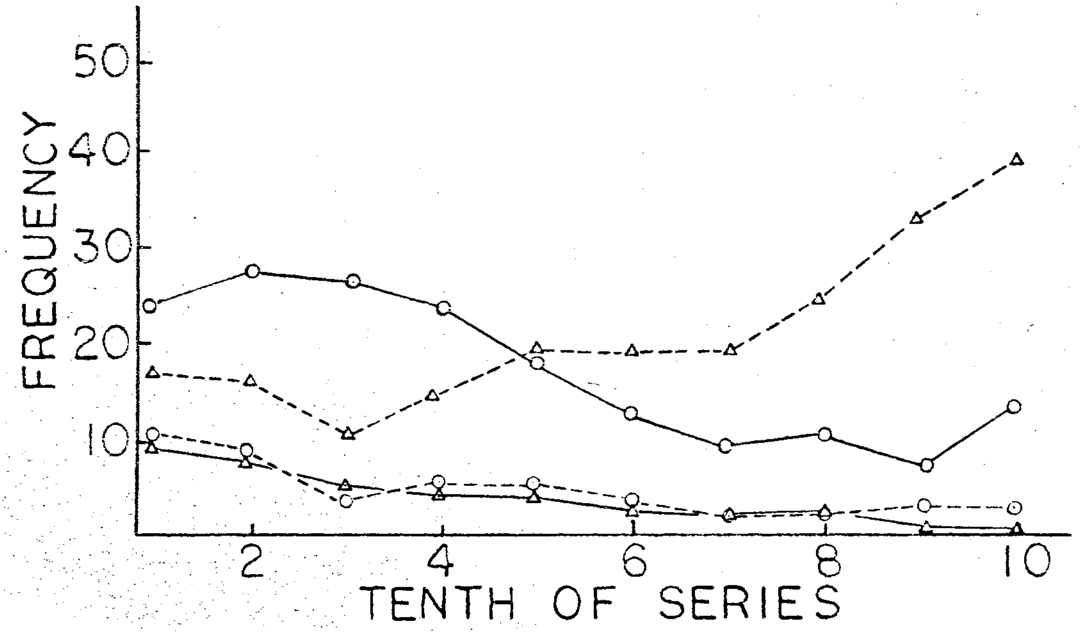

Figure 25. Average Frequency of Air Snapping Periods (Circles with Solid Lines), Nest Pushing (Triangles and Broken Lines), Conveyance of Vegetation (Circle and Broken Line), and Conveyance of Bottom Debris (Triangle and Solid Line) in a 10-Minute Period During Each Tenth of 3 Spawning Series.

The increase in nest pushing frequency throughout the remainder of the spawning series is due primarily to the deposition and arrangement of eggs within the nest. Long periods of pushing may be observed as the male snaps at the water surface within the nest, collecting eggs which are replaced into the nest. Occasionally, more exuberant pushes occur. These may function to shake poorly fastened eggs free or they may simply be attempts of the fish to remain at the surface.

## Use of Plant Fragments and Bottom Debris

Plant fragments from floating or rooted plants and bottom debris consisting generally of small plant fragments and other detritus were used throughout the series in equal quantities except at the end.

The average frequency of carrying plant fragments and bottom debris to the nest in 3 typical spawning series was 10 and 11 trips per 10 minutes, respectively, during the first tenth. Throughout most of the remainder of the series the two behaviors remained equally frequent between 4 and 7. With conclusion of the series, however, use of bottom debris became infrequent, averaging 1.8 and 1.1 trips per 10 minutes during the last 2 tenths. Use of plant fragments during this time remained at 4.0 and 4.1 trips per 10 minutes. Unlike nest pushing and air snapping, which increased in frequency at the conclusion of the series, bottom debris and vegetation use shows no such increase (Figure 25).

## Post-Spawning Care

### Incubation Period

Eggs hatched from 18-26 hours after deposition. Exact incubation duration was difficult to determine since in order to observe eggs it was necessary to manipulate the tank cover, causing the males to become extremely disturbed. The most rapid egg maturation occurred within approximately 18 hours in surface water temperature of 32 C. The eggs were nestled in the moist vegetation within 15 cm of a 25-watt incandescent tank light. Since the top of the tank was enclosed in a reflector, thus not permitting any great degree of air circulation over the moist eggs, the temperature of the vegetation remained within a degree of the surface water.

Maximum hatching time was 26 hours. This was in a tank with surface water temperature of 30 C; the eggs were also suspended in a moist nest at the surface or above.

### Defense of Nest and Young

In 7 out of 11 spawnings, males generally remained beneath the nest when the tank was disturbed in order to observe eggs or fry. In 4 cases the males fled.

Those males remaining beneath the nest during disturbance to the tank invariably oriented facing the disturbance and erected all median fins and thrust pelvics forward from the body. One male showed extreme aggression during disturbance of the nest when a lens was being used to determine egg development. As was common in every case in which the male did not flee, his median fins were raised and the body was oriented with the snout directed toward the point of disturbance 1-3 cm beneath the nest. After assuming such a position the fish swam up through the nest striking the lens which was being held 5-6 cm above the nest. The same type of disturbance was repeated 5 additional times, once within an hour of the initial attack and 4 times thereafter at approximately 12 hour intervals. In every case but the last the lens was attacked.

From the commencement of spawning up to a week after egg hatching most males retained strict territoriality preventing any other fish from approaching the nest. Throughout this entire time, fish moving in the vicinity of the nest were approached with median fin erection and were viciously chased. It was not uncommon for females to be restricted in movement almost entirely for this time period.

A great weakness in nest defense of the male is his ineffectiveness in chasing fish from beneath it, once they arrive there. Such a situation arises during spawning when the male appears insufficiently aggressive to keep unreceptive females from entering the nest. Females may also enter beneath the nest when the male is away or is distracted by some other activity; such females often fail to orient in response to the displays of the male and push the nest with their snout. When eggs are present the pushing sometimes leads to egg eating. Once this occurs even the most aggressive males have some difficulty removing the female. Most aggressive males, however, drive the female from the nest within several seconds by tail beating. Severe biting by the male under the nest was rare, but occasionally a male unable to evict the female by tail beating and butting would seize her pelvics in his mouth and use them to pull her from the nest.

Once a female ate eggs she usually attempted to do so repeatedly. On one occasion after 4 hours of successful spawning the female entered the nest and began feeding on eggs. While the male attempted to remove her, a second female came from shelter and after pushing the nest for a minute also began feeding. During this time the male succeeded on several occasions in temporarily removing a female from the nest but with 2 females to cope with and his relatively reduced aggressiveness beneath the nest, this was ineffective. Less than 50 eggs survived this behavior and the nest was badly torn apart since the females remained in the nest for approximately 6 minutes before the male succeeded in evicting them.

In the majority of cases, however, when unreceptive females entered beneath the nest and hesitated to commence appropriate reproductive behavior, they were approached directly and confronted by aggressive displays from the male. If they failed to flee within 10-30 seconds, they usually were attacked and bitten. However, unlike most other situations in which aggressiveness is detected by fin erection and/or tail beating, the median fins of the male were usually depressed slowly as the dorsum was leaned toward the female. If the female fled, she was chased aggressively, if not, she was attacked and bitten. The degree of severity of attack beneath the nest seldom reached that commonly achieved elsewhere in the tank.

Since nest defense during parental care may elicit maximum aggressiveness from the male, the explanation of median fin erection in various encounters as being a sign of aggressiveness appears not to be as elemental as might first appear. There is considerable disagreement concerning the function of median fin erection. For example, Barlow

(1962), as do most authors, regarded median fin erection as a display typical in situations of conflict between flight and aggression. Baerends (1957) stated that fin erection is dependent on attack motivation or is a defense mechanism in some spiny-rayed species. Myrberg (1965) on the other hand considered fin erection as a behavior related to locomotor coordination rather than motivational state. Miller and Hall (1968) although agreeing basically with Myrberg feel that the lateral spread has an obvious signal function which may develop as a result of reinforcement during individual ontogeny.

Males defended the nest up to 9 days after spawning. Nest defense and mere territoriality are somewhat similar and vary primarily in the intensity of aggression shown by the male appearing to be dependent on the nature of the total stimulus situation. At one extreme, aggressiveness other than mild chases, intention movements, or fin erections are elicited when a subordinate approaches within several centimeters of the nest. At the other extreme a male defending a nest will attack females at the opposite end of the tank if they move into view. All degrees of aggressiveness between these extremes exist.

