PRE- AND POST-SPAWNING BEHAVIOR IN THE BLUE GOURAMI, *TRICHOGASTER TRICHOPTERUS* (PALLAS), AND THE PARADISE FISH, *MACROPODUS OPERCULARIS* (LINNAEUS)

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PREFACE

The objectives of the present investigation are to:

(1) Describe the motor patterns for seven presumably functional classes of behavior in *Trichogaster trichopterus* and *Macropodus opercularis*.

(2) Determine the length of reproductive cycles and the characteristic diel rhythmicity of spawning activities.

(3) Evaluate the influence of precipitation, barometric pressure, and water temperature on the presence of a nest and the onset of spawning.

(4) Determine if activity cycles exist by measuring fluctuations in daily activity.

(5) Compare the changes in the composition of behavior during the spawning cycle.

Dr. Rudolph J. Miller served as major adviser and was extremely helpful during all phases of the study. Drs. Roy W. Jones, Troy Dorris, L. Herbert Bruneau, and Larry T. Brown served on the advisory committee and edited the manuscript.

Donald E. Maritt suggested the method for computer analysis of the data. James Butler was instrumental in writing the computer programs and was helpful in expediting the work in the Computer Science Department. Dr. Dale D. Grosvenor, Director of the University Computer Center, was most encouraging.

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CHAPTER I

INTRODUCTION

This investigation is concerned with the pre- and post-spawning behavior of the blue gourami, Trichogaster trichopterus (Pallas) and the paradise fish, Macropodus opercularis (Linnaeus). The study attempts to determine whether environmental factors influence the spawning cycle. Breeding pairs of fish were observed in aquaria. The behavioral differences between the two species are compared.

Qualitative descriptions of the observed behaviors are given, and a quantitative analysis of 23 of them follows. The functional classes of behavior investigated are: Patrolling, maintenance, comfort movements, agonistic, migratory, courtship, and parental behavior.

Previous investigations that are particularly pertinent to this study are the works of Forselius (1957), Miller (1964), Greenberg, Zijlstra, and Baerends (1965), Hall (1966a), Ward (1966), and Miller and Hall (1968).

Forselius (1957) described the reproductive behavior patterns of anabantids, with particular reference to the genus Colisa. He also discussed their systematics, ecology and endocrinology.

Miller (1964) studied the social organization of T. trichopterus with special emphasis on motor patterns, territoriality, hierarchy, nest building, and spawning behavior.

Greenberg, Zijlstra, and Baerends (1965) gave a quantitative description of the changes in the average daily frequencies of occurrence of various pre- and post-spawning activities performed by males and females of *Aequidens portalegrensis* during the spawning cycle. They found the frequency distribution of courting activities during the pre-spawning period followed optimum curves. They noted that the curves for different activities usually varied slightly in phase, with some activities reaching their maximum gradually, others more abruptly.

Hall, (1966a) compared the qualitative and quantitative aspects of courtship and reproductive behavior in breeding pairs of *Trichogaster leeri*, *Trichogaster trichopterus*, and *Macropodus opercularis*. He found a striking similarity in courtship patterns between the two *Trichogaster* species and a dissimilarity to *M. opercularis*. He also noted that the reproductive behavior in *M. opercularis* is characterized by greater male-female cooperation than in the *Trichogaster species*. This included female nestbuilding and egg and fry retrieval.

Ward (1966) studied the paradise fish, *M. opercularis*, under laboratory conditions. He discussed the qualitative and quantitative differences in locomotory, feeding, sexual, parental, and agonistic behaviors between domestic and wild caught fish. He found that courtship and mating behavior were qualitatively similar in domestic and wild paradise fish, with some differences in the quantitative aspects. He also noted that male-female pairings exhibited less aggression during a 10-minute test than either male-male or female-female pairings.

Miller and Hall (1968) presented a detailed quantitative description and causal analysis of courtship and breeding activity in *T. leeri*. Emphasis was placed on bout analysis, with 15 different types of bouts distinguished. They found that bouts initiated by females are more likely to terminate in a clasp or spawning than those initiated by males. Evidence was cited to show that male aggressiveness tended to be slightly higher in most male-initiated bouts. Female butting was interpreted as a signal for sexual readiness with a strong suggestion that it is also used as a self-protection device in the absence of female readiness to spawn. Additional discussion was devoted to the factors that lead to increased courtship activity by the male after the terminal spawning. They also suggested that failure of the female to respond to male courtship was followed by increased male aggression a few hours after spawning.

Additional relevant papers dealing with the reproductive behavior of fishes are: Barlow (1962, 1964), Picciolo (1964), Hall (1966b), Rainwater (1967), Hall and Miller (1968), and Wimmer (1970).

The effect of environmental factors on the activity cycles of fish have been investigated by Allen (1959), Alabaster and Robertson (1961), Davis (1964), Swift (1964), Groot (1965), Kwain and McCrimmon (1967), and Marshall (1967).

CHAPTER II

MATERIALS AND METHODS

This study was conducted in the constant temperature room of the Oklahoma State University Aquatic Biology Laboratory from January, 1965 to January, 1968. Room temperature ranged from 24-27° C. during the course of the study.

Fish Stocks

Fifteen pairs of _T. trichopterus_ and 15 pairs of _M. opercularis_ were maintained during the study. Qualitative descriptions were based on these breeding pairs of fish. Quantitative descriptions during a 64-day period were based on four pair of each species but intermittent observations during a 30 hour period were based on 12 pairs of each species. Fish of both species were originally obtained from aquarium dealers in Oklahoma City and offspring from this stock were used in the study.

Physical Conditions

Glass aquaria were used, ranging in size from 57 x 16.5 x 30 cm. to 61.5 x 23 x 31 cm. with volumes of 28.5 liters (7½ gallons) to 38 liters (10 gallons), respectively. One breeding pair of fish was maintained per tank. To insure uniform quantitative results the fish used in the daily observations as well as the 30-hour intermittent studies were all placed in 28.5 liter tanks.

Each aquarium was provided with a gravel bottom approximately 2-3 cm. deep, a clay pot shelter, a thermostatically controlled heater, and a standard aquarium thermometer. Water temperatures were maintained between 27-29°C. (80-84 F.). Aquatic plants included *Myriophyllum* sp., *Naias* sp., and *Vallisneria* sp.

Lighting was provided by fluorescent reflectors and individual aquarium reflectors with 25 watt incandescent lamps. A 12-hour photoperiod was maintained by means of electric timers. Lights-on period began at 0600 and ended at 1800 hours.

Feeding

Fish were fed daily, usually two hours before the morning observation and shortly after the afternoon observation. *Daphnia*, dried foods, and *Chironomus* larvae were utilized.

Fish Size and Age

All fish were breeding age when paired. Sizes ranged between 5 to 8 centimeters and 3 to 6.5 centimeters, standard length for *T. trichopterus* and *M. opercularis*, respectively. An attempts was made to pair males and females of both species into four categories (see Table I):

1. Large male and large female.
2. Large male and small female.
3. Small male and small female.
4. Small male and large female.

TABLE I

FISH SIZES - STANDARD LENGTH IN CENTIMETERS*

Tank No.	Category	6/26/65	9/2/65
	T. trichopterus		
B2	Small male	5.95	6.55
	Small female	5.55	5.63
B6	Large male	7.64	7.94
	Small female	5.75	5.96
B10	Small male	5.36	6.13
	Large female	6.32	6.35
B17	Large male	6.33	6.44
	Large female	6.24	6.55
	M. opercularis		
P4	Small male	3.76	4.84
	Small female	3.69	4.12
P7	Large male	5.58	5.74
	Small female	5.14	5.18
P8	Small male	3.31	4.53
	Large female	3.59	4.30
P14	Large male	5.90	5.94
	Large female	4.93	5.07

*Centimeter measurements taken with a Helios calipers.

Recording Equipment

Qualitative descriptions of behavior were aided by use of notebooks and prepared data sheets.

Photographic analysis was useful in the qualitative descriptions; a Leica 35 mm. camera, a Bolex 16 mm. movie camera with electric motor, and a Bell and Howell time analysis 16 mm. movie projector were utilized.

Quantitative data were obtained with the use of an Esterline-Angus event recorder and keyboard, Esterline-Angus tape reader, and a time-measurement ruler; the data were transcribed into matrix tables. These tables listed "begin and end time" in seconds for all behaviors during an observation period. The tables were then keypunched for use on an IBM 7040 computer for further analysis.

Observations

Daily observations of each aquarium were made to determine nest size and position, water temperature, spawning time, disposition of eggs or fry, male and female coloration, and behavioral patterns. Quantitative data were obtained with the use of the Esterline-Angus event recorder over a 64-day period from June 30, 1965 to September 1, 1965. The recorder was run at a chart speed of 1½ inches per minute. Quantitative records were taken each morning and afternoon, during the 10-minute observation periods, respectively, for each pair of fish. At the end of an observation period the color pattern, nest size and position, presence of fry or eggs, and water temperature were recorded.

Routine for Analysis

Following a preliminary observation period of several months the relevant behavioral units were determined and seven presumably functional classes of behavior were designated. During this period, qualitative descriptions were initiated which facilitated the recording of the quantitative data that followed. The classes of behavior were set up on the basis of these qualitative descriptions and on their apparent related functions.

In the study of activity cycles, graphs of activity patterns for individual fish, over 30-hour periods, were quite similar. For this reason, an average frequency and duration of behavior for males or females of the same species was calculated for each 10-minute observation period. The absence of spawning activity within several days of the 30-hour periods might partially explain the uniform fluctuations. Therefore, the data could be averaged with some degree of confidence.

To study pre- and post-spawning activity, the daily activity patterns of individuals were again compared. These comparisons revealed that activity patterns for individuals of the same species were usually similar within several days of spawning. Because of this, behavior patterns for all fish were analyzed for an 11-day period, five days before and five days after spawning. Since the curves for individual fish of the same species were similar, the data for each activity were averaged daily for four fish. These figures represent the mean total time spent in performing one particular activity during 20 minutes of daily observation, a combination of the morning and afternoon periods. The time for related activities could then be added together to give total activity in a presumably functional class of behavior. For example, total agonistic activity would include all the time recorded for each of the activities listed under this category (see page 18).

Data for individual motor patterns revealed that some activities occurred infrequently during the observation period. For this reason, quantitative analysis of these activities was not always possible. Other behaviors slightly more frequent were placed with their functional groups of behavior and summed as total group activity. For the more common activities, graphs of both individual and summed activity patterns were analyzed.

Each recording period was divided into its respective number of seconds (e.g. 600 seconds). Frequency was recorded simply as the number of times a particular behavioral event occurred during the observation period. Duration was recorded as the total number of seconds utilized for that particular behavior. An average duration per behavioral unit was obtained by dividing the total duration by the total frequency for any observation period. Time was recorded in seconds.

The frequency of expiration of bubbles during surface and subsurface blowing was also measured. Inspirations during surface blowing were not measured since it was impossible to determine before hand whether bubble blowing was to follow. In many instances, numerous inspirations occurred without bubble blowing. Miller (1964) states that T. trichopterus inspire 1-40 times prior to bubble blowing.

CHAPTER III

BEHAVIORAL DESCRIPTION AND TERMS USED IN THE STUDY

Motor patterns for Anabantoid fishes have been described in detail by Forselius (1957), Miller (1964), Hall (1966a), Ward (1966), and Rainwater (1967).

The descriptions that follow characterize the observed behavior patterns and point out the differences and similarities between the species studied. These descriptions serve as the basis for the subsequent quantitative analysis of *T. trichopterus* and *M. opercularis*.

During a 64-day period, June 30 to September 1, 1965, 38 motor patterns were monitored and tallied with an event recorder. As a matter of convenience, seven functional classes of behavior have been designated under which 29 of the 38 motor patterns are described. The functional classes of behavior are: patrolling, maintenance behavior, comfort movements, agonistic activity, migratory behavior, courtship and spawning behavior, and parental behavior. These categories are also useful in organizing the data for graphs of both the individual motor patterns and the summed functional group activities.

Patrolling

Interspersed between the performance of any two activities are periods when the dominant fish (usually the male) swims slowly around the tank. By definition, during this period there is no observable interaction between the male and female.

Patrolling is similar to the "patrolling maneuvers" of Anabantid fishes, described by Forselius (1957), who states that after guarding the nest for a while, a male begins to swim around his territory and, if no other fish is encountered, he returns to the nest. The swimming movements apparently are undirected and the patrols are repeated at fairly regular intervals.

During patrolling activity slow forward movement is maintained by constant beating of the pectoral fins, and rapid movement by lateral undulations of the body. In *T. trichopterus*, the dorsal fin and pelvic fins are partially or completely folded and adducted; the anal fin and the caudal fin may be partially extended or adducted. The caudal fin may be undulated slightly during turning maneuvers. In *M. opercularis* the median and pelvic fins are partially or fully appressed. Occasionally the drooping and partially extended caudal fin is undulated and moves from side to side. More frequently, the caudal fin is completely folded and forms a long narrow point. In both species, body orientation while swimming may be parallel or at varying angles to the surface.

Maintenance Behavior

The activities described as maintenance behavior are those concerned with the vital functions and day-to-day needs of the individual.

Inspiration

Both T. trichopterus and M. opercularis possess a labyrinth, an accessory respiratory organ characteristic of the family Belontiidae (Liem, 1963). The labyrinth is an adaptation to the shallow, stagnant, oxygen depleted waters of southeastern Asia in which they live. Inspiration or air gulping seems to be the predominant method for obtaining oxygen, although Hadley (1965) and Ward (1966) have shown that T. trichopterus and M. opercularis can survive without surfacing to gulp air for at least 173 and 96 hours, respectively, in water saturated with oxygen. Ward (1966) concludes that the frequency of air gulping appears to be directly related to water temperature and activity, and inversely related to age. Younger fish gulp air more frequently.

The term inspiration means a period during which a fish obtained atmospheric oxygen by surfacing, consisting of one too many gulps of air. No quantitative distinction was made between a single air gulp and continued gulping of air for extended periods, as is common in T. trichopterus; both cases were considered one inspiration and measured in terms of its duration. The number of inspirations during an observation period was tallied as the frequency.

Both the blue gourami and paradise fish take air into the labyrinth by swimming up to the air-water interface, and with the snout protruding 1-3 mm. above the water surface expel old air and take in a fresh supply. In T. trichopterus inspiration can take place while slowly swimming or in a stationary position; extended inspirations occur during the nestbuilding phase and last up to 130 seconds. Occasionally, gas bubbles pass out beneath the opercula as the fish leaves the surface.

In contrast to T. trichopterus, a stationary position is usually maintained by M. opercularis, but the fish may break the surface several times in rapid succession. Usually, the inspirations last one to two seconds; rarely more than nine seconds, and gas bubbles frequently escape from under the opercula.

When frightened, both species spend less time inspiring at the surface than normally. A submissive female, for example, spends most of her time hiding, leaving for only a few seconds to dart to the surface, inspire, and return to shelter. Ward (1966) suggests this would probably have adaptive value in the presence of surface predators.

Feeding

Both the blue gourami and paradise fish ingest dry and live food from the surface and intermediate depths, as well as from the gravel bottoms of the aquaria. Living food is preferred by both species. Surface feeding is most frequent when dry food is introduced.

Both species have similar feeding habits and postures. T. trichopterus, however, does show one form of surface feeding not observed in M. opercularis. Essentially, the fish maintains a stationary position while the mouth is opened and closed rapidly, approximately two times per second, sucking the food into the mouth. Usually, stationary surface feeding occurs first, and as the surface food disperses, is followed by food gulping. When swimming slowly at approximately 45° to the surface, the blue gourami maintains surface contact with the mouth, rapidly opening and closing the maxillaries about individual food particles. The dorsal and anal fins are partially erect and the caudal fin may be extended or partially drooping. Occasionally, the pelvic fins are rapidly extended forward and backward, in a lashing movement.

In subsurface feeding, *T. trichopterus* ingests food at varying body orientations. When feeding on *Daphnia*, young fish cautiously approach them with their pelvic fins thrust forward; however, adult or experienced fish appear to approach the *Daphnia* with deliberate dashing movements with their pelvic fins trailing. Occasionally, after repeated maxillary movement, the ingested material is spit out and reingested; this may occur several times and is commonly observed in both species.