When females are being severely harassed by males, they often assume positions making them as inconspicuous as possible, such as aligning their bodies inconspicuously along clumps of vegetation or in corners. If chased by the male, they also retain the position assumed when they take shelter and may remain there for as long as 20 minutes, usually until surfacing for air. Fish in such harassed states often move pectorals more rapidly than usual and maintain median fins in a partially erected position. As is the case in nonreproductive situations, the male becomes less aggressive at night and females come out of shelter more readily. They cannot, however, approach the vicinity of the nest without being chased.

## Maintenance of Nest and Progeny

Upkeep of nest and care of progeny are difficult to separate and are discussed together below.

Frequency of Air Snapping. Near the end of the spawning series the frequency of air snapping trips increased to more than twice the frequency occurring during mid to late series. In the 3 spawning series graphed in Figures 20, 23, and 24 increases of approximately 170, 100, and 25 per cent, respectively, occurred from late in the series to 2 hours or so after the final spawn. Within several hours of this peak the rate dropped to a level slightly above that evidenced late in the series. For example, in the 3 spawns mentioned above, air snapping trips approximately 6 hours after the final spawn in the series were executed 5 more, 2 more, and 3 less times per 10 minute period than late in the series. The rate of snapping stabilized somewhat at this level and continued until approximately 20-30 hours after the completion of spawning, at which time a general decrease occurred (Figures 20, 23, and 24).

The number of snaps per air snapping trip followed much the same trend as did the frequency of the trips themselves. Snaps per trip increased through the commencement of spawning and in some cases through the first half of the series. In 2 spawning series (Figures 20 and 23) maximum snaps per trip occurred at the commencement of spawning and reached an average frequency of 19 and 20 snaps, respectively, per trip. In a third spawning series (Figure 24) the maximum number (19) was reached midway through the series. In all 3 figures above the frequency per trip was lowest near the termination of the series, averaging only 4-6 snaps per trip. Following the conclusion of each series the frequency for an hour or 2 increased by 3-5 snaps. However, within 10 hours of spawning termination, snaps seldom exceeded 5 and within 24 hours they seldom exceeded 3.

During egg development the frequency of trips and snaps per trip was relatively high and bubbles were still being released in quantity beneath the nest. Bubbles at this time probably aided in carrying eggs higher into the nest. However, bubbles released during the post spawning phase did not accumulate in the nest either because of lack of mucous secretion in the mouth or more likely because of agitation of the nest produced by nest pushing. Nests often contained no bubbles several hours after spawning completion.

The significance of the reduced rate of air snapping occurring after the 20-30 hour period mentioned above is questionable since no regular release of bubbles beneath the nest follows inspiration. Undoubtedly some of these inspirations are for respiratory use by the male while others probably function in aiding the male to replace fry in the nest. After fry have hatched and begin to move around in the nest, and continuing for up to a week after hatching, most males move about beneath the nest taking into their mouths almost any small moving object. Many objects, including some fry were spit out at the spot they were ingested, others were brought to the vicinity of the nest and released as the mouth was pushed upward a centimeter or less beneath the nest.

During the many hours of observation only 7 fry were actually observed being taken into the mouth, 4 were mumbled about in the mouth and released where they were taken in, the other 3 were taken below the nest and presumably spit or released into the nest when the male thrust his snout into it. No inspirations were observed being made after ingestion of these 3 fry before placement in the nest. Many times, however, males with young in the nest acted as if they had caught a moving fry and preceded to snap air and release it into the nest. Only fish with fry in the nest were observed behaving in this way.

Frequency of Nest Pushing. In most cases after spawning completion the level of nest pushing dropped abruptly from the high frequency during spawning termination. For example, the 3 males mentioned above decreased nest pushing frequency approximately 50, 30, and 25 per cent per 10 minute period within 2 hours of spawning completion. With some exceptions the frequency of nest pushing occurring an hour or 2 after the end of the series was maintained for approximately 36 hours.

Nest pushing during this time consisted mainly of snapping and pushing with the snout into lower portions resulting in an occasional jet through the nest. This behavior was primarily concerned with collection of loose eggs and replacement in the nest.

Throughout approximately the first 30 hours only slight variations were observed between day and night frequencies of nest pushing (Figures 20 and 23). After this period pushing frequency corresponded closely with nonreproductive activity patterns. Throughout the first 20-30 hours after spawning, nest pushing remained consistantly high (Figures 20, 23, and 24) showing no low periods of behavior characteristic of nonreproductive fish between midnight and 3:30 a.m. For example, in 3 spawning fish (Figures 20, 23, and 24) nest pushing frequency averaged only 2 snaps less per 10 minute period between 2:00 and 3:00 a.m. than at 12:00 and 6:00 a.m. immediately after the spawning series. During the second lights-out period following the spawning series, however, the same 3 fish pushed the nest 6-8 times less per 10 minutes than the first. Thus, the normal low in behavior occurring between 12:00 and 3:00 a.m. was absent when eggs were in the nest. The level of nest pushing also remained high through the first lights-out period but after hatching returned to typical diurnal rhythms (Chapter IX). This decline in nest pushing which occurs at approximately the time of hatching is perhaps due to presence of the fry and may indicate less need for parental care for larvae than for eggs.

In each of the 3 cases mentioned above the day following spawning, nest pushing reached a high near 2:00 to 3:00 p.m., near the frequency of the preceding day. For example the afternoon following spawning the 3 males averaged approximately 23, 20, and 20 nest pushes in a 10 minute period. Twenty-four hours later they averaged 20, 20, and 19. Nest pushing always decreased greatly after the second day and the highest frequency of nest pushes in the 3 males on the third day was 5 and the lowest 3.

After the third day, nest pushing remained at a relatively low level varying between 2-8 pushes in a 10 minute period, increasing and decreasing primarily with the time of day. The length of time males continued this behavior varied. It was usually one of the last parental care behaviors to cease. The longest period any male continued nest pushing was 6 days, but most stopped within 3 days.

Intensity of Nest Pushing. Once the larvae are about 24 hours old nest pushing becomes less forceful. It appears that there is no longer an attempt to keep the nest compact and pushes are administered lightly, perhaps as the maturing fry are replaced into the nest. They are no longer forced into the nest but may be released among lower fragments hanging from the nest.

Within several days, nests become less compact and fragments in the nest drift apart. During this time nests often increase up to twice their prespawning diameter.

Thus it appears that nest pushing serves three major functions: placement of materials during nest construction; facilitation of egg collection, deposition, and aeration; and replacement of larvae and fry during later stages of the reproductive cycle.

Use of Plant Fragments and Debris. Although plant fragments occasionally are added for a short time after the completion of the spawning series, addition of bottom debris is rare. By the time the larvae have attached, material other than bubbles are no longer brought to the nest except for an occasional piece of vegetation that has become dislodged and is hanging from the nest or within several centimeters of it.

On only two occasions was vegetation brought to the nest more than one day after spawning completion, and this proved to be a period of nest building preceding a second spawning series.

# CHAPTER IX

# DIURNAL BEHAVIOR

In measuring diurnal activity the total frequency of chases and displays were used as an index of agonistic behavior and the duration of patrolling or random swimming was used to represent general non-agonistic behavior.

## General Activity Level

### Non-Agonistic Behavior

Two phases of behavior will be included here, Patrolling and Inspiration.

Patrolling. A higher level of non-agonistic activity occurred at mid-morning than any other time during the day, averaging approximately 270 seconds per 10 minute period for each of 3 fish in 16 tanks. An increase from the low levels of lights-out activity commenced approximately 2 hours before lights-on at which time the average duration of random swimming per 10 minute period for the same fish was 25.3 seconds (Figure 26). During the hour immediately preceding lights-on, activity by the same fish reached 84.5 seconds patrolling per 10 minute period. This period of increased activity reached a maximum of 264 seconds patrolling per 10 minutes after 2-5 hours. Activity declined from this point until shortly after 3:00 p.m. when it was less than half (105 seconds per 10 minutes) that which occurred during the morning peak.