M. opercularis frequently gulps air and food particles simultaneously when surface feeding, while passing gas bubbles out beneath the opercula. The mouth protrudes slightly above the surface and the pectoral fins beat rapidly to maintain the body position at 30 to 45 degrees to the surface. The median fins are partially erected while the pelvic fins are extended ventro-anteriorly. Usually, after ingesting a food particle at the surface, *M. opercularis* drops two to five cm. below the water's surface. This contrasts with the feeding pattern usually observed for mature *T. trichopterus*, which frequently maintains surface contact for 5 to 50 seconds, if undisturbed. However, young fish appear to gulp food and then back away from the surface, one cm. or less.

When feeding on *Daphnia* near the surface, *M. opercularis* moves forward rapidly, stops, and ingests the prey. When feeding on *Daphnia* near the bottom, the body may assume angles of 30-180 degrees to the bottom. Frequently, the anal and caudal fins are folded while the dorsal fin is partically erected when engulfing the food. Considerable time is spent in searching the bottom debris; any small moving organisms are immediately ingested. Plant parts and gravel are occasionally nipped. Most often (than not) the orientation when searching in this manner is almost vertical. Occasionally young fry are chased but few ingestions have been observed.

Resting

Blue gouramis and paradise fish maintain a stationary position which usually lasts for more than five seconds with a range of 1 to 300 seconds. Maximum durations up to 300 seconds were recorded at night.

During the day, T. trichopterus is most frequently observed in a stationary position 13-25 cm. from the aquarium bottom; however, submissive males and females occasionally hide under pot shelters or rest in dark corners along the gravel bottom. At night, a bottom resting location is more common.

While remaining stationary at intermediate depths, the body axis is parallel with the water's surface. The median fins are partially erected and the pectoral fins are beating rapidly. The pelvic fins are variously positioned from directly forward to extending laterally or adducted.

When resting on the bottom the median fins are partially folded, the pectoral fins are extended to provide support, and the pelvic fins are adducted. Occasionally the pelvic fins are abducted ventrally, forming an inverted V and providing support for the body and raising it approximately 1½ cm. above bottom.

With the approach of a female, a resting male will usually give a lateral display while maintaining his resting position; occasionally the male will approach the female or chase her if she flees. If a resting male is very close to the surface he frequently gulps air without changing his position.

M. opercularis rests frequently between activities. In general, it rests more often and for longer periods than *T. trichopterus*; the duration of one resting period ranges from 1-300 seconds with an average duration of 50 seconds. In contrast, *T. trichopterus*' resting ranges from 1-128 seconds, with an average duration of 30-35 seconds.

M. opercularis frequently rests on the leaves of aquatic plants in the upper half of the tank. If resting near the surface the body axis is parallel to the surface but tilts slightly upwards when a bubble of air is needed. Occasionally a fish near the surface will rise slowly several centimeters toward the surface to inspire with no perceptible fin movements. Infrequently, a paradise fish will passively sink to the bottom with no accompanying fin movements. On the bottom a slight lateral tilting is noted unless the fish is braced by the wall of the aquarium or plants, etc. Fin positions are similar to the fin positions of bottom resting *T. trichopterus*.

Resting *M. opercularis* males will usually exhibit a lateral display sometimes accompanied by an opercular spread when approached by a female; the interaction may lead to an abbreviated circling bout and either break off or continue into a male butt and chase. After a bout of nestbuilding a male frequently posts himself beneath the nest for several seconds.

Comfort Movements

The motor patterns described as comfort movements appear to remove a temporary discomfort suffered by the fish. Usually a particular body part or area is affected. Baerends and Baerends-Van Roon (1950) state that all comfort movements have one common feature: before the movement is carried out the animal is restless, but after it, the fish appears to feel more comfortable.

Yawning

This activity often occurs for one or two seconds after long bouts of bubble-blowing or aggressive encounters. The jaws are opened widely and extended maximally; the median fins are partially extended and the pelvic fins abducted anteriorly. The motor pattern appears similar in the two species.

Chafing

Chafing is the deliberate brushing of the body against some object. The first noticeable sign of imminent chafing activity is a slight increase in fluttering of the pectoral fins and an apparent visual fixation on a chafing object. The fish will then slowly approach the plant, thermometer, pot shelter, or other object. Several millimeters from the object the fish will simultaneously fold the fins, accelerate, and tilt the body laterally, either toward or away from the object, so that the body wall brushes against it. Frequently, several chafes (two to five) are performed in quick succession especially after a prolonged male-female aggressive encounter.

Flexing

Flexing resembles a male spawning reflex lasting one to two seconds. In both *T. trichopterus* and *M. opercularis* the head and tail are bent into a U-shape without a female in the embrace. Median fins are partially folded. On one occasion a *M. opercularis* male performed a flexing movement followed by swimming inhibition and a spawning roll. Flexing behavior is more frequent several days before or after spawning in both species. In a few instances isolated males were observed exhibiting flexing behavior.

Ward (1966) observed flexing in nestposting *M. opercularis* male fish during mating. He suggested the behavior appeared to be an "overflow activity" where a highly activated male apparently responded to a sub-optimal stimulus. Evidently, a sight of a female can act as the stimulus.

Agonistic Activity

The blue gourami and paradise fish exhibit patterns of agonistic activity which differ mostly in detail. In a few instances, a particular motor pattern is missing in one species. Several agonistic patterns serve in courtship bouts as well as territorial disputes. Much of the agonistic activity in both forms is quite stereotyped, and was recorded in the following categories.

Approach

Approach includes cases occurring during courtship and agonistic interactions. An approach usually consists of one fish swimming directly toward another, in either an exploratory or seemingly aggressive manner; a mutual approach occurs occasionally. Approach speed apparently depends upon many factors: the size and familiarity with the mate, the position of both fish relative to the nest site, the state of reproductive readiness of both fish, etc. Usually, a slow cautious approach is noted but rapid approaches are common during territorial defense by the male and courtship advances by the female.

During social encounters some distance from the nest site, _T. trichopterus_ and _M. opercularis_ females may swim by the male slowly and evoke little or no reaction. Usually, the median fins are partially folded, and the pelvic fins trailing; the pectoral fins beat slowly providing the major propulsive force. This is typical when either partner is patrolling or feeding. A slow approach is also executed when either partner approaches the other and ingests an extending fecal plug.

During agonistic encounters _T. trichopterus_ usually approach each other slowly with the pelvic fins flicking rapidly anteriorly and laterally, with varying degrees of lateral display and the caudal fin spread. When rapidly approaching, the dorsal and pelvic fins are adducted and the anal and caudal fins relaxed, while the pectoral fins and body undulations provide the propulsive force. Spawning females will swiftly approach a male under the nest and immediately butt him several times on the caudal peduncle; he usually responds by rubbing (see below).

During courtship and some aggressive interactions, _M. opercularis_ make a slow cautious approach. A variety of body and fin modifications occur; e.g., median fin erection, opercular erection, S-shaping, and extension of pelvic fins. During a rapid approach, the dorsal and anal fins are adducted and frequent halts are common followed by a lateral display.

Both species show horizontal orientation during the approach; but with _M. opercularis_ it can range from a slight head up position to an almost vertical approach by the female, called tail wagging. On other occasions lateral tilting away from the partner at an angle of 45 degrees serves as a submissive posture while approaching.

Lateral Display

A lateral display basically consists of median fin erection, and is frequently performed during an approach. It is the predominant display during courtship and aggressive encounters in both the blue gourami and paradise fish.

During courtship the male may be oriented at any angle to the female, but usually is directly in front of her or parallel to her (Miller, 1964). During prolonged and intense displays the male becomes quite dark.

In both species, the median fins may be partially to fully extended. In _T. trichopterus_, the caudal fin droops slightly in low intensity displays, but is curved upward with the caudal peduncle during intense displays, making the fish appear bowed in the middle (Miller, 1964). The pelvic fins are usually brought forward and occasionally are positioned laterally and moving rapidly.

During low intensity displays, _M. opercularis_ partially extends the median fins, and this often occurs when the female takes a lateral oblique appeasing posture. If the display is intense, the median fins are fully extended, the pelvic fins are extended ventro-anteriorly and occasionally laterally so that a wider inverted V is formed. The body axis is usually tilted slightly upward.

At maximum intensity, the lateral display in both species is modified so that the body is curved laterally into an S-shape (sigmoid) curve. The display often develops into other activities such as tail beating, biting or butting, though these may occur simultaneously with the lateral spread (Miller, 1964).

In pairs of *M. opercularis*, when the two fish are swimming parallel, an aggressive or courting male will give an intense lateral display, usually form its body into a sigmoid posture and vibrate. This may last for a few seconds and the male will then reverse his orientation, head-to-tail, and continue his display for as much as eight seconds; the female will usually respond in a similar manner.

During the descriptive phase of the study, the durations of low and maximum intensity lateral displays were measured. However, during the quantitative phase, all intensities were recorded under the one type.

Opercular Erection

This display consists of extending the branchiostegal membranes and the gill covers maximally. It is commonly observed during a frontal display or lateral spread display in *M. opercularis* but is very rare in *T. trichopterus*. A displaying male may be in front of or face the female. During a frontal display, the opercular erection is maximal and the median fins may or may not be extended. Lateral displays frequently include opercular erection; a mutual display is common when neither partner is completely dominant. Opercular erection in female *M. opercularis* is less pronounced and infrequent.

Opercular ocelli are well developed in *M. opercularis* and attacks are commonly directed at the side of the head near them. A frontal display with opercular erection is often followed by an attack while lateral display is not (Hall, 1966a).

Body Vibrating

During this study, body vibrating has been observed only in *M. opercularis*. Forselius (1957) defined it as a spasmodic vibration that pervades the whole fish body from head to caudal fin. It occurs (in both partners) as a mutual threat and may be repeated several times in succession.

A pair maintains parallel orientation while their bodies are in an S-shape, head-to-tail position. A mutual lateral display ends with a rapid beating of the pectoral fins of each fish and a body vibration. Maintaining a head-to-tail position, the two fish turn 90 to 180 degrees while vibrating, so that the head of each fish is moving toward the tail of the other fish (Ward, 1966). Since body vibrating occurred during the period of the lateral display, they were recorded together.

Butting and Biting

Butting is a strong thrust of the lips against the opponent's body without the grasping attempts of biting. It seems to be a milder form of aggression than biting. Biting begins with the mouth open; if the other fish remains stationary or cannot successfully flee, the attacker grasps the body or fin with its teeth, sometimes even shaking its head while biting (Miller, 1964). Butting and biting are frequently indistinguishable and were recorded together.

Median fins are fully erected during butting or biting. Butting and biting frequently develop into chasing, although appeasement postures sometimes inhibit further attack.

Female butting and biting occur mainly during courtship encounters. Typically, a *T. trichopterus* female darts from a shelter up to the male under the nest and butts him sharply on the side or caudal peduncle for 3-10 seconds (Miller, 1964). This seems to inhibit male attack and frequently is followed by male rubbing. During the courtship of *M. opercularis* the female butts the male for only one to two seconds; the male responds by curving, an invitation posture.

Mouth Fighting

During a bout of mouth fighting, the two fishes approach each other face to face; the median and caudal fins are maximally spread. In *T. trichopterus*, the pelvic fins are moving rapidly during the encounter, and in *M. opercularis* they are extended downward.

Frequently, the two fish approach each other slowly using only the pectoral fins to advance; then open the mouth and attempt to bite and hold the antagonist's lips (mouth-locking; sensu Forselius, 1947). Simultaneously, the caudal part of the body undulates violently while trying to drag the opponent backward.

Mouth fighting was observed in both the blue gourami and paradise fish, most frequently when the male and female were equally aggressive or when the female was slightly larger than the male.

Mouth locking did not exceed 39 and 14 seconds for *T. trichopterus* and *M. opercularis*, respectively. Ward (1966) reported that jaw locks for *M. opercularis* did not usually exceed one to two minutes and occasionally lasted nine minutes.

Chasing

Chasing involves fleeing of one fish with another in pursuit, usually biting or attempting to bite the subordinate. The fleeing fish usually swims away from the attacker at moderate to high speed with fins folded. Male chasing is common in both aggressive and aborted courtship encounters. In *T. trichopterus*, it occurs after spawning when the female recovers from swimming inhibition and swims slowly away from the nest. Chases may be brief or prolonged, single or repeated (Hall, 1966a). Females of both species have been observed chasing males in aggressive encounters. In one instance a female *T. trichopterus* chased a male continuously for 46 seconds butting him several times during the chase.

During a slow chase, pursuing *T. trichopterus* and *M. opercularis* may exhibit a lateral display. While fleeing, *T. trichopterus* frequently maintained a partial median fin erection; fleeing *M. opercularis* usually did not and the caudal fin was also folded forming a long posterior point. During rapid chases, the fins of the pursuer and pursued of both species were folded.

Appeasement Posturing

Both sexes of blue gouramis and paradise fish exhibit appeasement postures. It is most often seen in females being harassed by males, but subordinate males may also show it. Median fins are folded, the caudal fin often droops, and the fish often tilts laterally. Sometimes the head or tail is elevated. Appeasement appears to be only mildly successful in inhibiting male aggression. Lateral and vertical appeasement are commonly seen in *M. opercularis* females while approaching males under the nest (Hall, 1966a).

Migratory Behavior

Migratory behavior is observed in both *T. trichopterus* and *M. opercularis* males and females. The males tend to exhibit this behavior more frequently, probably because their territory includes most of the aquarium. The motor patterns are similar in both species. The fish swims incessantly, often for more than 30 minutes, up and down near the sides of the aquarium. The median fins are folded and the pelvic fins trail. The movements are jerky and the fish stays in the bottom half or intermediate depths of water (Forselius, 1957). The behavior is reminiscent of the pacing back and forth of caged cats.

Forselius (1957) suggests that this behavior can only be interpreted as a manifestation of spawning migration, not as a searching for a mate. However, within the confines of an aquarium, the increased movement of the males does appear to attract the female. If she is in spawning condition, she more frequently approaches the male during his fluttering movements. Sevenster (1961) terms this behavior "fluttering" and interprets it as migratory behavior in three-spined sticklebacks. Citing Van Iersel (1953), Sevenster (1961) states that non-reproductive males (e.g., in winter) do not flutter in such a persistent way, unless they have been treated with testosterone propionate. Sevenster, therefore, regards fluttering as the first indication of reproductive motivation. He states that within a few hours it was gradually replaced by fighting followed by the assumption of dominance by one of two males in a tank.

Migratory behavior may be interrupted by inspiration for one or two seconds or short periods of bottom feeding. A male may show migratory behavior without being influenced by any activities or movements on the part of the female, who frequently is in hiding. On occasion, a female will approach a fluttering male who responds with a lateral display and continues his fluttering movements. If the female is more aggressive and begins to butt, the male flees.

Courtship and Spawning Behavior

During early courtship, a number of displays may be utilized by both sexes. A few of these displays include elements of aggressive behavior; e.g., lateral display and opercular erection by the male, and female courtship butting in _T. trichopterus_. Descriptions of these aggressive elements are given in the preceding section.

The motor patterns included under this section normally occur only during the sexual encounters of a spawning bout. Ethograms of courtship and spawning activities are given in Hall (1966a, 1966b, 1968), and Hall and Miller (1966). Courtship frequently begins with the male making a slow cautious approach toward the female, or occasionally a female will approach the male. In either case, the male will present a lateral display, usually at right angles to the longitudinal axis of her body.

The following descriptions roughly approximate the courtship and spawning sequences. Additional details on courtship and spawning patterns are discussed by Miller (1964), Hall (1966a), Ward (1966), and Hall and Miller (1968).

Leading-to-the-Nest

This behavior is observed in males of both species. It commonly occurs in early phases of a spawning sequence and occasionally in post-spawning males. The male approaches the female, gives a lateral spread, then turns and slowly swims back to the nest, with the body in a sigmoid curve and the fins maximally erected. Leading may take the form of a series of halts and advances toward the nest. A male may stop, back up, then turn and swim toward the female to begin again. If the female is sexually responsive she may follow the male to the nest where other courtship activities ensue. *T. trichopterus* males occasionally drive the females to the nest by swimming beside her maintaining a full lateral spread display and pushing her with head and body toward the nest (Miller, 1964). Driving-to-the-nest was not observed in *M. opercularis*.

Tail-Wagging

Tail-wagging is commonly performed by *M. opercularis* females as a distinct part of the coursthip repertoire. During this study, males were not observed performing this activity, but Hall (1966a) states that inferior males may exhibit the preliminary J-shape pattern. Tail-wagging is not performed by *T. trichopterus* males or females.

Typically, tail-wagging begins as a J-shape appeasement posture when the female approaches the male. The longitudinal axis of the female's body is perpendicular to the bottom of the tank with the head pointing upward. Flexure of the caudal fin and caudal peduncle results in a distinct J-shape which is usually maintained for one to two seconds. This develops quickly into tail-wagging. It consists of low frequency undulating movements of the caudal fin with the caudal peduncle of the fish in a vertical or near vertical position. Tail wagging resembles tail beating, an aggressive behavior, except that the body is oriented differently and the frequency of undulation is lower (Hall, 1966a).

Tail wagging in young females appears to be more frequent and more pronounced, and undulations of the caudal peduncle seem to have greater amplitude. A tail-wagging female may approach a male leading with her lateral, dorsal, or ventral body wall; her orientation is almost perpendicular with the bottom (75-90 degrees). The pectoral fins beat rapidly, the pelvic fins are maximally extended, and the dorsal and caudal fins are partially extended. The caudal peduncle undulates rapidly, providing the main propelling force.

When the female first approaches the male she may butt him at the pelvic fin insertion and then one or two times on the midbody in line with the anterior end of the dorsal fin.

Rubbing

Rubbing occurs only in *T. trichopterus*. Frequently, when the male is under the nest, nestposting or during bubble blowing, the female approaches him swiftly and butts him several times. The male then drops down under her breast and slowly rocks back and forth for 5-130 seconds. Usually, the two fish face the same direction, but infrequently the body axis of the male is at an angle to that of the female. The dorsal fin of the male is completely depressed, and usually brushes against the breast and belly of the female. His anal fin is partly or fully spread and the pelvic rays extend forward and outward 130-180 degrees. The dorsal fin of the female is partially folded, while her anal fin is spread wide and her pelvic fins are held diagonally backwards (Miller, 1964).

During rubbing the male is darkly colored. If rubbing is interrupted and broken off, he will chase and butt the female repeatedly until she reaches cover; when he returns to the nest he is usually paler in color.

Circling, Clasping, Spawning Roll, and Egg Emission

In *T. trichopterus*, after a prolonged bout of rubbing, the male curves his body and swims in a circle. The female remains roughly perpendicular to the male in the center of the circle, with her snout above his dorsum, just anterior to the origin of the dorsal fin. As the male circles, his body curves more tightly into a U-shaped flexure, and the female places herself against his side with her head protruding beyond his back. If these movements are carried out properly, the male then clasps the female tightly. The anal fins of both fish and the caudal fin of the female begin to vibrate. This vibration continues as the female bends her caudal peduncle upward and the clasped pair roll over so that her vent is directed upward. Both fish then shake violently as the gametes are released (Miller, 1964).

Little or no circling is evident in *M. opercularis*. During a preliminary bout a pair may orient in a head-to-tail fashion and perform a mutual lateral display ending with a vibration. A ripe female will usually approach the male directly and at right angles and butt him along the lateral line. The male then forms his body into a U-shape, with his head and tail pointing toward the female. Median fins are partially spread. The female enters the U-shape fold of the male as he tightens his grip and both fish beat their pectoral fins rapidly. Median fins of the female are folded. The two fish then roll over slowly and release the gametes. Egg emission, in both species, most frequently occurs just below the male's nest. The eggs may be ejected into the nest, or more commonly they float upwards into it. After release of the eggs and sperm, both fish appear immobile, and sink towards the bottom.

Swimming Inhibition

Swimming inhibition is a trance-like state occurring in both species immediately after spawning and pseudospawning bouts. After the male loosens the clasp both the male and female lose their orientation to one another and are relatively immobile for 2-13 seconds. They both may sink far below the nest before recovering. The female of both species tends to recover first, and in *T. trichopterus* swimming inhibition often ends abruptly with the female fleeing and male chasing. The male quickly returns to the nest and begins egg retrieval. In *M. opercularis* the female often remains and aids in nest-care and egg retrieval (Hall, 1966a).

Parental Behavior

A strict definition of parental behavior would include any behavior elements or patterns that begin just after fertilization of the eggs and end when the parents no longer retrieve or defend the young. However, nestbuilding activities do occur before spawning. Bubble blowing commonly precedes courtship and appears to attract the female. This behavior is intimately involved in the survival of the eggs and fry. The incorporation of early nestbuilding in this section provides the opportunity for an interesting comparison of pre- and post-spawning events.

Parental care begins with the collection of the eggs by the male after spawning. The eggs are mouthed then spit into the nest. A great deal of time is spent in rearranging the nest, blowing new bubbles, mouthing and retrieving the eggs, and defense of the nesting site. In addition, the male positions himself just below the nest and appears to create a current of water across the bottom surface of the nest. Nest care continues for approximately four to seven days. During this time, the fry are continuously retrieved and returned to the nest, and eventually the male loses all interest in the nest and fry.

Bubble Blowing

Most anabantoid fishes build bubble nests as reported by Braddock and Braddock (1959), Forselius (1957), Hall (1966a), Miller (1964), Pal and Southwick (1966), Smith (1945), and Ward (1966).

In *T. trichopterus*, only the male constructs a bubble nest, whereas both sexes of *M. opercularis* build a nest. Usually if a nest is constructed by the female it is small and apparently non-functional. Occasionally, the female will help the male build the functional nest. However, if the male is removed from the tank, the female will actually maintain the nest and care for the fry.

Two major patterns of nestbuilding were: Surface bubble blowing and subsurface bubble blowing. In addition, jetting and opercular emission of bubbles were infrequently noted. Surface bubble blowing was only performed by male *T. trichopterus*; it commonly occurred throughout the spawning cycle. Subsurface bubble blowing was performed by the males of both species and the female *M. opercularis*. In *T. trichopterus* males, subsurface blowing commonly occurred the day of spawning and as a frequent postspawning activity.

In *M. opercularis* males subsurface blowing occurred throughout the spawning cycle and on the spawning day. Surface blowing tends to form shallow, extensive nests, whereas subsurface blowing tends to form deeper and more concentrated nests.

When blowing surface bubbles, the male *T. trichopterus* usually circles actively beneath the nest, with snout up and body at about a 30 to 45 degree angle with the surface. The dorsal fin is depressed partially against the body with the rayed portion loosely spread but not extending above the surface. During a female approach, a lateral display can be maintained while nestbuilding. Alternate strokes of the pectoral fins and movements of the upper part of the caudal fin maintain the fish in one spot. Position changes are affected by combined action of the caudal and pectoral fins. The pelvic fins hang downward at approximately a 30 degree angle away from the body. The anal fin is relaxed. Infrequently, the male will hover at the surface with his mouth protruding from the water and gulp in air up to several minutes, close his mouth and then spew out a cluster of bubbles. This method is used frequently to produce a bubble nest that consists of a single layer of bubbles or scattered clusters of bubbles.

During subsurface blowing, the male surfaces, gulps air from 1 to 40 times, and then drops below the surface (or nest) about three centimeters. As the male backs away from the surface the pelvic fins swing forward and he usually makes a quarter turn either clockwise or counterclockwise. While in a horizontal position, he releases bubbles from the mouth. When the bubbles are released the caudal peduncle swings upward. Bubbles from under the gill covers often occur at the end of a series of bubble-blowing movements at the surface and most commonly after the nest has been deepened (Miller, 1964). Nests are usually constructed in corners or along the sides of the tank; vegetation is not actively incorporated into nests.

As previously mentioned, both male and female M. opercularis construct a bubble nest by releasing bubbles below the surface. The male alternates between periods of nestbuilding and patrolling, occasionally approaching the female. When bubble blowing, the male gulps air at the surface, his body oriented at a 75 degree angle. As the mouth protrudes above the surface it is opened and the opercular flap is quickly opened twice per air gulp. Backing away from the surface two to four centimeters in an almost vertical position, the male makes a quarter turn and releases bubbles into the nest. Gulps of air are made at the edge of the nest and released near its center; this tends to deepen the nest. Occasionally, streams of bubbles are emitted from under the gill covers after the nest has deepened. Usually, the partially erected caudal and dorsal fins undulate noticeably. The pelvic fins rotate forward during inspiration. The pectoral fins beat rapidly during inspiration in concert with undulations of the caudal fin. The quarter turns are accomplished with alternate beating of the pectoral fins.

The female appears to build nests in a similar manner; her nests are not as large and are usually more diffuse. Several hours before spawning, the female may begin to blow bubbles near the male's nest. This activity is usually followed by tail wagging, by the female, apparently in an attempt to approach the male under the nest.

Most male nests are placed in a corner or side of the tank. Occasionally, vegetation serves as a matrix for the nest, but nests entirely devoid of vegetation are also constructed.

Jetting

This behavior is usually performed by post-spawning males of both species, when a stream of air and water is shot through the nest. It appears to aerate the eggs and fry in the frothy nest. Ward (1966) states that eggs are sucked in and then forced outward into the nest with the stream of water. During this investigation, no eggs were observed ejected into the nest during jetting.

In a few instances, *T. trichopterus* males were observed jetting without a nest or eggs present; however, jetting was more frequently observed when eggs were in the nest or between periods of nestbuilding just prior to spawning.

In *M. opercularis* males, jetting is interspersed between subsurface blowing and mouthing of eggs in the nest. It is performed both in the center and along the edges of the nest from one to three times in rapid succession, two to five seconds apart, with each jetting lasting one to two seconds. In an almost vertical position, the snout extends into the nest, and after two convulsive gulps of air a rather steady stream of water shoots upward at least two to five centimeters.

Nestpushing

Nestpushing is performed by the males of both species at almost right angles to the surface; it consists of forceful butts with the snout, penetrating into the nest. The median fins are partially or completely folded with the pectorals beating rapidly.

Forselius (1957) suggests this behavior facilitates oxygen diffusion from the air to the eggs and fry at the bottom of the nest.

Retrieving

Eggs are retrieved and deposited in the nest after each spawning bout; this activity continues until most of the eggs are collected. Dislodged eggs and fry are constantly returned to the nest.

In *T. trichopterus*, only the male returns eggs or fry to the nest. After spawning the male spends much time sucking eggs into his mouth and blowing them into the nest, often with some bubbles. There is a tendency to retrieve eggs and young that have drifted away from the nest. Some males have been observed retrieving eggs from one part of the nest and placing them in another (Miller, 1964). As the fry become large enough to swim actively, the retrieving movements of the male gradually diminish. Six to eight days after hatching, the male apparently loses active interest in retrieving the fry. Occasionally, males were observed chasing fry, returning to the nest site, and ejecting the non-existing fry 15 to 30 days after hatching. Many males were seen chasing fry 20 days after hatching, but only a few were successful in catching and eating them.

Both male and female *M. opercularis* retrieve eggs after spawning. The female apparently carries the eggs to the periphery of the nest and the male retrieves them from this position. Occasionally, a female will retrieve fry two to three days old and place them near the edge of the nest. Following most spawning sequences, the female will approach the male under the nest, in a tail-wagging display, and retrieve one to five eggs and deposit them at the nest periphery. After retrieving and ejecting the eggs into the nest the male occasionally chases the female away. The male commonly releases 1 to 10 eggs approximately two centimeters below the nest after retrieval. The number of retrieves varies considerably. On the spawning day, males have been observed retrieving eggs 18 to 23 times per minute. Following spawning, the male commonly bites off clusters of eggs in the nest, mouths them repeatedly, and replaces them in the nest.

Retrieval of eggs or fry is usually performed at an 80 degree angle to the surface. The pectoral fins beat rapidly, while the partially folded dorsal and caudal fins undulate. The anal fin hangs downward and the pelvic threads are folded.

Attacking Snails

Snails are frequently observed gliding on or near the nests of both the blue gourami and paradise fish. The response of both species to the snails is the same: immediate attack. These attacks occur frequently during periods of intense nestbuilding and one to three days preceding and following spawnings. Attacks are infrequently noted at other times. Only the males were observed attacking snails.

In *T. trichopterus*, the male swims directly toward a snail near the nest and with the mouth open delivers several strong thrusts. The snail usually drops to the bottom of the tank, frequently followed by the male. At this point the male swims away. On one occasion, a dark nestbuilding male attacked a snail near the nest. It held the snail in its mouth for five seconds while shaking its head violently from side to side; the snail then fell to the bottom and was ignored.

M. opercularis males usually approach a snail cautiously, observing it for several seconds before attacking in a similar manner.

Terms

Bout. A social interaction between a male and female; it may contain any number or combination of activities described (Hall and Miller, 1968).

Pseudospawning Bout. A pseudospawning bout refers to a series of male-female sexual encounters, similar in form to a spawning bout, but differing in that one or both partners fail to release gametes. It includes clasping, the spawning roll, and swimming inhibition.

Spawning Bout. A spawning bout refers to the series of male-female sexual encounters which lead to the extrusion of gametes by both partners. It is concluded with aggressive male behavior; e.g., butting or chasing just after swimming inhibition (Hall and Miller, 1968). This is similar to the "spawning cycle" of Forselius (1957).

Spawning Sequence. This refers to the complete series of male-female interactions (bouts) comprising prespawning, spawning, and post-spawning activities (Miller, 1964; Miller and Hall, 1968). These sequences are of variable duration, but usually last two to five hours. These are comparable to "mating cycles" of Forselius (1957).

Spawning Interval or Cycle. The time elapsed between two spawning sequences. It can be as little as two days but frequently more than 10 days.

CHAPTER IV

REPRODUCTIVE FACTORS

Under certain conditions, _T. trichopterus_ and _M. opercularis_ males are able to spawn every few days. According to Mathis (1940), _Betta splendens_ males exhibit similar spawning intervals. Van Iersel (1953) reports that after several fertilizations, _Gasterosteus aculeatus_ males have a recovery period of several days in which there is a decrease in sexual responsiveness. This decrease appears to be directly influenced by fertilization and the onset of fanning. Hall (1966a) found that _T. leeri_ males spawn every few days for approximately a month, then enter a period of dormancy for several weeks or months.

Spawning Intervals

The data collected during this study indicate a somewhat different pattern. Several times males spawned a few days apart followed by periods of no spawning. More frequently, however, spawning intervals were longer than 11 days.

In one instance, a _T. trichopterus_ male spawned with a female on 19 and 21 July 1965. During the next 26 days, a nest was sporadically maintained by the male until 16 August, when they spawned again. In another case, a male spawned on August 12, 1965 and maintained a nest almost up to the time of the next spawning on August 29, 1965. Similar examples were observed for _M. opercularis_.

It seems likely that T. trichopterus and M. opercularis males are physiologically capable of spawning every two or three days for short periods of time. The capacity for successive spawnings could be adaptive, especially if the original clutch of eggs is destroyed or infertile. In a few instances, the parents consumed the eggs and then spawned again within a few days. Longer intervals may be adaptive in that they permit the male to maintain uninterrupted nest care. Since nest care and retrieval do not last more than 7-10 days past spawning, and more frequently 5-7 days, the length of spawning intervals may be largely determined by the spawning readiness of the female (Tables XV and XVII, Appendix).

Table XV in the Appendix lists the intervals between spawning sequences in T. trichopterus females. It shows that "short" intervals between successive spawning sequences were followed by "longer" intervals and vice versa. Thus, following spawning intervals of 2, 11, and 17 days, the succeeding intervals increased to 26, 41, and 24 days, respectively. Whereas spawning intervals of 26, 37, and 64 days were followed by substantially shorter intervals of 8, 22, and 21 days, respectively. In addition, intervals of at least 11 days were recorded for four of five females observed. Hall (1966a) recorded spawning intervals of at least 10 days for five of eight T. leeri females observed.