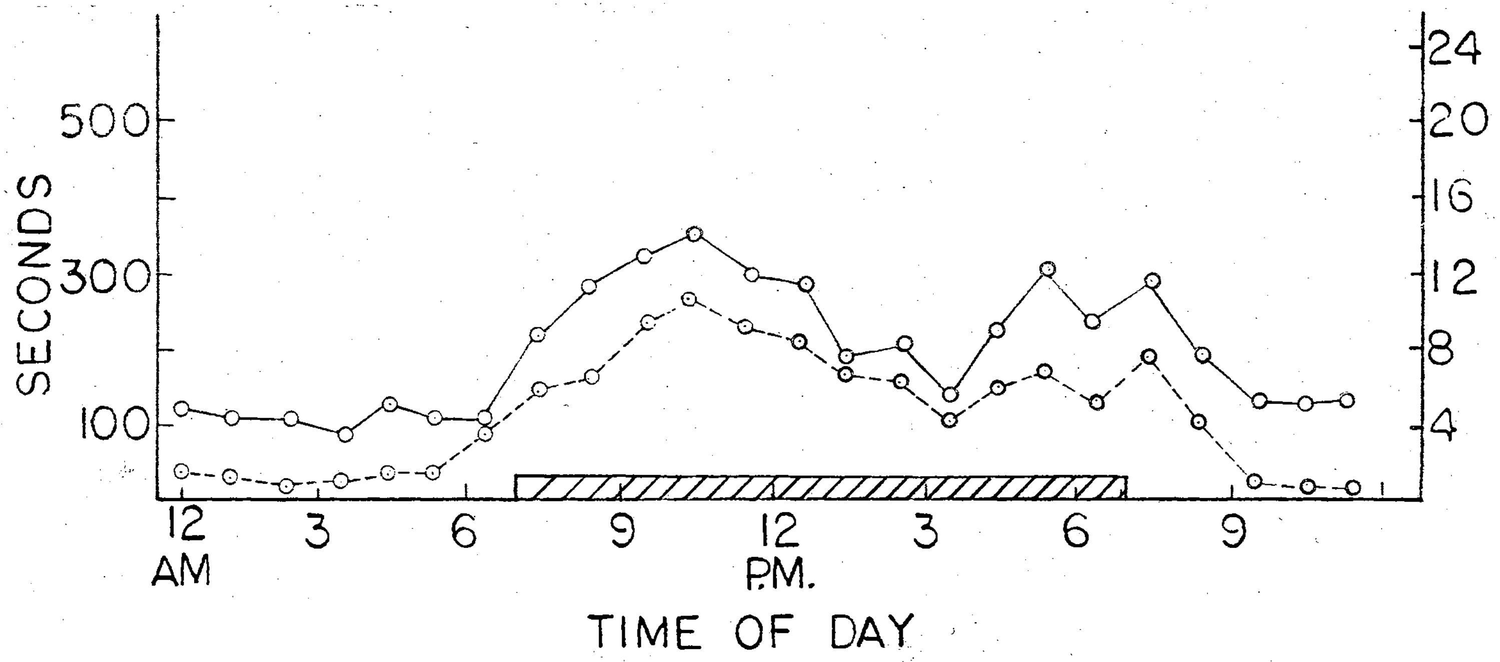

Figure 26. Average Duration of 1 Patrolling Trip (Solid Line and Right X-Axis) and Total Patrolling (Broken Line and Left X-Axis) per 10 Minute Period Throughout a 24 Hour Period in 15 Tanks. Hatched Bar = Lights-on.

Although not detectable in Figure 26, approximately 70 per cent of the tanks observed showed a temporary slump in activity of approximately an hour duration at some time between 8:00 a.m. and noon. Since the exact hour of low activity varied from one tank to another it was not evident in Figure 26, which represents the average duration for 15 tanks. The rate of activity decreased as much as 20 per cent in several cases. The mid-morning slump, however, can be observed to some degree in Figure 27 since this represents an average for only 6 tanks.

The mid-afternoon slump was followed by a late afternoon surge of activity (163 seconds per 10 minutes) which in turn subsided to 114 seconds of activity during the hour prior to lights-out.

Once again following lights-out there was another short period of increased activity lasting between 1 and 2 hours with a high of 185 seconds of patrolling per observation period.

Darkness appeared to reduce aggressive behavior and the fish, particularly subordinate ones, came out into open water for longer and more frequent periods of time, swimming about the tank with relatively little harassment from dominant fish.

This characteristic of subordinate fish leaving shelter the instant following lights-out is most noticeable in situations in which a fish is extremely aggressive and has been keeping subordinates under cover. Such behavior is common in tanks with nest building males.

From about 3 hours after lights-out to 2 hours before lights-on, activity was consistently at a low level and patrolling activity varied from zero to 164 seconds of activity per 10 minute period for any one fish and the average duration for fish in the 16 tanks had an

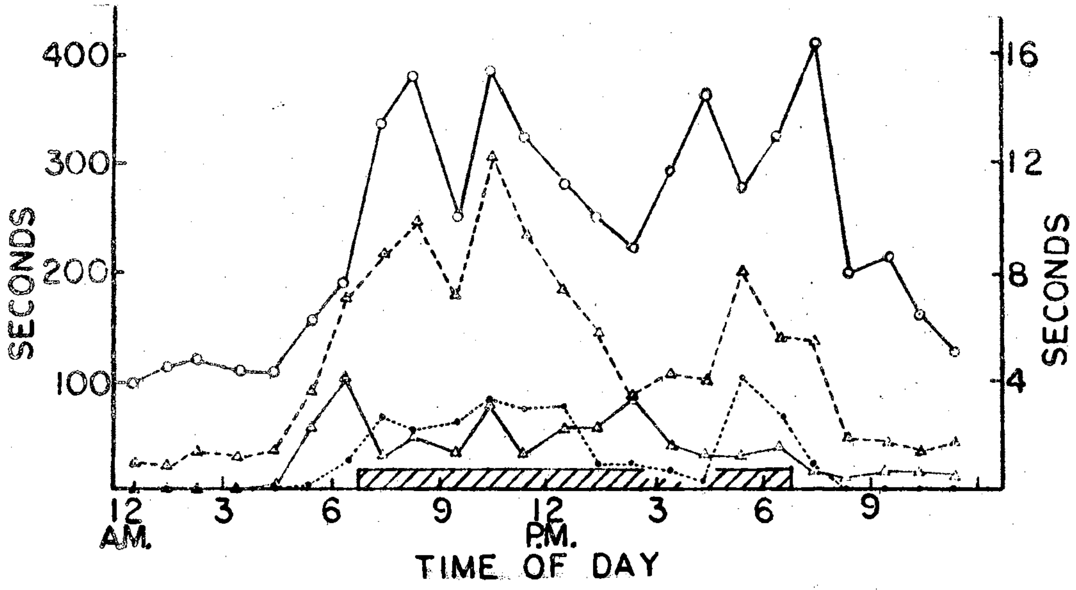

Figure 27. Average Duration of Patrolling (Triangle with Dashes-Left Axis), Duration of Each Patrolling Trip (Circle with Lines-Right Axis), Frequency of #3 Chase (Dot with Dashes-Right Axis), and Frequency of #1 and #2 Chases (Triangles with Solid Line-Right Axis) per 10 Minute Period Through 24 Hours in 6 Tanks. Hatched Bar = Lights-on.

average of 22.7 seconds. The lowest level of activity is reached in the early morning from 5-6 hours before lights-on.

The duration of patrolling periods increase and decrease during a 24-hour period much the same as the total duration of patrolling discussed above. The greatest difference is in the duration of individual patrols. For example, durations of individual patrols during the 3 hours before lights-on changed very little and had an average of 4.8, 4.2, and 4.2 seconds, respectively. Total time patrolling during the same time, however, was 25.3, 39.7, and 84.5 seconds, respectively. Therefore, while no prolonged patrols occur there is an increase in total patrolling duration.

Activity increased gradually with the approach of lights-on at approximately the same rate in tanks which were in almost total darkness as in several tanks in which the light was increased gradually over several hours before lights-on (Figures 26 and 27).

Inspirations. As mentioned earlier, the inspiration of air included two types: surface inspiration and dashes-to-surface. Neither of these behaviors followed the same general trend followed by patrolling and aggressive behaviors.

The frequency of surface inspirations varied from 0.5 inspiration to 1.9 every 10 minutes and had an average of 1.2. As may be seen in Figure 28, throughout a 24-hour period frequency of surface inspirations are relatively constant but appear to be most frequent 3 hours before lights-on and 2 hours after lights-out when the average number of inspirations was 1.9. Frequency during lights-on varied from 0.5 to 1.9 and had an average of 1.3. This lower rate of inspiration in spite

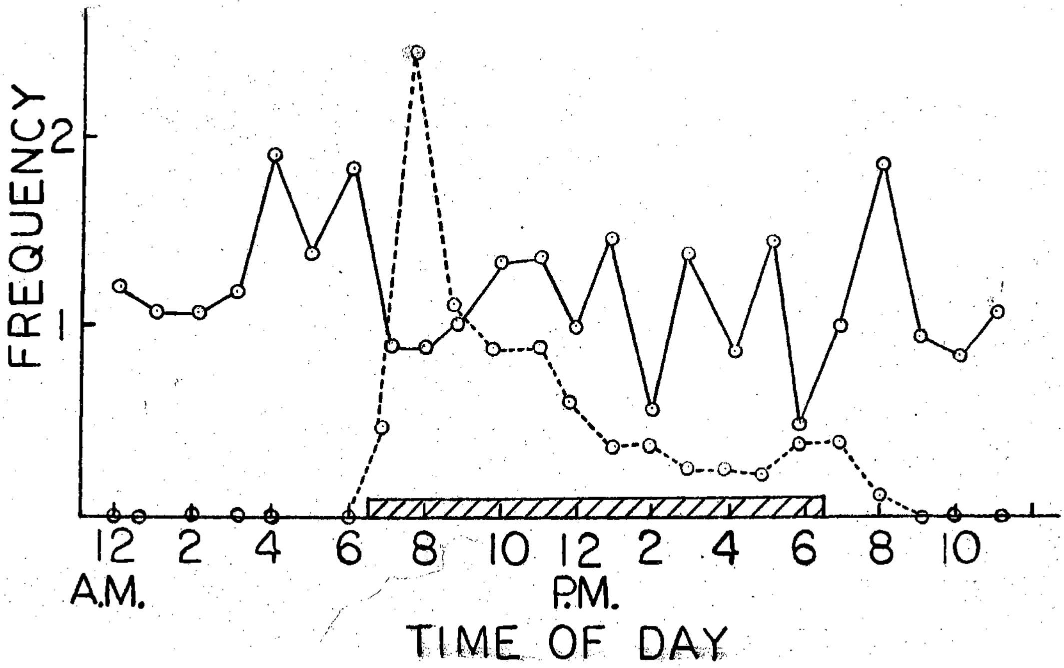

Figure 28. Average Frequency of Dashes-to-Surface (Broken Line) and Surface Inspiration Trips (Solid Line) per 10 Minute Period Throughout 24 Hours in 11 Tanks. Hatched Bar = Lights-on.

of increased activity during lights-on is probably due to a higher rate of dashes-to-surface during this time.

Dashes to the surface occurred almost entirely during lights-on, varying from 0.4 to 2.2 dashes every 10 minutes (Figure 28). Dashes commenced at lights-on and reached maximum frequency an hour or two thereafter, declining from that point until one hour before lights-out when a slight increase occurred, continuing for 2 hours.

Increases in dashing to the surface coincide closely with the periods of the day when territories and social behavior are less pronounced. They often appear to be performed by several fish rather than individuals. If this behavior is primarily an allelomimetic social behavior it may explain the fact that no such dashes occur during lights-out when fish are unable to maintain visual contact with one another. Perhaps also slowly executed inspirations occur at night when predators, territory defenders, and the like are less active. During the day, however, dashes-to-surface are more common since they decrease the chance of damage from hostiles. During times when territories are held aggressively, as in nest construction or parental care, dashes-to-surface are rarely executed by either male or female.

## Agonistic Behavior

To some extent agonistic and non-agonistic activity increased and decreased together. Several exceptions existed, however.

Most data concerning chases discussed in this section are based on an average of 16 24-hour periods of observation, 10 minutes each hour.

During lights-out chases were infrequent and remained at an average of less than one chase per 10 minute period from 9:00 p.m. to 4:00 a.m. During this time Type #3 chases were rare and chases were of Types #1 and #2, indicating again a loss of aggressiveness after lights-out due perhaps to elimination of stimuli (Figure 29).

As patrolling began to increase at 4:00 a.m., chase frequency increased also, from 0.6 chase at 4:00 a.m. to 8.5 at 6:00 a.m. per 10 minute period. Approximately 80 per cent of the chases during this peak of behavior were Type #2 chases.

Although a rapid decrease in total chases occurred from 6:00 to 9:00 a.m. the decline was due primarily to a drop in less aggressive Types #1 and #2 chases which decreased to 1.3 at 9:00 a.m. Actually, Type #3 chases were most frequent and increased rapidly the hour after lights-on, from 1.5 at 6:00 a.m. to 4.2 at 7:00 a.m. They remained more frequent than the less aggressive ones through most of the lights-on period.

A second peak in aggressive behavior occurred from 10:00 a.m. to 1:00 p.m., reaching an average of 8.6 chases every 10 minutes. Occurring almost simultaneously with this high in aggressive activity was the mid-morning high in patrolling, which peaked at 10:00 a.m., while chases appeared to reach maximum an hour later at the point which patrolling commenced to decline. Unlike the first peak, just prior to lights-on, which consisted mostly of non-aggressive chases, this late morning high consisted of approximately 60 per cent Type #3 chases (Figure 29).

Following this pre-noon high a continuous decrease in the frequency of chases occurred, reaching a low at 4:00 p.m. of 3.8 chases

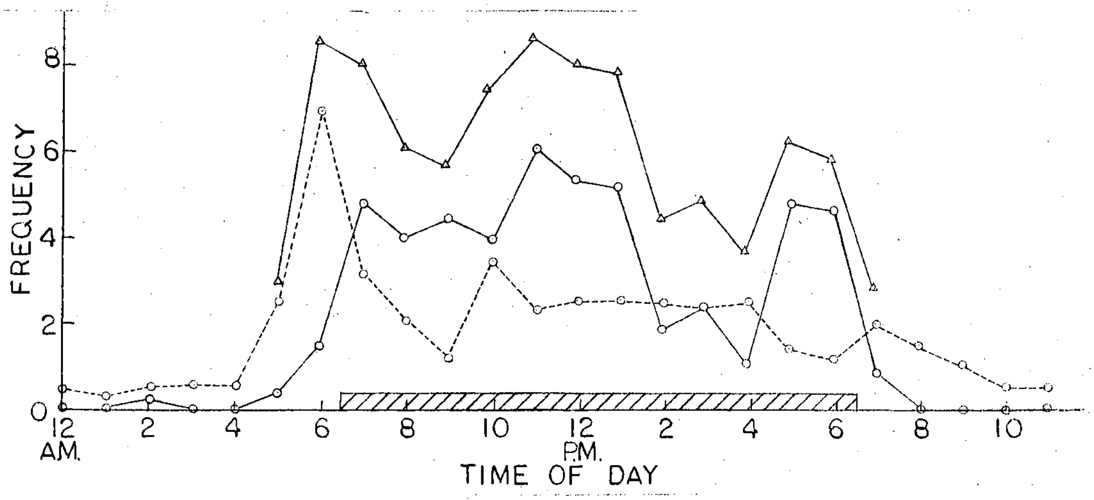

Figure 29. Average Frequency of #1 and #2 Chases (Circles with Broken Line) and #3 Chases (Circles with Solid Line) per 10 Minute Periods Throughout 24 Hours in 16 Tanks. Triangles with Solid Line = Total Chase and Hatched Bar = Lights-on.

per 10 minute period. The frequency of both chases and patrolling reached their lowest point during daylight hours between 2:00 and 5:00 p.m. This period is the only time during lights-on that Types #1 and #2 chases exceed those of Type #3. Thus, loss of aggressiveness correlates closely with periods of non-patrolling.

Between 5:00 and 7:00 p.m. a third and last peak of activity occurred during which the frequency of chases increased 2-3 per observation period. This increase corresponded closely with a pre-lights-out increase in patrolling. Again, Type #3 chases greatly exceeded less aggressive ones, reaching 4.8 and 1.7, respectively. Tanks showed an increase in patrolling the hour following lights-out, but few showed an overall increase in aggressive Type #3 chases (Figure 29).

Although in some exceptional cases chases continued to remain at a relatively high frequency after lights-out, in most cases there was a sharp decline to 11:00 or 12:00 p.m., from which time a consistently low level of activity was maintained. In almost every case, however, Types #1 and #2 chases were more frequent than Type #3 chases. With darkness, aggressiveness clearly declines.

There is no question from the above data that aggressive behavior increases and decreases with patrolling activity. Perhaps the simplest explanation of the correlation of these activities is merely the fact that with increased movement more encounters occur, resulting in increased agonistic behavior. This explanation, however, does not always hold true, especially during the increase in patrolling after lights-out at which time total frequency of chases declines. This also does not explain the hour lag between peaks in patrolling and aggressive behavior. A third point of uncertainty is that of the rapid increase of chases existing prior to lights-on, which increases at a rapid rate only to decline while patrolling continues to increase. The early pre-lights-on increase in aggressiveness is perhaps due to reestablishment of territories and/or hierarchy as the fish commence moving about the tank.