These data lend support to the hypothesis that T. trichopterus females may undergo a period of gonadal recrudescence following a spawning sequence. A minimum spawning interval of two to four days may be essential. Barlow (1964) reported that a female Badis badis was able to spawn every seventh day with a minimum of about four days. Hall

(1966a) found that after numerous spawning sequences (as many as 6 in 26 days by one female), *T. leeri* females undergo a "rest period" or period of rejuvenation.

The mean average spawning interval for *T. trichopterus* was 21.2 days (Table XV, Appendix) and the mean average spawning interval for *T. leeri* was 7.1 days (Hall, 1966a). No spawnings were recorded during the months of May, October, and November (Table XVI, Appendix).

Spawning intervals for *M. opercularis* females (Table XVII, Appendix) show a similar pattern. "Short" intervals between successive spawning sequences were followed by relatively "longer" intervals and vice versa. For example, following spawning intervals of 4, 5, 6, and 21 days, the succeeding intervals increased to 64, 25, 18, and 81 days, respectively. Whereas spawning intervals of 18, 25, 29, 44, 55, 64, and 75 days were followed by "shorter" intervals of 7, 21, 21, 28, 44, 35, and 9 days, respectively. Three of six females showed an increase in succeeding interval length following a "short" spawning interval. In seven instances the length of time between spawnings for all six females decreased following an extended "rest period". Also intervals of at least 18 days were recorded for seven of eight females observed.

The mean average interval for *M. opercularis* was 27.6 days (Table XVII, Appendix) and the mean average interval for the same species, calculated from Hall (1966a), was 6.4 days. Spawnings were recorded from May through November (Table XVIII, Appendix).

Discussion of Spawning Intervals

The spawning intervals of both *T. trichopterus* and *M. opercularis* males indicate a similar capability to spawn every few days. Short cycles may be disadvantageous. Hall (1966a) reported that male fertility appears to decline when repeated spawnings occur one day apart. Barlow (1964) found that *Badis badis* males will sometimes spawn successively with two females on the same day. In such instances, many of the eggs remain unfertilized.

During this study, decreased fertility of eggs following two day spawning intervals did not occur. The tentative hypothesis is that a minimum spawning cycle for the males studied is two days. However, more data are desirable, since these few observations cannot reflect the range of individual variation.

Female *T. trichopterus* and *M. opercularis* show spawning intervals with similar characteristics. "Long" intervals were followed by relatively "shorter" intervals and vice versa (Tables XV and XVII, Appendix). There is a distinct difference in the character of spawning intervals between this study and Hall's (1966a) study. The mean average spawning interval during this study was considerably higher. A number of variables could account for this difference. Water temperatures, food schedules, lighting, age and condition of fish, total number of spawnings, and differences in fish stocks. The last variable, individual differences between members of the same species, seems the most likely answer. Of course, differences between species as *T. trichopterus* and *T. leeri* might occur, but the data derived from the study do not settle this question. For example, when comparing the lengths of spawning intervals between *M. opercularis* females in the two studies the contrast is even greater (27.6 versus 6.4 days). Perhaps the number of spawnings from which the data are derived is not sufficiently large. There were 19 *T. trichopterus* and 30 *M. opercularis* spawnings during this study.

Hall's (1966a) data on spawning intervals were derived from 32 T. leeri and 21 M. opercularis spawnings. These sample sizes may not be large enough to detect actual trends. In all future studies of this kind a minimum of 50 spawnings should be observed.

Another aspect of the data from the two studies is worthy of consideration. Hall's (1966a) data show much shorter intervals for both species. In this study, the spawning intervals were considerably longer. This may reflect nothing more than individual variation in the length of spawning intervals. This could result from any of the variables previously mentioned, especially short intervals, because of females in "good reproductive condition" and longer intervals for females in "poor condition".

The significance of the data seems to be that after a spawning, a female may require a period of at least two to four days to "recuperate". After several successive spawnings, a female may require an even longer spawning interval than usual. In addition, after "long" spawning intervals it seems likely that the succeeding intervals would be "shorter". This may simply reflect the improved "physical condition" and "spawning readiness" of the female.

Diel Rhythmicity of Spawning Activities

T. trichopterus showed a definite diel rhythmicity of spawning activities. On spawning days, the mornings were characterized by reduced activity in both sexes with occasional male nestbuilding. In the afternoons, both partners were more active, and most spawning sequences began after 1200 hours. Pre-spawning courtship activities were in progress by early afternoon and 18 of 19 spawning sequences occurred between 1300-2000 hours. Table II shows the number of spawnings in progress per hourly interval with 41 of 50 (82%) occurrences recorded during this same period. Hall (1966b) reported that most (80%) of the *T. leeri* spawnings occurred between 1000-1400 hours.

During this study, more *T. trichopterus* spawnings were in progress between 1800-1900 hours than at any other time. The median hourly interval was 1600-1700 hours. No spawnings were recorded prior to 1100 hours and none continued after 2200 hours. The average duration of a *T. trichopterus* spawning sequence was 2.52 hours (Table III).

M. opercularis exhibited a slightly different pattern of spawning activity. On spawning days, nestbuilding usually began during the late morning or early afternoon and most spawning sequences started after 1500 hours. Of 30 spawnings, 26 took place between 1800-2300 hours. The number of spawnings in progress per hourly interval is given in Table II with 57 of 68 (84%) occurrences recorded during this same period. Hall (1966b) reported a peak in spawning activity between 1600-1700 hours for *M. opercularis* with 85% of the spawning bouts occurring between 1500-2000 hours.

During this study, more *M. opercularis* spawnings were in progress between 2100-2200 hours than at any other time. The median hourly interval was 2000-2100 hours. No spawnings were recorded prior to 1400 hours and none continued after 2400 hours. The average duration of a *M. opercularis* spawning sequence was 2.15 hours (Table III).

The photoperiod during Hall's study was 12 hours long. Automatic timers set the light period from 0600 to 1800 hours. The same regimen was followed during this study.

TABLE II

NUMBER OF SPAWNINGS PER HOURLY INTERVAL*

Hourly Intervals	Number of Spawnings in Progress	
	_T._ _trichopterus_	_M._ _opercularis_
1100 - 1200	2	-
1200 - 1300	4	-
1300 - 1400	4	-
1400 - 1500	5	2
1500 - 1600	4	3
1600 - 1700	7	2
1700 - 1800	7	2
1800 - 1900	8	9
1900 - 2000	6	12
2000 - 2100	2	14
2100 - 2200	1	15
2200 - 2300	-	7
2300 - 2400	-	2

*The number of spawnings in progress per hourly interval. A spawning sequence that began at 1100 and ended at 1400 was recorded under each of the three hourly intervals included.

TABLE III

COMPARISON OF DIEL PATTERNS OF SPAWNINGS PER HOURLY INTERVAL

	Hopkins *T. trichopterus*	Hall* *T. leeri*	Hopkins *M. opercularis*	Hall* *M. opercularis*
Number of Spawning Sequences (n)	19	15	30	9
Most Spawnings Began After	1200	1000	1500	1200
Most Spawnings	82%-1300-2000	80%-1000-1400	84%-1800-2300	85%-1500-2000
Median Hourly Interval	1600-1700	1200-1300	2000-21000	1700-1800
Peak Spawning Activity Per Hour	1800-1900	1100-1200	2100-2200	1600-1700
Peak Spawning Per Three-Hour Period	1600-1900	1100-1400	1900-2200	1600-1900
Midpoint of Peak Period	1730	1230	2030	1730
NO Spawnings Before	1100	0900	1400	1300
After	2200	1800	2400	2000**
Average Time Per Spawning Sequence	2.52 hrs (n=19)	3.93 hrs*** (n=12)	2.15 hrs (n=30)	4.15 hrs (n=1)

*Data either derived or calculated from Hall (1966a, 1966b). The data are given in the number of spawning bouts per hourly interval.

**Hall (1966a, 1966b) reported that on one occasion, a spawning was observed at 2232 hours. He also stated that on three other occasions eggs were discovered in the morning that could only have been spawned the preceding night.

***Hall (1966a, 1966b) gives an average spawning time for *T. trichopterus* of 3.82 hours for two complete spawning sequences.

Discussion of Diel Rhythmicity of Spawning Activities

When comparing the diel spawning activity of the two species, it appears that the greatest number of T. trichopterus spawnings per three-hour period occurred between 1600-1900 hours and for M. opercularis between 1900-2200 hours. Both T. trichopterus and M. opercularis showed sharp declines in the number of spawnings in progress per hourly interval following their peaks at 1800-1900 hours and 2100-2200 hours, respectively (Table II).

The M. opercularis used in this study exhibited a later diel spawning pattern than did T. trichopterus. A reasonable parameter for comparing these differences would seem to be the midpoints of the peak three-hour spawning periods. The midpoint for T. trichopterus is 1730 hours and for M. opercularis is 2030 hours. From Hall (1966a), the midpoints for comparable three-hour periods were calculated. The midpoint for T. leeri was 1230 hours and for M. opercularis was 1730 hours (Table III).

Observational notes also support the thesis that M. opercularis exhibit a later diel spawning pattern than do T. trichopterus. Certain aspects of the data derived from this study and Hall's (1966a, 1966b) study can be compared. Most T. trichopterus and M. opercularis spawnings observed occurred between 1300-2000 and 1800-2300 hours, respectively. T. leeri characteristically spawned earlier than T. trichopterus (Hall, 1966a, 1966b).

The average duration of a T. trichopterus spawning sequence is slightly longer than a M. opercularis sequence. Hall's (1966a, 1966b) data show the reverse. One reason for this difference could be the determination of the beginning and ending of a spawning sequence which is subject to individual interpretation. The second reason for the difference in average spawning durations may simply be the numbers of spawnings reported. During this study 19 *T. trichopterus* and 30 *M. opercularis* spawnings were observed compared to 9 *M. opercularis* spawning sequences reported in Hall (1966a) (Table III).

CHAPTER V

FACTORS ASSOCIATED WITH THE PRESENCE OF A NEST

Daily records were maintained to determine if precipitation, barometric pressure and water temperature were contributing factors in influencing the presence of a nest.

The Effect of Precipitation

During the study, it was noted that preceding and during periods of daytime precipitation, individual fish of both species exhibited intense nestbuilding behavior frequently followed by spawning. The fish appeared to respond to the changing weather conditions. A burst of activity, mostly nestbuilding, occurred several hours before the rainfall. Barograph readings usually reflected distinct changes in pressure at this time.

Since the fish in this study were kept in aquaria in a laboratory with no windows, it seems reasonable to assume that precipitation per se did not have a direct effect on their behavior. However, the data were statistically tested to determine the validity of this assumption. It is also possible that the fish responded to changes in barometric pressure.

Allen (1959) showed that the movement of silver salmon, *Oncorhynchus kisutch*, and chinook salmon, *O. tschawytscha*, to the spawning grounds was directly associated with only one of the many physical factors measured. Falling barometric pressure affects chinooks, while night-time precipitation was important for silver salmon. Allen (1959) states that fall chinook salmon generally spawn in the larger rivers where inadequate flows due to a lack of rainfall do not usually interfere with spawning. He suggests that silver salmon have become adapted to spawning in small streams where low flows, due to a lack of rainfall, often influence the time and place of spawning. They seem to move onto the spawning grounds in response to environmental factors associated with increased stream flow, but silver salmon appear to require a more definitive stimulus.

Both _T. trichopterus_ and _M. opercularis_ are found in streams, canals, ditches, lakes, ponds, swamps, and rice fields of Southeast Asia (Smith, 1945; Forselius, 1957; Innes, 1956). Although both species occur in areas affected by monsoons they are allopatric. When the monsoon rains come and the water level rises in the marshes and ponds these species begin to migrate from the deeper, permanent waters where they have spent the dry season, to rice fields and shallow inundated swamp areas (Forselius, 1957). Nestbuilding and spawning behavior are probably influenced by environmental factors associated with the monsoon season, such as rainfall and falling barometric pressure. Thus, it seemed reasonable to check these factors to determine if they have an effect on behavior in the laboratory.

Precipitation was measured at the weather station on the Oklahoma State University campus. Weather records were obtained from the Oklahoma Section of the U. S. National Summary Annual for 1965.

A frequency distribution of precipitation over a 211-day period (April 21 to November 17, 1965) showed that precipitation occurred approximately 23% (49 days) of the time (Table IV). During the 49-day precipitation period, T. trichopterus and M. opercularis constructed 21% and 23%, respectively, of all the nests observed. Furthermore, on 21 of the 211 days, less than 0.10 inch of precipitation was recorded. This represents 10% of the total period. By comparison, T. trichopterus and M. opercularis constructed 8% and 9%, respectively, of all nests present during this same period.

The range of rainfall may also be compared with the frequency of nest presence. Sixteen percent of all nests constructed, by each species, occurred at five precipitation levels, indicated by asterisks in Table IV. The 54 T. trichopterus and 67 M. opercularis nests were present on 34-precipitation days. This represents 16% of the 211-day observation period. In contrast, almost 77% (162 days) of the 211-day period were days without precipitation. During this same period, T. trichopterus constructed 79% (261) and M. opercularis constructed 77% (317) of all nests observed.

Contingency tables were also used to test the hypothesis that precipitation influenced the presence of a nest. For T. trichopterus, the x^2 from Table XIX in the Appendix was 0.110 with a probability between 0.70 and 0.80. The x^2 for M. opercularis was 9.540 with a probability between 0.005 and 0.001 (Table XX, Appendix).

The Effect of Barometric Pressure

Barometric pressure was measured at the weather station at the Oklahoma State University campus. The barograph charts were used to assess the daily fluctuations in mean barometric pressure. Figures 1 and 2 show the number of days and the number of nests present over the

TABLE IV

FREQUENCY DISTRIBUTION OF PRECIPITATION, NUMBER OF OBSERVATIONS, AND NESTS PRESENT OR ABSENT DURING A 211-DAY PERIOD (APRIL 21 TO NOVEMBER 17, 1965)

			T. trichopterus				*M. opercularis*			
				Nests				Nests		
Precipitation (inches)	Number of Days	Frequency %	Number of Observations	Absent	Present	Frequency Nests Present %	Number of Observations	Absent	Present	Frequency Nests Present %
4.00–4.99	1	0.47	8	8	-	-	10	5	5	1.21
3.00–3.99	-	-	-	-	-	-	-	-	-	-
2.00–2.99	1	0.47	5	4	1	0.30	3	1	2	0.48
*1.00–1.99	5	2.37	22	13	9	2.73	22	12	10	2.43
0.90–0.99	-	-	-	-	-	-	-	-	-	-
0.80–0.89	-	-	-	-	-	-	-	-	-	-
0.70–0.79	1	0.47	8	6	2	0.61	8	4	4	0.97
0.60–0.69	3	1.42	8	4	4	1.22	6	0	6	1.45
0.50–0.59	1	0.47	-	-	-	-	-	-	-	-
*0.40–0.49	3	1.42	24	17	7	2.13	28	17	11	2.68
0.30–0.39	4	1.90	10	6	4	1.22	6	2	4	0.97
0.20–0.29	4	1.90	12	9	3	0.91	9	2	7	1.70
*0.10–0.19	5	2.37	28	16	12	3.65	27	18	9	2.19
*0.01–0.09	10	4.74	37	24	13	3.95	33	14	19	4.61
*Trace	11	5.22	54	41	13	3.95	51	33	18	4.37
0	162	76.78	863	602	261	79.33	908	591	317	76.94
Total	211	100.00%	1079	750	329	100.00%	1111	699	412	100.00%

*The ranges of precipitation during which the greatest number of nests were observed.

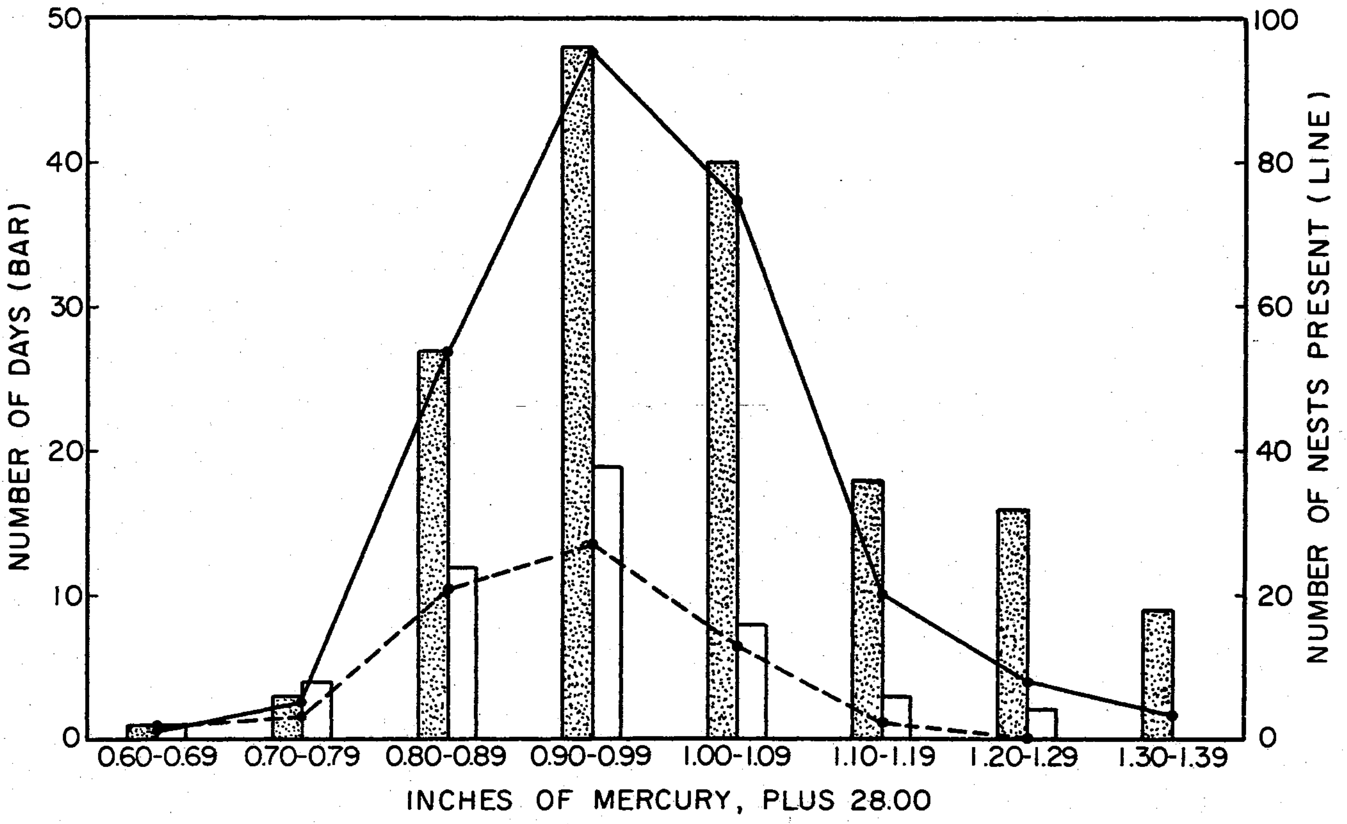

Figure 1. Daily Mean Barometric Pressure During 211 Days, April 21-November 17, 1965 (Bar) and Number of T. trichopterus Nests Present at the Various Pressures (Line)

n = 162 dry days (shaded bar);
n = 261 nests present on dry days (solid line);
n = 49 wet days (clear bar);
n = 68 nests present on wet days (dashed line).

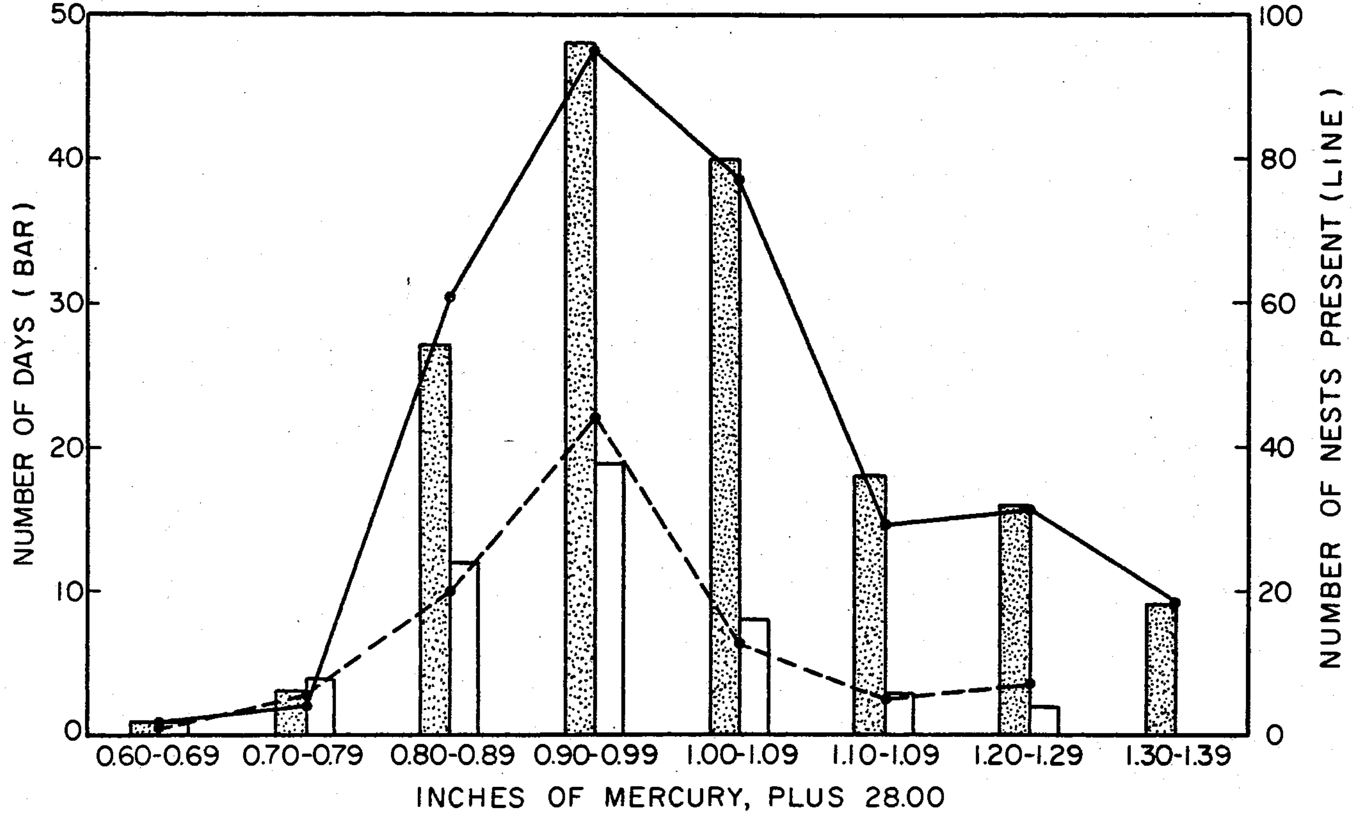

Figure 2. Daily Mean Barometric Pressure During 211 Days, April 21-November 17, 1965 (Bar) and Number of *M. opercularis* Nests Present at the Various Pressures (Line)
n = 162 dry days (shaded bar);
n = 317 nests present on dry days (solid line);
n = 49 wet days (clear bar);
n = 95 nests present on wet days (dashed line).

entire range of mean barometric pressure. Both T. trichopterus and M. opercularis showed almost identical distributions and paralleled the range of daily mean barometric pressure.

Figures 1 and 2 also compare precipitation with mean barometric pressure and show that barometric pressure is normally distributed on dry days. This record extended over the entire 211-day period. However, during periods of precipitation, there were more days, 73% (36 days), with the barometric pressure below 29.00 inches of mercury, than above it (13 days). During the 162 dry days, the barometric pressure was evenly divided above and below 29.00 inches of mercury. The most frequent range of mean barometric pressure for both wet and dry periods was 28.90-28.99 inches of mercury. The greatest number of wet, 38.78% (19), and dry, 29.63% (48), days were recorded within this range. T. trichopterus constructed 39.71% and 36.40% of all nests on both wet and dry days, respectively, within this range. Similarly, M. opercularis constructed 46.32% and 29.97% of all nests on both wet and dry days, respectively, within this range (Figures 1 and 2).

However, the number of days recorded below 29.00 inches of mercury (115 days - 54.50%) did not quite equal the number of days at 29.00 and above (96 days - 45.50%). This point was selected because the median value was between 28.99 and 29.00 inches of mercury. When making similar comparisons between mean barometric pressure and the numbers of nests present there was an even greater disparity. For T. trichopterus, was 208 (63.22%) nests present when the pressure was below 29.00 inches of mercury and 121 (36.78%) nests at 29.00 and above. M. opercularis constructed 232 (56.31%) nests during periods when the pressure was below 29.00 and 180 (43.69%) nests when the pressure was recorded at 29.00 and above (Table XXI, Appendix).

The relative frequency of nests present for both species on wet days above and below 29.00 inches of mercury was almost identical to the relative frequency of wet days at these pressure ranges (Table XXI, Appendix).

The presence or absence of nests were also compared with the daily trend in mean barometric pressure. Tables XXII and XXIII in the Appendix show that *T. trichopterus* and *M. opercularis* construct almost equal numbers of nests regardless of whether the barometric pressure is rising or falling. When the daily mean barometric pressure was rising or falling, *T. trichopterus* constructed 46.80% (154) and 49.24% (162), respectively, of all nests present during a 211-day period. During this period, 48.34% (102) of the days showed a rise and 47.39% (100) of the days a fall, in the daily mean barometric pressure. Only 4.26% (9) of the days in the 211-day period were recorded with no net change in daily mean barometric pressure. On these days both species constructed less than 5% of the total number of nests recorded. In fact, *M. opercularis* showed only 19 nests present out of 40 observations during periods of no net pressure change. On the other hand, *T. trichopterus* showed an even smaller number of nests present, 13 out of 41 observations during the same period.

The Effect of Water Temperature

Water temperatures were measured with a standard laboratory thermometer. During the period from April 21 to November 17, 1965, a total of 1079 and 1111 nest observations were made for T. trichopterus and M. opercularis, respectively.

During this period T. trichopterus constructed 329 nests. Almost 50% (162) of these nests were constructed when water temperatures ranged between 82° to 84° F. The optimum temperature was 82°F with 62 nests present. Since only 37% (402) of all observations were recorded in the 82° to 84°F range, it appears that as water temperatures reach this range, T. trichopterus males are more likely to build a nest (Figure 3).

During this same period, M. opercularis constructed 412 nests. Approximately 56% (231) of these nests were constructed when water temperatures were between 80°-83°F. The optimum temperature for nest-building appears to be 80°F with 66 nests present. Almost 55% (605) of the observations were made when the water temperatures were within this range. In this case, the evidence for a relationship between water temperatures 80°-83°F and the presence of a nest seem inconclusive. At best, one can say that M. opercularis exhibits a wider tolerance to water temperatures and may begin optimum nestbuilding at lower water temperatures than T. trichopterus (Figure 3).

Tables XXIV and XXV in the Appendix show that for both species more nests were present when water temperatures were fluctuating (rising or falling) than when they were stable (no change). However, the relative occurrence of nests closely followed the relative occurrence of the different states of temperature change, suggesting that this factor was not critical for either species.

The possibility that water temperature influenced the size of a nest constructed by the fish was considered. Nest sizes of several

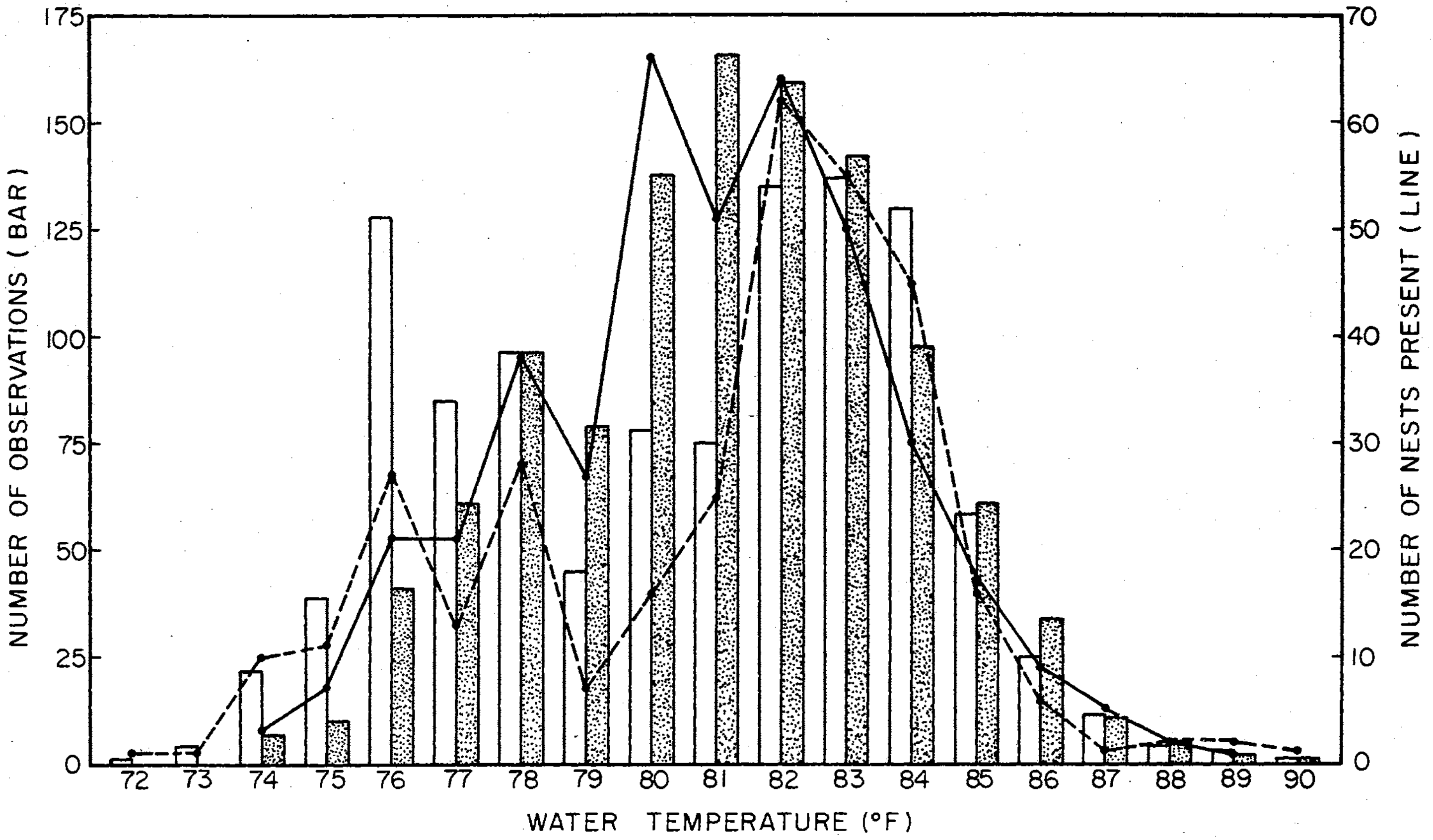

Figure 3. Number of T. trichopterus and M. opercularis Observations (Bar) and Number of Nests Present for Each Species at Various Water Temperatures (Line)
n = 1079 T. trichopterus observations (clear bar);
n = 1111 M. opercularis observations (shaded bar);
n = 329 T. trichopterus nests present (dashed line);
n = 412 M. opercularis nests present (solid line).

pairs of T. trichopterus and M. opercularis were recorded from May to November. The hypothesis that an increase in nest size is associated with rising water temperatures was not supported by laboratory observations. In fact, nest sizes, for both species, tended to increase and decrease in relatively equal numbers, regardless of rising or falling water temperatures. For example when water temperatures rose 61 nests increased in size and 55 decreased, while 39 remained unchanged. When water temperatures were falling 51 nests increased in size and 46 decreased, while 33 remained unchanged. Chi-square tests of this data yielded probabilities greater than 0.70 for both species.