## Reproductive Compared to Nonreproductive Behavior

Data used in analysis of nonreproductive and reproductive behaviors are based on 5 tanks each containing 1 male and 2 females. Behavior was recorded each hour for 10 minutes for a period of 24 hours (Figure 30). The day following the first observation periods peat moss was added to a depth of 5-10 cm on the bottom of each tank. After 6 days a second series of observations was made. One male began nest construction within 24 hours of the second observation series, and within 72 hours all males were constructing nests.

### Total Patrolling Duration

During lights-on, patrolling decreased considerably at the onset of spawning behavior and possessed an average duration per 10 minute period of 149.9 seconds compared to 183.5 seconds before the onset of reproductive behavior, a decrease of 18.4 per cent.

The only time during light hours in which the duration of patrolling in reproductive behavior significantly exceeded nonreproductive was between 7:00 and 9:00 a.m. during which time it was 20 per cent greater and had reached a peak for the 24 hour period (Figure 30). Following this early peak of activity patrolling in reproductive fish declined sharply from 247 seconds between 8:00 and 9:00 a.m. to 114

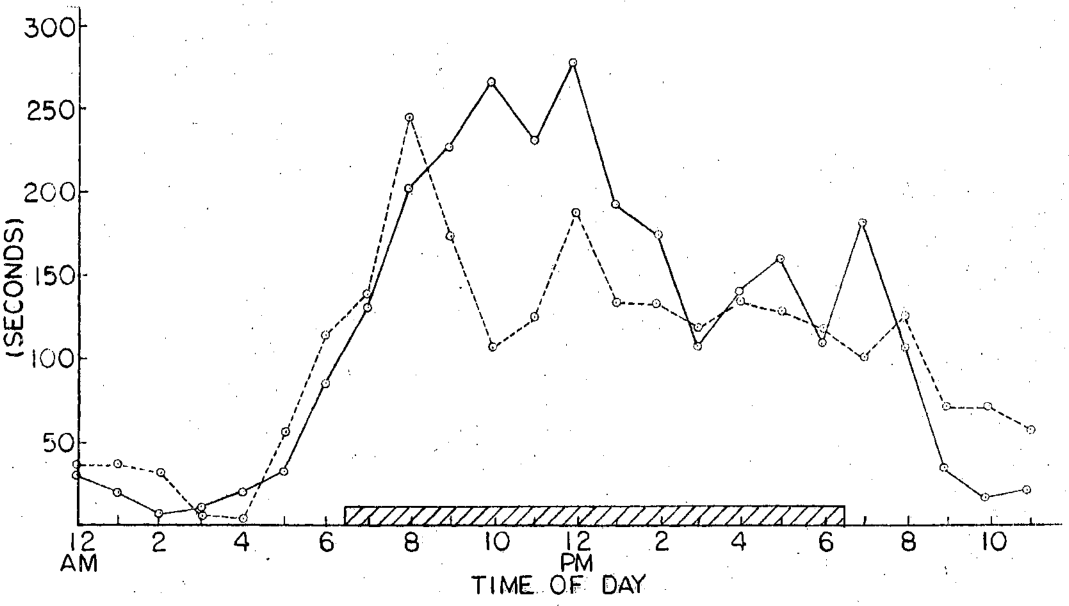

Figure 30. Average Total Patrolling Durations During the Reproductive (Broken Line) and Nonreproductive (Solid Line) Phase per 10 Minute Period Throughout 24 Hours (15 Fish). Hatched Bar = Lights-on.

seconds between 10:00 and 11:00 a.m. and remained below nonreproductive for most of the light hours.

This 7:00 a.m. peak in patrolling by reproductive fish may perhaps be explained again by an early initial activity in establishment of the territory of the male. During the period of inactivity which followed, the male usually remained at the site of the future nest.

With few exceptions patrolling duration during lights-out was the reverse of that found during lights-on and the average of patrolling during the nonreproductive period was 50.7 while it was 61.9 during reproductive behavior, an increase of 22 per cent.

### Duration of Individual Patrols

Unlike total patrolling duration, single patrol durations were longer in reproductive than nonreproductive periods with respective highs of 48.4 and 14.9 seconds, and averages for a 24-hour period of 17.9 and 7.8 seconds, respectively. Thus, the reduction in total patrolling duration is accompanied by longer individual patrols and reduction of patrolling frequency. Perhaps more pronounced situations of this type developed into fluttering or migrating (Figures 30 and 31).

### Chases

Contrary to what might be expected, the overall frequency of chases did not increase with the onset of reproductive behavior. Types #1 and #2 chases remained much the same with an average of 2.1 in nonreproductive and 2.2 in reproductive periods and Type #3 chases declined from an average of 3.1 to 2.4 chases per 10 minutes (Figure 32).

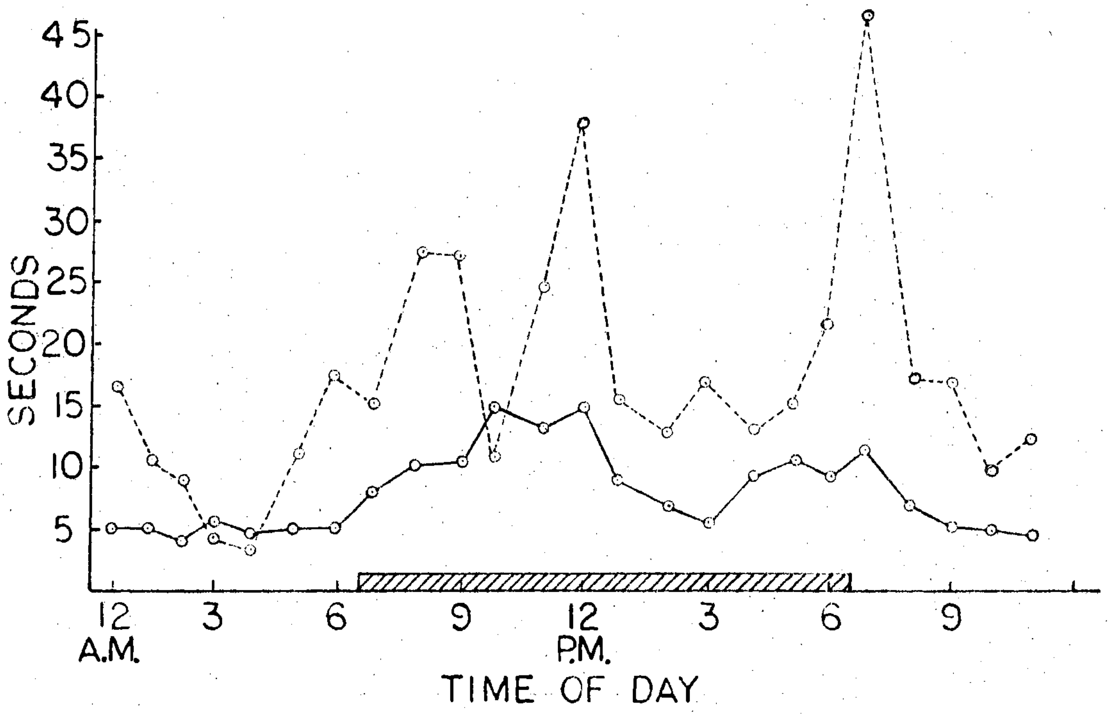

Figure 31. Average Duration of an Individual Patrol 1 Day Before (Solid Line) and 6 Days After (Broken Line) Lowering of the pH (15 Fish). Hatched Bar = Lights-on.