Discussion

Precipitation did not prove to be a reliable factor in predicting future nestbuilding. This is not particularly surprising since the fish were not outdoors. Other variables such as absolute humidity were not measured. The relative occurrence of nests paralleled the relative occurrence of both wet and dry days. Therefore, rainfall outside the laboratory did not appear to be correlated with nestbuilding of fish kept in aquaria.

Contingency tables were used to test the relationship between the presence of a nest and rainfall. The χ^2 figure for T. trichopterus indicated that there was no association between precipitation and the presence of a nest. The χ^2 figure for M. opercularis was significant at the 0.001 level (Tables XIX and XX, Appendix). However, this does not prove that precipitation does influence the presence of a nest. Precipitation seems to be associated with another variable, barometric pressure, which may, in turn, influence both spawning and the presence of a nest. For example, during the study it was determined that rainfall was more likely to occur at "lower" barometric pressures. In fact, 73% (36 days) of the wet days were recorded with pressures below 29.00 inches of mercury. Therefore, if nestbuilding is more frequent at "lower" pressures, it would also be secondarily associated with rainfall. This might explain the significant figure for _M. opercularis_ indicating an association between rainfall and the presence of a nest.

When the presence of a nest is compared to barometric pressures above and below 29.00 inches of mercury, there does appear to be a slight difference between the two species. Table XXI in the Appendix shows that 63.22% of the _T. trichopterus_ nests and 56.31% of the _M. opercularis_ nests were present on 54.50% of the days recorded below 29.00 inches of mercury. This indicates that _T. trichopterus_ may be slightly more sensitive to "lower" pressures than _M. opercularis_ and, therefore, are more likely to build bubble nests than _M. opercularis_ under these conditions. Since the relative frequency of nests present on wet days, for both species, paralleled the number of days above and below 29.00 inches of mercury, it seems logical to conclude that precipitation outside the laboratory has no effect on the presence of a nest in aquaria. Apparently the presence of a nest is also not affected by the mere rise or fall in barometric pressure. However, the construction of a nest might depend on either the degree of rise or fall or whether the rise or fall is occurring during a "high" or "low" pressure trough. Neither of these factors proved significant in this study. The data tend to weakly support the hypothesis that barometric pressure below 29.00 inches of mercury may stimulate _T. trichopterus_ to build nests and act as a permissive factor at this level for _M. opercularis_.

Occasionally, increases in nest size follow significant changes in barometric pressure. This may be the result of a secondary effect, since intense nestbuilding is usually associated with spawning, which frequently follows abrupt changes in barometric pressure. Therefore, it appears that the onset of spawning and its attendant physiological changes can trigger nestbuilding and control nest size.

At best "warmer" water temperatures probably do have a permissive effect. In *T. trichopterus* aquaria, water temperatures between 80°-84°F appear to enhance nestbuilding. *M. opercularis* seem to be less sensitive, building nests at temperatures between 75°-85°F.

M. opercularis appear to have wider tolerance limits to water temperature and barometric pressure than *T. trichopterus*, particularly when nestbuilding. This is not surprising since they are a more northerly species and show little if any geographical overlap with the *Trichogaster* species. Liem (1963) proposes that a *Macropodus*-like stock is ancestral to the Trichogasterinae, the subfamily to which the *Trichogaster* species belong. Evidently, *Trichogaster* developed in a more southern climate and their tolerance to water temperature and barometric pressure is more limited than *Macropodus*. This apparent decrease in tolerance to water temperature and barometric pressure would seem to support Liem's (1963) suggestion that the *Trichogaster* species are a more advanced form than *Macropodus*.

CHAPTER VI

SPAWNING FACTORS

Three environmental factors (precipitation, barometric pressure, and water temperature) were considered in an attempt to determine if they were associated with the onset of spawning.

The Effect of Precipitation

As indicated in Chapter V, it seemed worthwhile to determine if nestbuilding by fish kept in aquaria was associated with precipitation outside the laboratory. The same consideration was given to the possibility that precipitation in some way influenced the onset of spawning.

Table XXVI in the Appendix shows that of 49 total spawning sequences, 31 occurred in association with precipitation either the previous day, the same day, or the day following the spawning or in any combination. It also shows that only 18 of the 49 spawnings occurred during periods of no rain. Contingency Tables XXVII and XVIII in the Appendix give the probabilities of precipitation-related spawnings (PRS) for the two species. They are between 0.10 and 0.20 and 0.20 and 0.30 for T. trichopterus and M. opercularis, respectively.

Contingency tables testing a possible relationship between precipitation on the spawning day only showed probabilities of 0.50 to 0.60 and 0.9995 for T. trichopterus and M. opercularis, respectively, (Tables

XXIX and XXX in the Appendix). These probabilities suggest that precipitation outside the laboratory did not influence the onset of spawning.

Since rainfall is closely associated with changes in barometric pressure, it is more likely that, at least under laboratory conditions, barometric pressure may provide spawning and nestbuilding cues.

The Effect of Barometric Pressure

Barograph records revealed that barometric pressure frequently followed a circadian rhythm. Approximately 0800 hours each day the high pressure point was attained and at 1800 hours the low pressure point was reached. Because of the cyclic nature of barometric pressure, a mean was calculated for each day during the study period and used in comparing spawning data. The daily mean barometric pressure was determined by calculating one-half of [daily minimum + daily maximum].

Birukow (1964) stated that changes in barometric pressure are highly correlated with changes in the number of photo negative grain weevils, _Calandra granaria_, traversing a given area at a given time of day. Lefeuvre (1960) reported that _Misgurnus_ [Cobitis] _fossilis_, a mud burrowing fish, is very sensitive to changes in weather and has been called a "weather fish". Allen (1959) stated that chinook salmon, _Oncorhynchus kisutch_, responded to falling barometric pressure by moving to the spawning grounds. Preceding and during severe weather (rainstorms), _T. trichopterus_ and _M. opercularis_ were quite active in this researcher's laboratory.

To determine if spawning was associated with changes in barometric pressure, both graphical and statistical methods were applied to the barometric and observational data.

Figure 4 shows the fluctuations in the daily mean barometric pressure during a 211-day period. The frequency of spawning and individual spawning days are indicated by species. Of the 211 days, 100 were recorded with a falling mean barometric pressure and 102 were rising. Nine days were recorded with no change in mean barometric pressure from the preceding day (Table XXXI, Appendix). An equal number of spawnings were recorded on days when the mean pressure was rising (23) or falling (23) and only three spawnings occurred when the mean pressure was the same for two consecutive days (Table XXXII, Appendix). Precipitation was almost equally divided between days of rising (25) and falling (22) mean barometric pressure (Table XXXIII, Appendix).

Twenty-two percent of the spawning sequences occurred on 22% of the days with precipitation. Seventy-eight percent of the spawnings occurred during 77% of the days without precipitation (Table XXXIV, Appendix).

The change in barometric pressure between the preceding day's mean and the pressure at the start of spawning the next day ranged from 0.00 to 0.35 inches of mercury (Table XXXV, Appendix).

At an undetermined number of hours preceding each spawning, it seemed likely there might be an absolute high or low pressure point. By scanning the old barograph charts, the absolute high or low pressure point was determined and the number of hours it preceded each spawning ascertained. A maximum pressure change occurred at an average of 11.6 hours preceding each of the 49 spawnings. By marking off a point

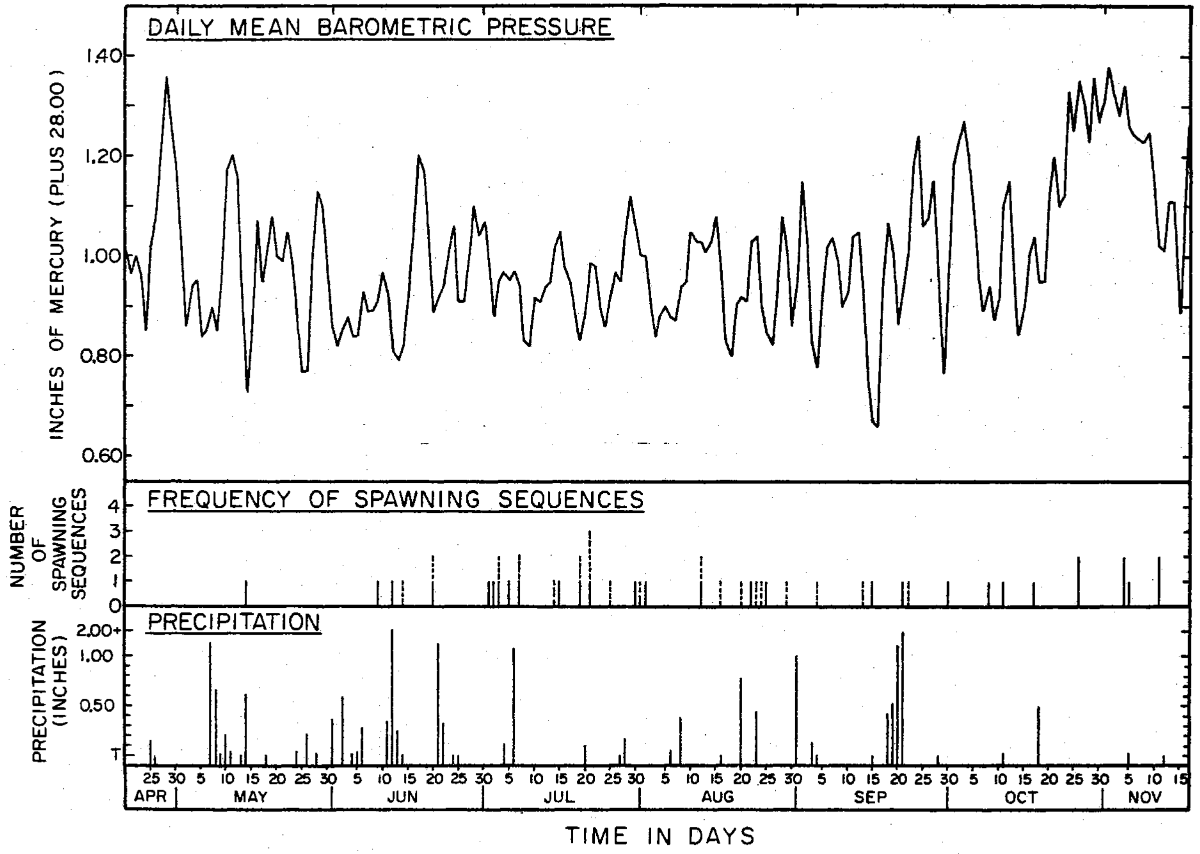

Figure 4. Frequency of Spawning Sequences Compared to Occurrence of Precipitation and Fluctuations in Daily Mean Barometric Pressure During 1965 (Mean Barometric Pressure is the Mean of one-half [Daily Maximum and Daily Minimum])

n = 8 pairs of *T. trichopterus* with 19 spawning sequences (dashed line).

n = 10 pairs of *M. opercularis* with 30 spawning sequences (solid line).

approximately 12 hours before each spawning on the old barograph charts, the net change in barometric pressure was determined. More spawning sequences seemed to occur if, during the preceding 12-hour period, the barometric pressure was falling (36 spawnings) rather than rising (11 spawnings). Only two spawnings occurred when the pressure showed no appreciable net change during the 12-hour period preceding spawning (Table V). The distribution of positive and negative changes in pressure 12 hours preceding spawning are shown in Table VI. The table is skewed toward the larger negative net changes in pressure. The largest number of spawnings, five in each class, occurred when the pressure was falling with net changes of -0.16 and -0.06 inches of mercury.

Net changes in falling pressure during the 12 hours preceding a spawning averaged 0.11 inches for both species. The net change for rising pressure averaged 0.07 inches for both species (Table VII).

Trends in rising and falling barometric pressure were analyzed by three methods: Trends during the 12 hours preceding spawning, discussed above; long term trends (day-to-day mean barometric pressure); and short term (hourly absolute pressure trends). There were 22 spawnings following rises and peaks in pressure on day-to-day mean barometric pressure (Figure 4). On a short term basis (hourly changes in pressure) there were four spawnings when the barometric pressure was rising and 43 spawnings when it was falling. Two spawnings occurred following no change in pressure (Table VIII).

Long and short term differences in the number of spawnings result from the method by which they are tallied. For example, on July 20, 1965 the mean barometric pressure was 28.88 inches and on July 21, when a *T. trichopterus* spawned, it was 28.99 inches. This represents a net

TABLE V

TRENDS IN BAROMETRIC PRESSURE DURING THE TWELVE HOURS PRECEDING SPAWNING

	Rising	Falling	No Change	Total
T. trichopterus	6	12	1	19
M. opercularis	5	24	1	30
Total Number Spawning Sequences	11	36	2	49

TABLE VI

NET CHANGE IN BAROMETRIC PRESSURE TWELVE HOURS PRECEDING SPAWNING

	Net Change (Inches of Mercury)	Number of Spawning Sequences		Total
		T. trichopterus	*M. opercularis*	
Barometric Pressure Rising	+ 0.15			
	0.14			
	0.13	1		1
	0.12			
	0.11	1		1
	0.10		1	1
	0.09		1	1
	0.08			
	0.07			
	0.06			
	0.05			
	0.04		1	1
	0.03	1	1	2
	0.02	1	1	2
	+ 0.01	2		2
	0.00	1	1	2
Barometric Pressure Falling	- 0.01			
	0.02			
	0.03	1		1
	0.04			
	0.05	2		2
	0.06	2	3	5
	0.07			
	0.08		3	3
	0.09		2	2
	0.10	1	3	4
	0.11		4	4
	0.12		3	3
	0.13		3	3
	0.14	1		1
	0.15	2		2
	0.16	3	2	5
	0.17			
	0.18			
	0.19			
	0.20			
	0.21			
	0.22			
	0.23		1	1
	0.24			
	- 0.25			
	Total	19	30	49

TABLE VII

CHANGES IN BAROMETRIC PRESSURE DURING THE TWELVE HOURS PRECEDING FORTY-NINE SPAWNINGS

	Rising	Falling
Minimum Change	0.01	0.00
Maximum Change	0.13	0.23
Average*	0.07	0.11

*Same average for both species.

TABLE VIII

THE NUMBER OF SPAWNING SEQUENCES BASED ON SHORT AND LONG TERM TRENDS IN BAROMETRIC PRESSURE

	Rising	Peak	Falling	Valley	No Change	Totals
Long Term*	4	18	9	15	3	49
(Day to Day)	22		24		3	
Short Term**	2	2	13	30	2	49
(Hour to Hour)	4		43		2	

*Based on daily mean barometric pressure from Figure 4.

**Based on hourly readings from the barograph charts.

change of +0.11 inch. When the spawning is plotted by long term methods, based on the two daily means, the T. trichopterus spawning occurs on a pressure peak. If the same spawning is plotted by short term methods, based on hourly barograph readings, the spawning follows a distinct drop in pressure. This spawning is then tallied as one which occurred after a fall in barometric pressure. The short term method appears more sensitive to slight changes in pressure. The long term method, dealing with daily means, may not always reflect the hourly changes in barometric pressure. Therefore, the sudden changes in pressure which coincide with spawnings, and appear to influence them, can only be detected on an hourly basis.

Additional comparisons can also be made. If the number of spawning sequences are plotted against barometric pressure at the beginning of spawning, a normal distribution is obtained. The range of pressure with the highest spawning frequency was 28.90-28.99 inches (Figure 5). When the number of spawning sequences is compared to mean barometric pressure on the spawning day, a similar normal distribution is obtained. Also the range of pressure with the highest spawning frequency was the same as above but with fewer spawnings (Table XXXVI, Appendix). Both Figure 5 and Table XXXVI in the Appendix show T. trichopterus spawning over a narrower range of barometric pressure than M. opercularis. A reduced number of spawnings compared to M. opercularis may account for this difference in pressure range. T. trichopterus spawned 19 times during a four-month period, June-September, 1965 (Table XV, Appendix), compared to 30 spawnings during a seven-month period, May-November, 1965 (Table XVII, Appendix), for M. opercularis.

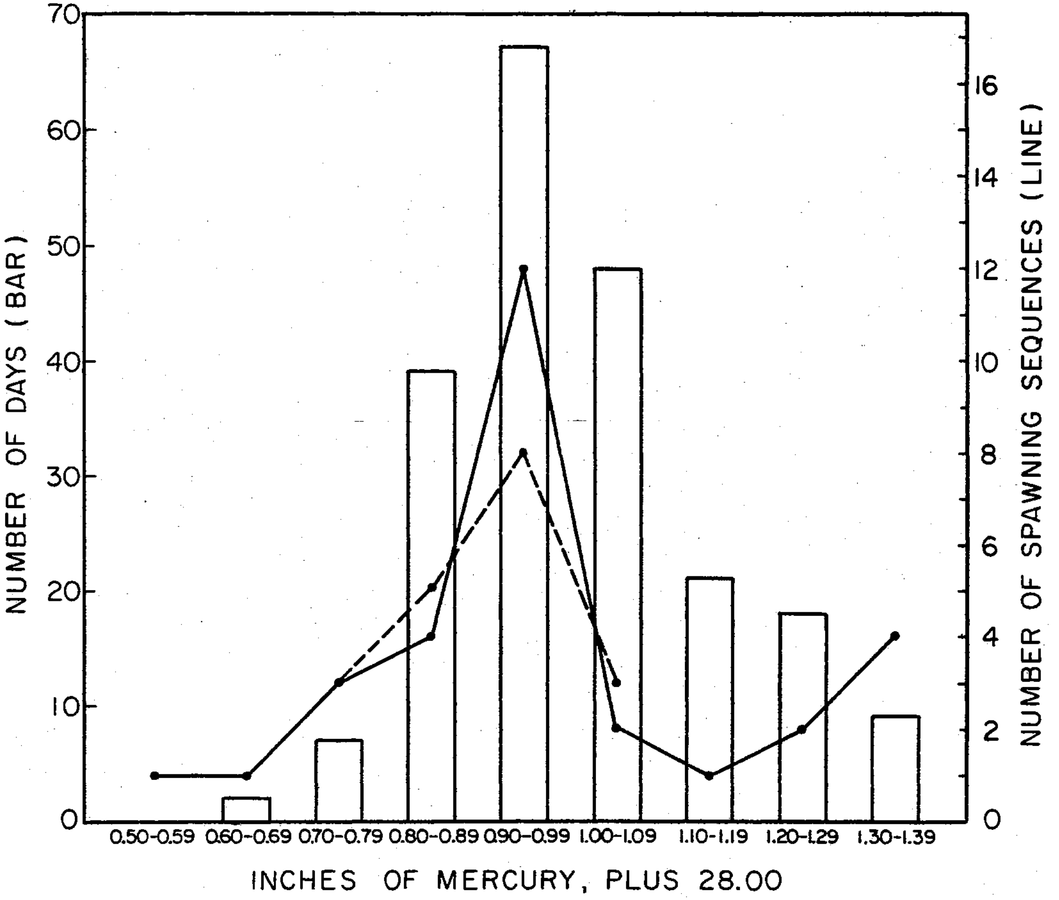

Figure 5. Daily Mean Barometric Pressure During 211 Days, April 21-November 17, 1965 (Bar) and Barometric Pressure at Beginning of Spawning Sequences (Line)
n = 19 <u>T. trichopterus</u> spawning sequences (dashed line);
n = 30 <u>M. opercularis</u> spawning sequences (solid line).

During June-September, 1965, the mean barometric pressure was confined to a range between 28.80-29.10 inches of mercury with few exceptions (Figure 4). T. trichopterus spawned six times (32%) during this period, between 29.00-29.09 inches mean barometric pressure. In the lower range, only one T. trichopterus spawning was recorded between 28.70-28.79 inches (Table XXXVI, Appendix). M. opercularis spawned over a wider range of barometric pressure. An increased number of spawnings (30 spawnings) over a seven-month period, May-November, 1965, may be partially responsible for the difference in distribution (Figure 5 and Table XXXVI, Appendix).

During April and May, the mean barometric pressure fluctuated more sharply than during June, July, August, and September, 1965. During October and November, the mean barometric pressure exhibited a rising trend (Figure 4). The lack of T. trichopterus spawnings during May, October, and November, seems unusual. These are the months with higher than average mean pressures, and additional study during January through May and October through December is necessary.

Over the seven-month period, April-November, 1965, the range of mean barometric pressure on the spawning day was between 28.60-29.39 inches (Figure 4). M. opercularis spawned throughout this range (Table XXXVI, Appendix), and also spawned once at 28.55 inches, producing a normal distribution similar to the distribution of mean barometric pressure (Figure 5). The frequency of spawning, in percent, in each mean pressure range, closely paralleled the distribution of days, in percent, under each pressure range. For example, 18% of the days in the 211-day study period were recorded between 28.80-28.89 inches; under the same pressure range, 16% of the spawnings occurred. Similarly, 32%

of the days were recorded at 28.90-28.99 inches and 37% of the spawnings occurred at this pressure range (Tables XXXVI and XXXVII, Appendix).

In conclusion, falling barometric pressure does seem suspect in influencing the spawning of *T. trichopterus* and *M. opercularis* in this author's laboratory. On the other hand, no specific range of pressure seems crucial. Yet, *T. trichopterus* did spawn more frequently at the lower pressure ranges (below 29.00). *M. opercularis* appears more tolerant, spawning at pressure ranges between 28.55 to 29.39 inches of mercury. Seventy-six percent of all spawning sequences (21 *M. opercularis* and 16 *T. trichopterus*) took place below 29.00 inches of mercury. Only 24% took place at 29.00 and above. Of these, 18% (9) were *M. opercularis* and 6% (3) were *T. trichopterus* spawning sequences.

The Effect of Water Temperature

The possibility that water temperature influences the onset of spawning in fishes has been suggested by Bullough (1961), Forselius (1957), and Van Iersel (1953).

Spawning temperature data were collected for 19 spawning sequences in *T. trichopterus* and 30 sequences in *M. opercularis*. The data were collected from seven pairs of *T. trichopterus* and ten pairs of *M. opercularis*. A standard laboratory thermometer was used. Spawning temperature data for the two species are shown in Tables IX, X, XI, and XII.

Most of the *T. trichopterus* spawnings were recorded between 80-85°F with 13 of 19 spawning sequences occurring within this range. The optimum temperature appears to be 83°F with six spawning sequences at this temperature (Table IX).

TABLE IX

SPAWNING TEMPERATURES IN *T. TRICHOPTERUS*

Temperature									
°F	°C	B2	B10	B11	B16	B17	B37	B46	Total
76	(24.40)			2					2
77	(25.00)			1		1			2
78	(25.55)						1		1
79	(26.10)				1				1
80	(26.65)	1			1				2
81	(27.20)								0
82	(27.75)	1	1						2
83	(28.30)	1	1		3	1			6
84	(28.85)	1							1
85	(29.40)					1		1	2
86	(30.00)								0
87	(30.55)								0
88	(31.10)								0
Total		4	2	3	5	3	1	1	19

TABLE X

SPAWNING TEMPERATURES IN *M. OPERCULARIS*

Temperature ^{o}F	 ^{o}C	P4	P7	P8	P14	P27	P28	P29	P31	P33	P34	Total
76	(24.40)											0
77	(25.00)						1				1	2
78	(25.55)					1			1			2
79	(26.10)				1				1			2
80	(26.65)		1					1	1		2	5
81	(27.20)			1								1
82	(27.75)	1	1	1	1			1	1			6
83	(28.30)			1			1	1		1		4
84	(28.85)	3										3
85	(29.40)		1									1
86	(30.00)	1		1			1					3
87	(30.55)											0
88	(31.10)							1				1
Total		5	3	4	2	1	3	4	4	1	3	30

TABLE XI

VARIATION BETWEEN SPAWNING TEMPERATURES AND THE PRECEDING DAY'S WATER TEMPERATURES (°F), (NUMBER OF SPAWNING SEQUENCES)

	1°	2°	3°	4°	5°	No Change	Total
T. trichopterus	9	4	-	1	-	5	19
M. opercularis	13	4	1	-	1	11	30

TABLE XII

NUMBER OF SPAWNING SEQUENCES OCCURRING AFTER FLUCTUATIONS IN WATER TEMPERATURE, (ONE DAY PRECEDING SPAWNING)

	Rise	Fall	No Change	Total	χ^2 Probability Values
T. trichopterus	10 (7)*	4 (7)	5 (5)	19	$0.30 > P > 0.20$
M. opercularis	13 (10)	6 (11)	11 (9)	30	$0.20 > P > 0.10$

*(Expected values).

Differences between spawning temperatures and the water temperatures on the day preceding spawning were small. Of the 19 spawnings, 13 were recorded with 1-2°F differences from the preceding day, 5 with no change in temperature, and only 1 took place with a change (rise) of 4°F (Table XI).

Almost 77% (23) of the 30 *M. opercularis* spawning sequences took place between 80-86°F. Fifteen of the 30 spawnings took place at 80, 82, and 83°F (Table X).

In 17 sequences a 1-2°F difference was noted between spawning temperatures and the preceding day's water temperature. In 11 sequences, no differences in water temperature were observed and on two occasions 3 and 5°F differences (fall) were noted (Table XI).

Both *T. trichopterus* and *M. opercularis* are capable of spawning over a relatively wide temperature range (77°-85°F). *T. trichopterus* data reveal a normal curve and *M. opercularis* data produced a curve which peaks in the lower, middle, and higher temperature ranges. Both show similar optimum spawning temperatures at 83° and 82°F.

The Change in Water Temperature

Van Iersel (1953) reports that by subjecting male *Gasterosteus aculeatus* L., a temperate water fish, to a sudden rise in temperature from 10° to 18°C (50° to 64.4°F) he observed a rapid development of the nuptial colors and a sudden appearance of various reproductive activities.

During this study, a record was kept of the fluctuations in water temperatures preceding spawning. Of the 49 spawnings, 23 occurred following a rise, 16 following no change, and 10 following a fall in water temperature. The number of spawnings following a rise in water temperature exceeded the number expected (23 to 17) and the number of spawnings following a fall was less than the number expected (10 to 18). The expected values were calculated from the relative frequencies of rising and falling water temperatures for all observations during the study. A chi square statistic testing these observations gives a probability value between 0.30 and 0.20 for T. trichopterus spawnings. The probability value for M. opercularis spawnings lies between 0.20 and 0.10 (Table XII). The data derived from these observations, therefore, do not convincingly confirm that the onset of spawning is influenced by rising water temperatures.

Although differences between spawning temperatures and the preceding day's temperatures were only 1-2°F it seems possible, however, that rising temperatures may be conducive for spawning. When females of both species are ripe sexually they may be more likely to spawn either after a period of constant temperature or following a slight rise in water temperature. Thirty-nine of the 49 spawnings occurred under these two conditions.

Both species showed an optimum number of spawnings at temperatures between 80-83°F, but M. opercularis exhibited greater tolerance in spawning over a wider temperature range than T. trichopterus (77-88°F and 76-85°F, respectively).

Because of the limited data, it is impossible to state unequivocally that rising water temperatures affect the onset of spawning. Constant or rising water temperatures seem to have at least a permissive effect; however, an experimental design to test this hypothesis is under consideration for a future investigation.

Discussion

During periods of impending precipitation, an increase in prespawning activity followed by spawning sequences was frequently observed. However, contingency tables testing a cause and effect relationship between precipitation and spawning did not prove significant. The various sensory modalities by which these fish might detect precipitation are not known. Presumably, in their native state, they may rely on visual cues, the lateral line, or on olfactory mechanisms. Under laboratory conditions, these air breathing fish have no way to detect precipitation directly. For this reason, it is not surprising that no direct correlation exists between rainfall and spawning despite our observations.

After analyzing several aspects of barometric pressure, it was found that more spawning sequences occurred if the absolute pressure was falling during the preceding hours. No particular range of pressure seemed essential in influencing spawning, although *T. trichopterus* spawnings appear to be restricted to the lower pressure ranges compared to *M. opercularis*, which spawn at a much wider pressure range. This may be partially due to the differences in distribution of the two fish species, with the more northern species (*M. opercularis*) subject to wider fluctuations in barometric pressure. Both species spawned more frequently when the barometric pressure was below 29.00 inches of mercury. However, *M. opercularis* also shows some flexibility in being able to spawn at the higher pressure ranges (above 29.09). These results support the hypothesis that both fish species appear to spawn more frequently when the barometric pressure is either falling or below 29.00 inches of mercury.

Both species spawned more frequently when the water temperatures were between 80-86°F. Also, 39 of the 49 spawnings recorded occurred when daily water temperatures were either constant or rising. *M. opercularis* appeared to have a slightly greater temperature tolerance, spawning at temperatures between 77°-88°F, compared to 76°-85°F for *T. trichopterus*.

The spawning data derived from this study compare favorably with Hall (1966b). In his study he reported the optimum range for *M. opercularis* to be 78°-83°F with 76% of the spawning sequences occurring within this range. Hall (1966b) also reports no clear-cut optimum spawning temperature for this species, but over 50% of the spawning sequences in this study occurred at 80°, 81°, and 82°F.

Apparently *M. opercularis* can spawn during extreme fluctuations of barometric pressure and water temperature. *T. trichopterus* did not spawn under these same conditions. This may reflect the more specialized nature of *T. trichopterus*.

CHAPTER VII

ACTIVITY CYCLES

Various aspects of fish activity cycles have been reported by Allen (1959), Alabaster and Robertson (1961), Swift (1964), David (1964), Marshall (1967), and Wimmer (1970). Most of these investigations were concerned with either isolating the environmental factors that initiated activity cycles or describing the rhythmic nature of these activities. With the exception of Allen (1959), all showed a correlation between an increase in fish activity with either the appearance or disappearance of light. Allen (1959) found that the movement of silver salmon (*Oncorhynchus kisutch*) into ponds coincided with nighttime rainfall.

During this study, 30-hour periods of intermittent observation (approximately 10 minutes every two hours) were made to determine if a diurnal-nocturnal activity pattern exists during nonreproductive periods in *T. trichopterus* and *M. opercularis* in the laboratory. A 12-hour photoperiod was maintained with the lights on at 0600 and off at 1800 hours.

Males of both species were considerably more active than females. For this reason more male activity patterns are presented, and, in general, they reflect the diurnal-nocturnal fluctuations for both sexes. The activity patterns for individual males over 24 hours were similar with only minor deviations.

In some instances, total duration in seconds was deemed the best measure of a behavior, since it distinguished between long and short bursts of an activity. In other cases, the frequency of a behavior was valuable in analyzing behaviors of either very long or very short durations, e.g., inspiration. Graphs of the frequency and duration of selected activities are presented in Figures 6, 7, and 8. Another parameter for measuring the rate of change in a behavior is the average duration per behavioral unit. For example, in patrolling, this shows the average duration of one patrolling trip (Figure 9).

Of the various behavior patterns monitored six classes of fish activity were chosen to show the cyclic fluctuations: Non-agonistic activity, male agonistic activity, migratory behavior, courtship, female activity, and total male activity.

Non-Agonistic Activity

Under this category, three male activities are included: patrolling, inspiration, and resting. The duration of patrolling or random swimming is used as an index of non-agonistic activity.