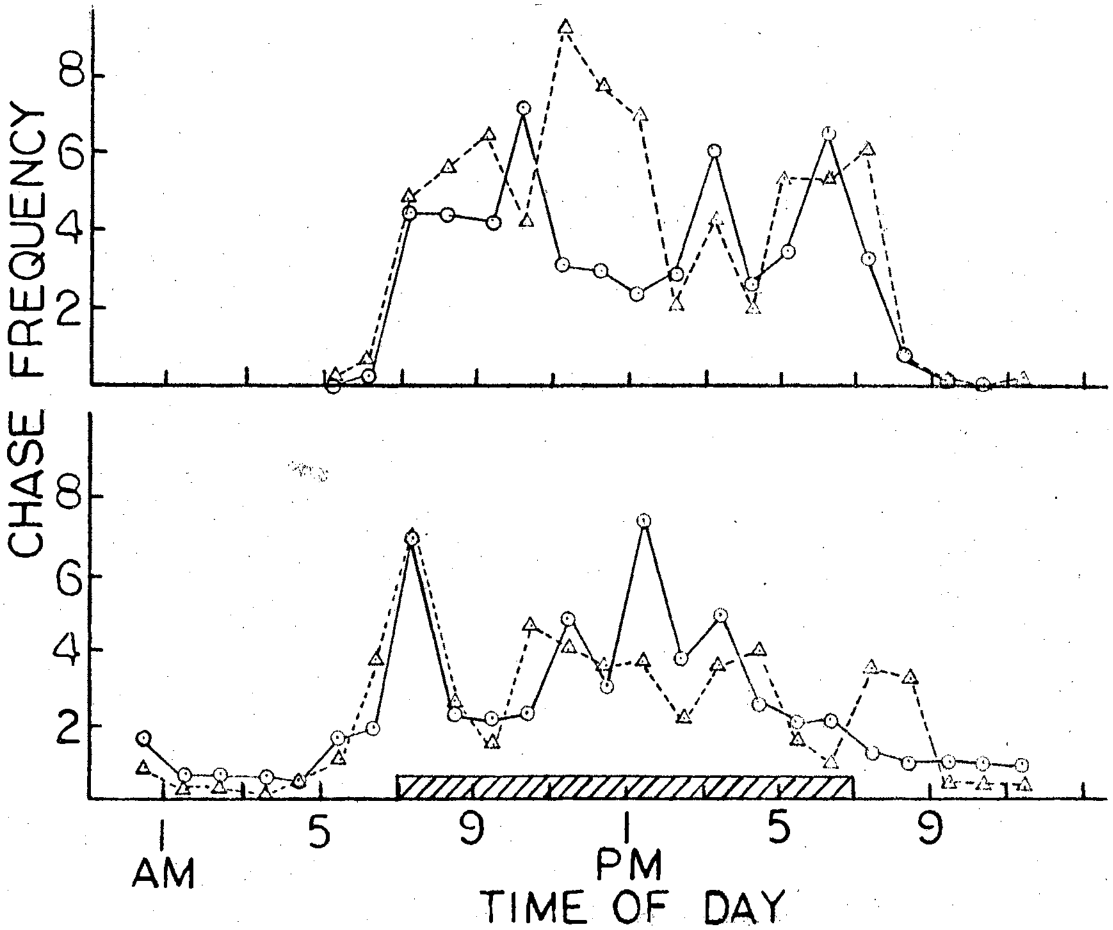

Figure 32. Average Frequency of Type #3 (Top Graph) and Types #1 and #2 Chases (Bottom Graph) per 10 Minutes Throughout 24 Hours 1 Day Before (Broken Line), and 6 Days Following (Solid Line) Lowering of the pH (15 Fish). Hatched Bar = Lights-on.

Distribution of Type #3 chases during daylight hours, however, was reduced in frequency between 7:00 a.m. and 2:00 p.m. from an average of 6.5 chases per 10 minute period during nonreproductive behavior to 3.8 during reproductive behavior, while at the same time Types #1 and #2 chases increased from 3.5 to 4.1 (Figure 32).

Several factors may be responsible for the above alteration in chasing. First, it is possible that at this point the female is reluctant to approach the male closely enough to elicit a chase, which increases in severity as the reproductive period continues. This could also account for the increased frequency of Types #1 and #2 chases in which the female eludes the male before eliciting severe aggressiveness. Secondly, the male also shows reluctance to leave his established nest site as shown by patrolling duration decrease. Finally, with the increase of other aggressive behaviors such as tail beating and fin displays (discussed below) the chase may become less important.

### Tail Beating, Lateral Displays, and Lateral Spreads

These three aggressive behaviors by the male increased in frequency during reproudctive behavior, occurring an average of three times each hour in nonreproductive male fish and 10.4 times in males in the reproductive phase. These behaviors occurred primarily during lights-on (81 per cent).

Because of the limited number of occurrences throughout the observation periods, it is difficult to obtain a good evaluation of trends over the 24 hours. It appears, however, that similar trends occur in these behaviors and in patrolling. There is also an indication that these behaviors are more erratic during reproductive behavior (Figure 33).

## Surface Inspiration

Surface inspirations almost tripled from an average of 0.9 every 10 minutes during the nonreproductive phase to an average of 2.5 several days before nest construction.

During the nonreproductive phase surface inspirations were more frequent during lights-out than during lights-on with an average per 10 minute period of 1.2 and 0.7, respectively. During the reproductive phase the reverse was true since the average frequency was 2.3 during lights-out and 2.8 during lights-on (Figure 34).

Two marked lows in inspiration frequencies occurred in both phases of behavior: following lights-on and at lights-out. This is most easily explained by concluding that the greatly increased rate of dashes-to-surface at lights-on and at lights-out furnish the fish with sufficient air so that surface inspirations are unnecessary.

The overall increase in respiration rate of reproductive fish reflects an increase in physiological processes and a general increase in activity rate. Possible relationships with dashes-to-surface will be further discussed below.

## Dashes-to-Surface

Dashes-to-surface by any fish in a 10 minute period varied from 0 to 7. The frequency varied generally according to the time of day, but was higher during the reproductive phase.

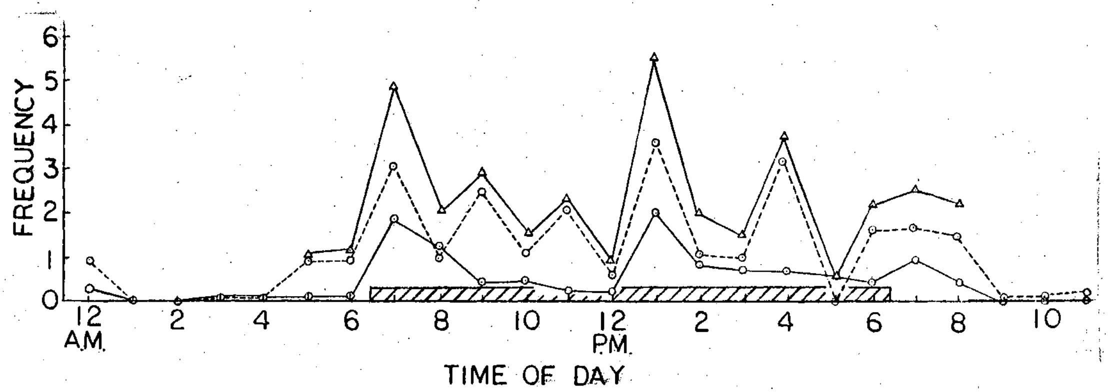

Figure 33. Average Frequency of Tail Beats, Lateral Spreads, and Lateral Displays per 10 Minutes Throughout 24 Hours 1 Day Before (Circle with Solid Line) and 6 Days After (Broken Line) Lowering of the pH (15 Fish). Triangles with Solid Line = Total of Before and After and Hatched Bar = Lights-on.

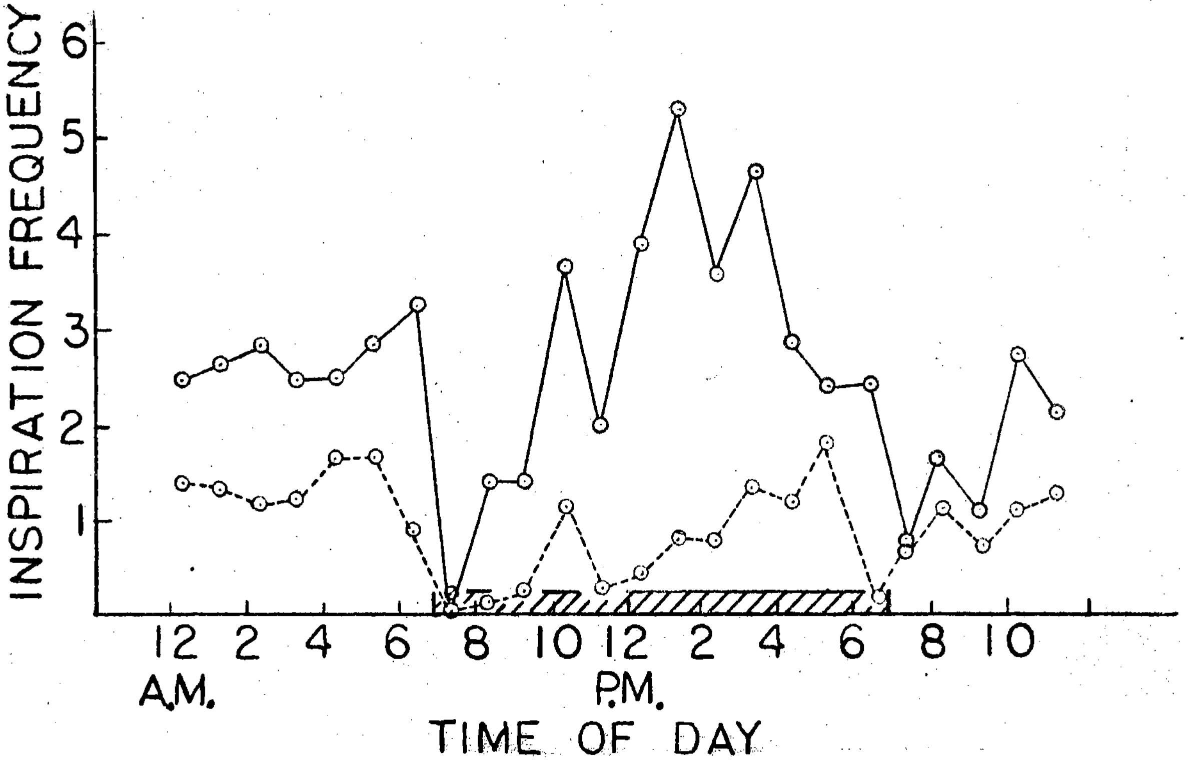

Figure 34. Average Frequency of Surface Inspirations per 10 Minute Period Throughout 24 Hours 1 Day Before (Broken Line) and 6 Days After (Solid Line) Lowering the pH (15 Fish). Hatched Bar = Lights-on.

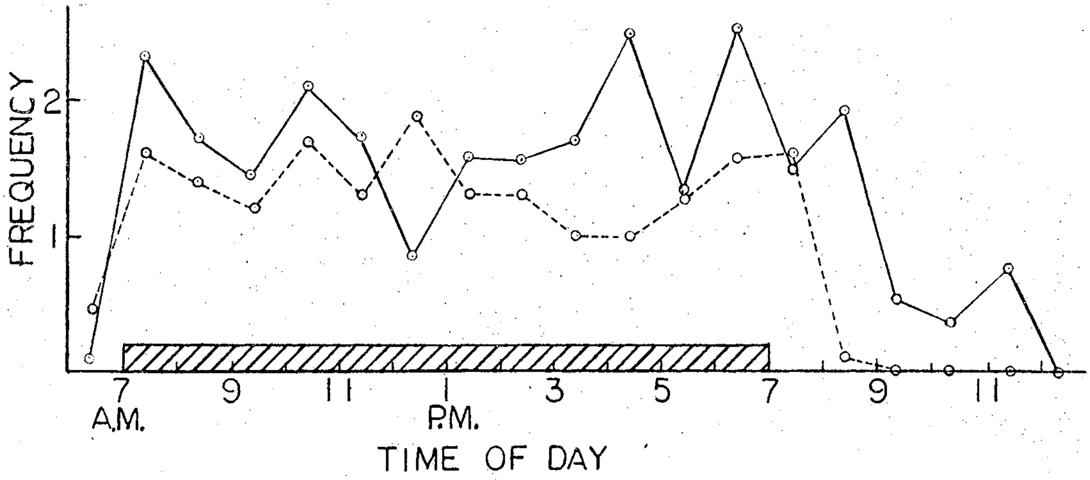

Figure 35. Average Frequency of Dashes-to-Surface per 10 Minute Period Throughout 24 Hours 1 Day Before (Broken Line) and 6 Days Following (Solid Line) Lowering of pH (15 Fish). Hatched Bar = Lights-on.

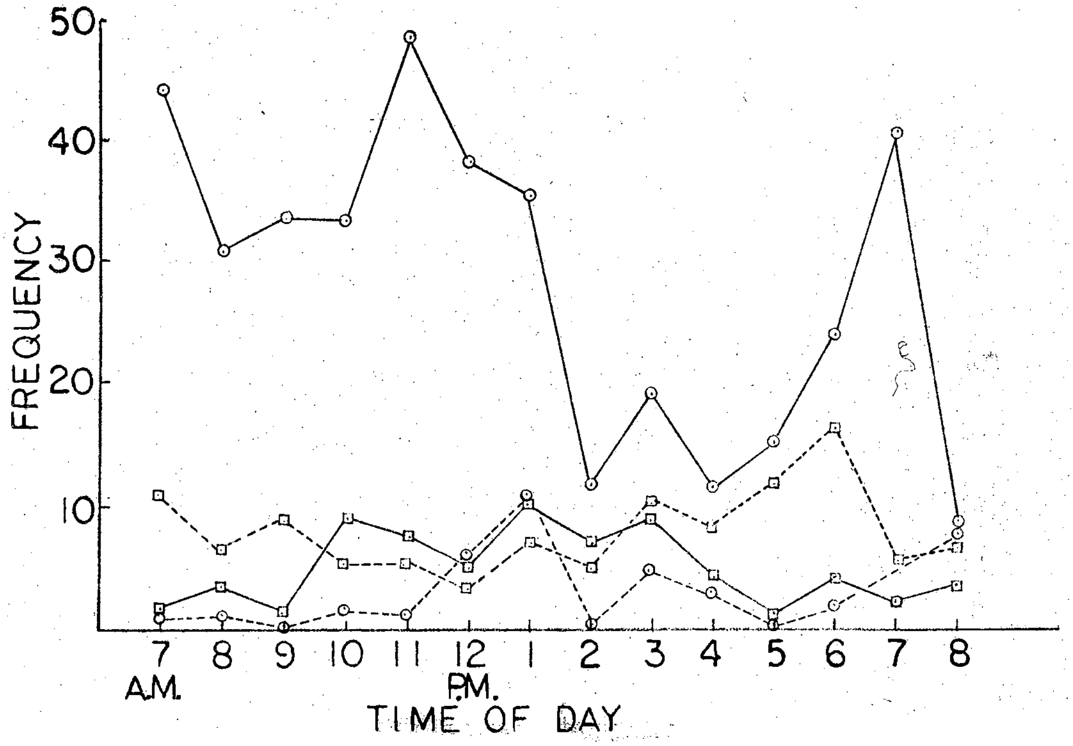

Figure 36. Frequency of Male and Female Initiated Encounters per 10 Minute Period Throughout 24 Hours 1 Day Before (Male = Circle and Solid Line, Female = Circle and Dash Line) and 6 Days Following (Male = Square with Solid Line, Female = Square with Dash Line) Lowering of pH (15 Fish). Hatched Bar = Lights-on.

male-initiated encounters 84 per cent lower, and female-initiated encounters 140 per cent higher. This clearly indicates that females approach the male much more frequently at this time (Figure 36).

The nonreproductive phase had two periods of maximum male-initiated encounters. One extended from lights-on to approximately 1:00 p.m. reaching a peak at 11:00 a.m. The second began an hour or two prior to lights-out and peaked approximately one-half-hour after lights-out. Low frequencies in the late afternoon ranged between 12 and 19 encounters. Male-initiated encounters during the reproductive period showed no pronounced high levels of activity other than an increase to approximately 17 encounters immediately prior to lights-out.

Encounters initiated by females in the nonreproductive phase showed a generally reciprocal trend to that of the males with lowest frequencies at lights-on and lights-out and the highest frequency at mid-day. The trend in the nonreproductive phase was similar to that of the male although much lower.

Females in the reproductive phase initiate more encounters than the male from 10:00 a.m. until 2:00 p.m. This was a time during which the male was remaining at the future nest site for extended periods and defending it aggressively. This was the first sign of increased female approach frequency and increased male response. By the time the nest was under construction, most encounters were initiated by the female. After the nest had been under construction for some time, the male again sought out the female to lead her to the nest if she did not approach it on her own accord. After several spawns it was generally no longer necessary for the male to lead the female and almost all encounters were female initiated.

# CHAPTER X

## SUMMARY

This paper includes qualitative descriptions of the behaviors of Trichogaster microlepis and quantitative aspects where deemed necessary to clarify qualitative data. Most data were obtained by observing tanks containing one male and two females for periodic 10-minute observations. During spawning behavior continuous observations were conducted for periods up to 24 hours.

Activity patterns were divided into agonistic and nonagonistic patterns and described in detail only when differing substantially from behavior of T. trichopterus and T. leeri.

Agonistic behavior appeared to be less vigorous in T. microlepis than other species of the genus and mouth fighting present in the other species was absent. Biting was infrequent except by nest guarding males and even butting was rare except by females during reproductive behavior. The most common female appeasement posture, "breasting," usually elicited by an approaching male was unique in that median fins were erected rather than folded as appeasement in most other species. Chasing, except by the male, was uncommon and escape by the female was usually accomplished readily from even the most severe chase by entering shelter and/or breasting.

Inspiration of air included two types, stationary-at-surface and dashes-to-surface, both of which appeared to be somewhat allelomimetic.

Ingestion of dry food occurred primarily at the surface but was taken at all levels. Actively moving organisms such as *Daphnia* were preferred to larger morsals of live food and ventral fins (pelvics) appeared to be used to locate food which was obscured from view.

Some behaviors occurring infrequently were: yawning, head jerking, mouth snapping, pseudo-clasping, and rocking.

The nest, constructed only by the male, was considerably more massive than that of either *T. leeri* or *T. trichopterus* and plant fragments, rare in above species, made up the bulk of the nest. The major materials used in construction were floating strands of *Ceratophyllum* and stems, leaves, and roots of *Vallisneria* which were often torn loose or uprooted. Although bottom debris was used, no sand or gravel was used as is sometimes the case in *T. leeri*.

The effect of age or past experience of the male on location, size, and materials or methods used for construction of the nest appeared to be minimal. Larger fish, however, had a tendency to construct somewhat larger nests probably due to their physical ability to utilize more inaccessible materials.

Nest construction could be predicted by the carrying of vegetation randomly about the tank by the male. Physical factors such as location and intensity of lighting, disturbance of the water, and location and density of vegetation affected the position of the nest.

Following each addition of construction material to the nest, air bubbles were released beneath it, unlike *T. trichopterus* and *T. leeri* which often remained at the nest inspiring air and releasing bubbles at the surface. Opercular air emission, common in both *T. trichopterus* and *T. leeri*, was rare in *T. microlepis*.

Following bubble release, the nest was often pushed with the snout (nest pushing). Perhaps this aided in the arrangement of the materials since T. leeri and T. trichopterus, which utilize little or no vegetation, lack this behavior.

Of 16 nests observed being constructed during the study, all were begun within 8 days of either changing the tank water (2 nests) or lowering of pH (14 nests). Alterations of temperature, turbidity, photo period, or addition of new fish had little or no apparent effect on enhancing reproductive behavior.

Male activity during early courtship was marked by increase in severity of chases and a decrease in movement throughout the tank. As he remained near his future nest site, females increased their approaches to him four fold.

By the time the nest was several hours under construction the female was usually forced to remain under shelter and ventured toward the male only after extensive and varied displays and leads by him. Once spawning started, however, male leads became less elaborate and most spawning bouts were female initiated since she usually went beneath the nest of her own accord while the male was preoccupied with nest care or air snapping.

Once the female arrived beneath the nest, she responded to the fin displays and tail-beating of the male by butting him. Butts were followed by an apparent loss of male aggressiveness and his display postures ceased as circling began.

During circling the female oriented with her snout at the dorsal fin of the male, following him around as he appeared to attempt to swim behind her, assuming a relative position to one another which was retained through the post-circle pause.

Circling periods varied in frequency and duration within an individual bout as well as within the spawning series. Circling periods when occurring more than once in a bout pregressively became shorter than the preceding circling, perhaps indicating a retention or summation of behavior in the bout to produce a spawn. Throughout most of the series, duration and total circling frequency per bout became shorter. Late in the series both circling duration and frequency per bout became longer.

Successful bouts usually possessed fewer circling periods than did unsuccessful ones and as the number of circling periods in a bout increased the probability of the bout being successful decreased. Of all bouts, successful or unsuccessful, possessing one or more circle periods, bouts with one circling period were most successful.

Following circling, the pair paused (post-circling pause) usually for several seconds less than circling, and changed little in relative position until the curve and clasp. Since little or no change of position occurred, the pause may have enhanced synchronization for execution of the clasp. Disorientation which occurred most often during the pause elicited displays by the male and butting by the female as circling was resumed.

Unlike circling, however, successive pauses in the same bout usually became progressively longer in both successful and unsuccessful bouts. In bouts with short circling periods, the duration of the pause was generally relatively long, and following long circling periods the pause duration was shorter. Thus throughout most of the spawning series the pause increased in duration as circling decreased, suggesting the possibility that time spent in the pause may have substituted partially for circling, and vice versa, and that the two may have summated to yield an optimum pre-clasp duration. Although the pause was absent in *T. trichopterus* and *T. leeri*, they both have additional behavior which lengthens the pre-clasp time.

The pause is terminated by the clasp as the male curves around the anterior of the female, bringing the genital orifices of the pair close to one another as the body of the female becomes perpendicular with head upward. The clasp varied less in duration than any other phase of the bout and once started the chance of a successful spawn occurring was approximately three to one. Duration of the preceding pause and location in the spawning series also had little or no effect upon the clasp duration.

As the peduncle of the female was brought upward the pair started to roll over and sex products were released. The clasp continued until the head and peduncle of the male were down, at which time the clasp was released and both fish fell away in a state of swimming inhibition. Time spent between rolling over and separation of the pair was longer after short clasps and shorter after longer clasps. They also increased as bout duration increased.

Swimming inhibition, if present, varied in duration and degree from one pair to another and was usually longer in males than females. The rapid recovery by the female often enabled her to escape from beneath the nest before being chased or attacked by the male.

The buoyant eggs were collected by the male either singly or several at a time depending upon their abundance, and were released into the nest as the snout was pushed into the structure. Eggs were then moved up through the nest by release of air bubbles below the nest, jetting, or nest pushing. Parental care by the male continued for several days during which time intruders were aggressively chased from the vicinity of the nest.

Most behaviors involved in nest construction and parental care such as air snapping, bubble blowing, conveyance of vegetation, and nest pushing vary predictably as to frequency and/or duration depending on the phase of the reproductive cycle. Release of air bubbles beneath the nest and conveyance of materials increased up to commencement of spawning at which time they decreased rapidly.

Nest pushing and, to a lesser degree, air snapping continued to be frequent throughout the first night and day following spawning, during which time fry hatched (incubation 18-24 hours). Nest pushing perhaps functioned in egg aeration and collection and deposition of eggs or fry which floated loose. For up to 9 days following spawning males vigorously attacked fish which ventured into the vicinity of the nest and on several occasions moving objects outside the tanks were attacked.

Most parental care, other than guarding of the nest area, continued for more than 30-40 hours following spawning, showing high and low periods of activity similar to nonreproductive diurnal rhythms.

In evaluating diurnal behaviors, durations and frequency of patrolling and inspiration were used to represent non-agonistic behavior and chases and lateral spreads and displays were used to represent agonistic behavior. Two peaks of patrolling occurred each 24 hours, one during mid-morning and a second less pronounced one which continued from an hour or two before to an hour after lights-out. Similar peaks of patrolling occurred during reproductive and nonreproductive phases except that during the former peaks in activity were considerably lower. As total patrolling became less, however, the duration of individual patrols increased considerably and perhaps developed into fluttering, common in some nest building males. Surface inspiration remained relatively constant, dashes-to-surface occurred only from lights-on to an hour after lights-out. During the reproductive phase surface inspirations increased considerably, particularly during the late afternoon and dashes-to-surface generally were somewhat higher, except during the spawning series, when they were absent.

Chases begin to increase shortly before lights-on and show one peak of activity shortly before lights-on, a second at noon, and a third prior to lights-out. During lights-out most chases were less aggressive (Types #1 and #2) and only after lights-on chases became aggressive (Type #3) and more numerous than Types #1 and #2. During lights-out aggressiveness apparently was at a minimum, perhaps because of the lack of visual stimuli. Also chases increase and decrease directly proportionate to the patrolling, suggesting that with increased movement over the tank more encounters occur, hence more chases result. Contrary to what might be suspected chase frequency does not increase during the reproductive phase as do tail beating and median fin displays. Perhaps less male patrolling or the increase in severity of chases when they do occur may be causes.

Within the onset of reproductive behavior there was an increase in female initiated encounters, especially during hours when the male was located beneath the nest. Female approaches reached their maximum during nest construction when the male was actively nest building.

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# VITA

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