Patrolling

During the day, both T. trichopterus and M. opercularis spend more than 40% of their time (averaging 240 seconds per 10 minute period for 12 males in separate tanks, each containing one male and one female) in patrolling activity. The highest levels of non-agonistic activity frequently occurred between 1000-1200 hours for T. trichopterus, averaging 352 seconds per 10-minute period for four males in separate tanks and between 0700-0900 hours for four male M. opercularis averaging 375

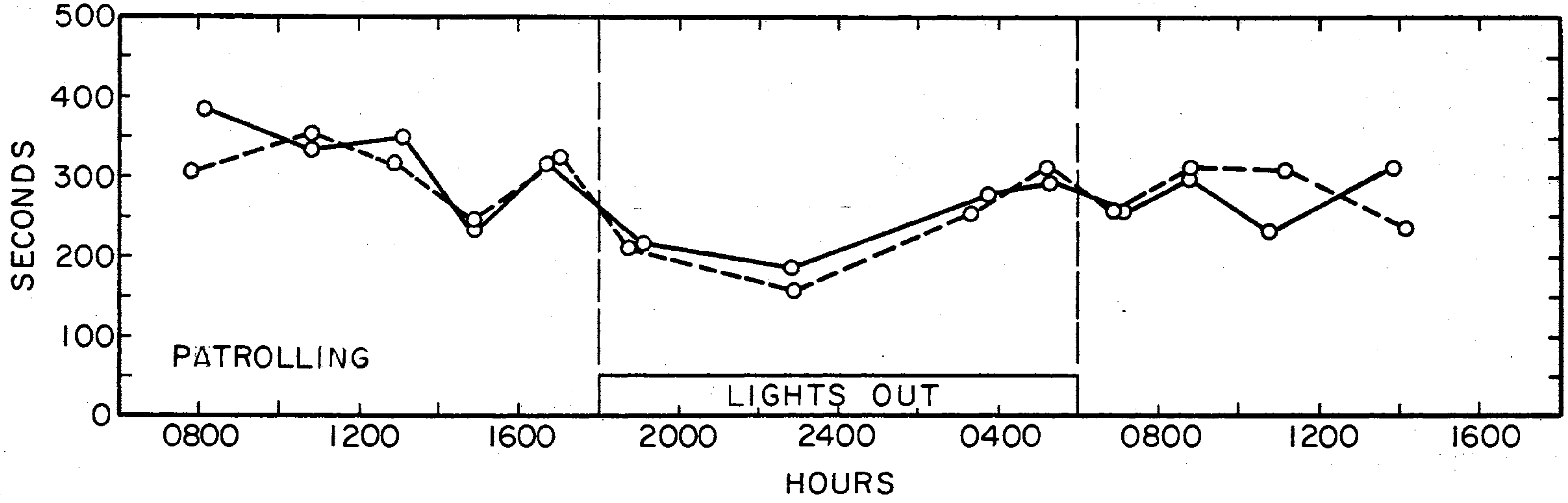

Figure 6. Total Patrolling Duration Per Ten Minutes (Average Values) Throughout a Thirty-Hour Period in Four Tanks Each of *T. trichopterus* (Dashed Line) and *M. opercularis* (Solid Line)

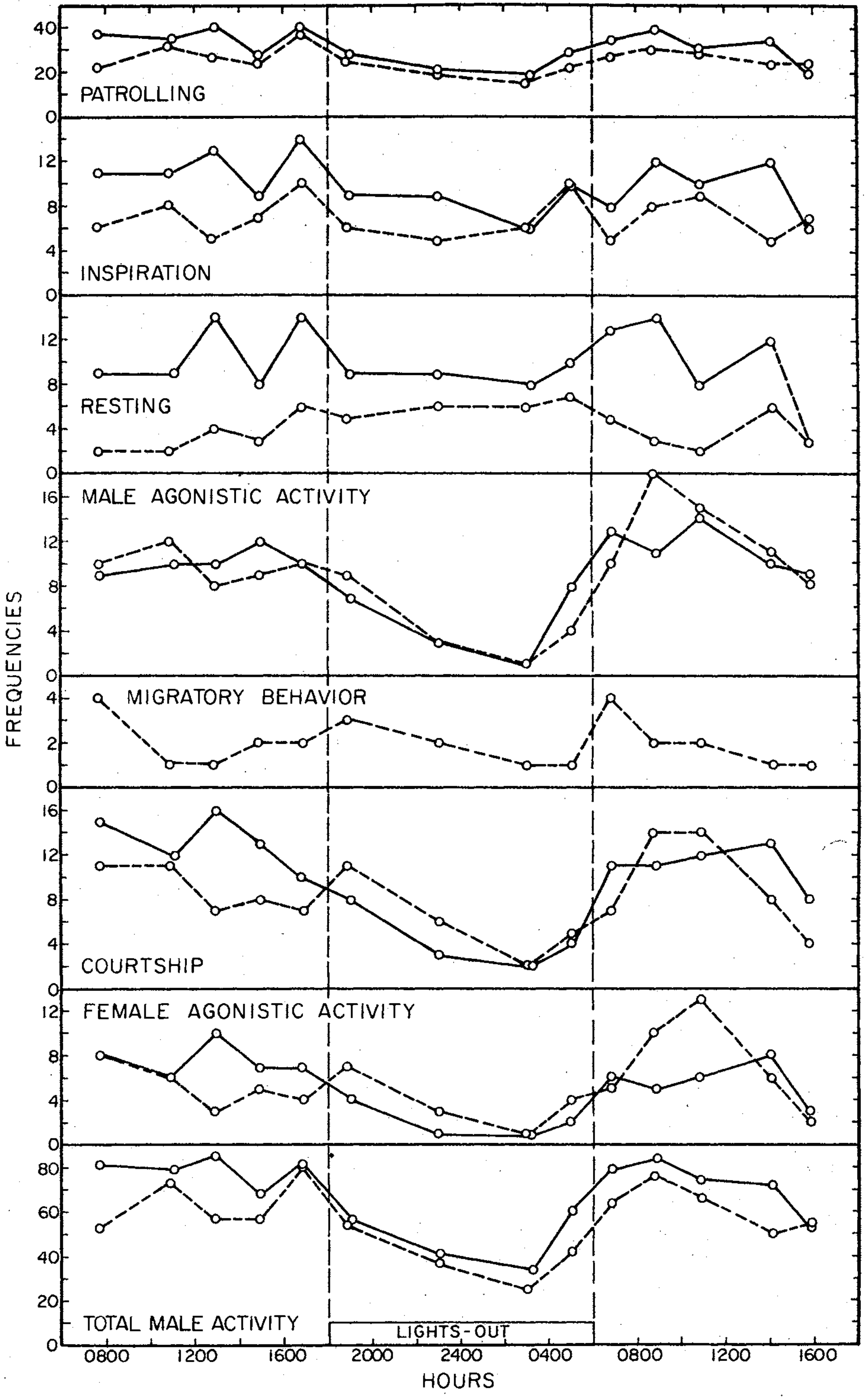

Figure 7. Average Frequencies of Eight Male and Female Activities Per Ten Minutes Throughout a Thirty-Hour Period in Twelve Tanks Each of T. trichopterus (Dashed Line) and M. opercularis (Solid Line)

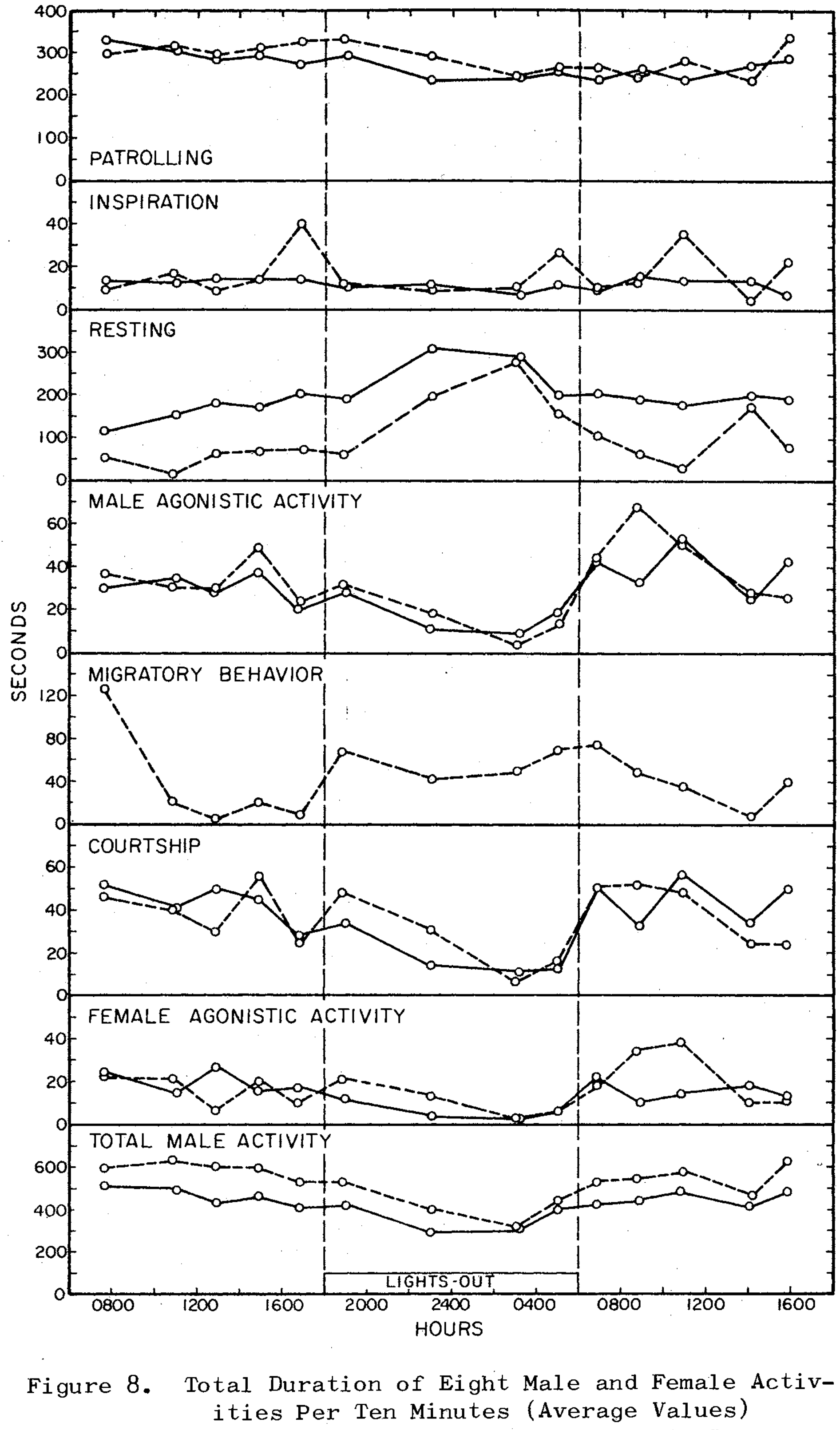

Figure 8. Total Duration of Eight Male and Female Activities Per Ten Minutes (Average Values) Throughout a Thirty-Hour Period in Twelve Tanks Each of T. trichopterus (Dashed Line) and M. opercularis (Solid Line)

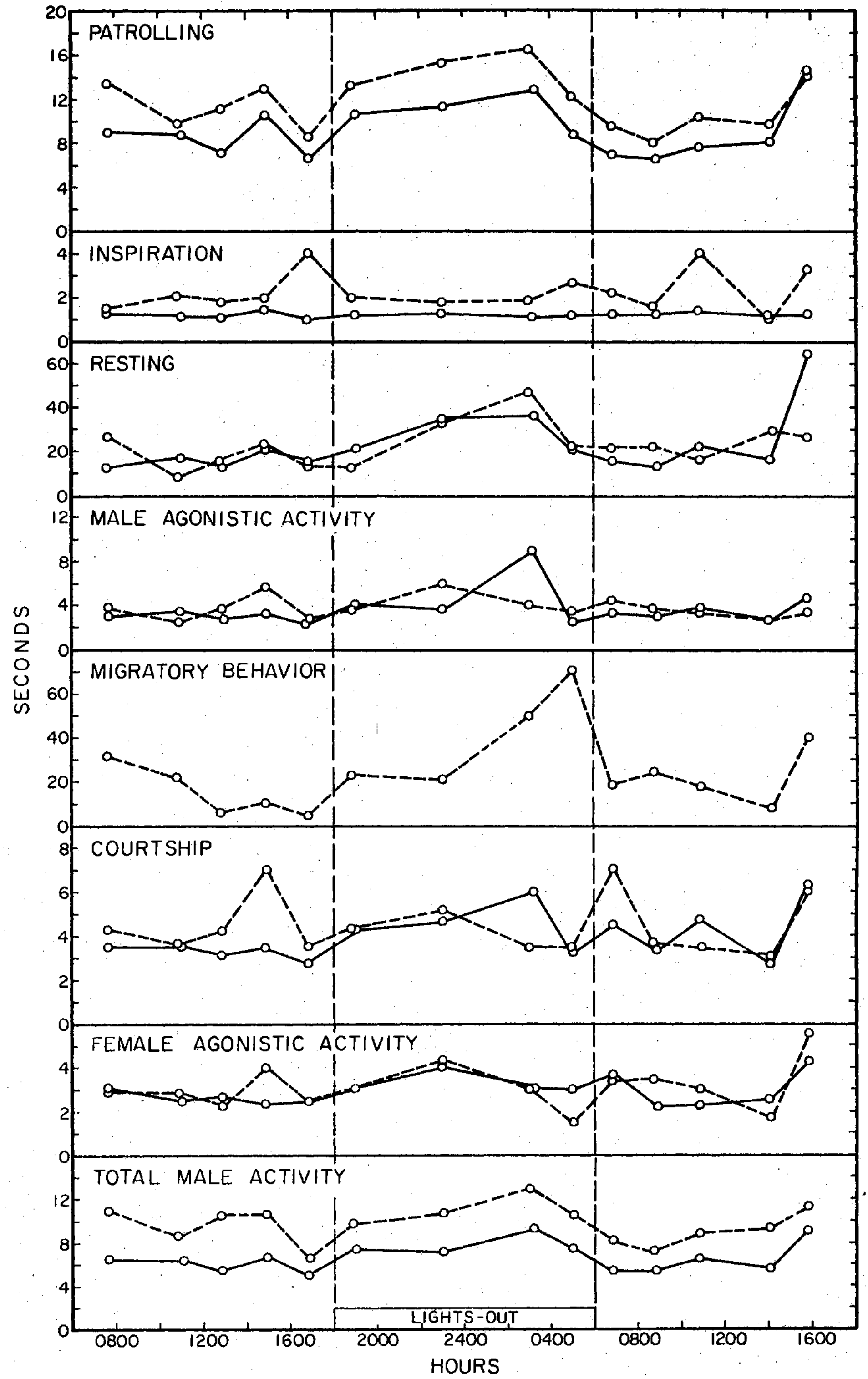

Figure 9. Average Duration of Eight Male and Female Activities Per Ten Minutes (Average Values) Throughout a Thirty-Hour Period in Twelve Tanks Each of T. trichopterus (Dashed Line) and M. opercularis (Solid Line)

seconds per 10-minute period (Figure 6). This contrasts sharply with the low levels of lights-out activity, for the same fish sometime between 1900 and 0400 hours. During this latter period the average duration of random swimming per 10 minutes for *T. trichopterus* and *M. opercularis* was 160 and 186 seconds, respectively. Activity began to increase approximately two hours before the lights-on period. During the hour immediately preceding lights-on, patrolling reached 331 and 296 seconds per 10-minute period for *T. trichopterus* and *M. opercularis*, respectively (Figure 6). Patrolling usually reached a maximum three to six hours later as indicated above. Activity declined from the morning high for both species, until approximately 1500 hours (range 1300-1700 hours) when it averaged 249 and 229 seconds per 10 minutes for *T. trichopterus* and *M. opercularis*, respectively.

Although barely detectable in Figure 8, approximately 75% of the tanks observed showed a temporary slump in activity of approximately one to two hours at some time between 0700 and 1200 hours. Because the exact hour of low activity varied from tank to tank, the mid-morning slump was not very evident in Figure 8, which represents the average duration for the males in 12 tanks. In several cases, the rate of patrolling activity, by both species, decreased as much as 40% but more frequently it decreased 10 to 20%. This compares favorably with Wimmer's (1970) observation, which reported mid-morning slumps up to 20% in patrolling activity for *T. microlepis*. The dip in morning activity can be observed to some extent in Figure 6, since this represents an average for only four males.

An afternoon slump was followed by a late afternoon surge of activity at 1700 hours (averaging 320 seconds per 10 minutes for four males of each species) which in turn subsided to 220 seconds of activity at 1900 hours, one hour after lights-out.

Occasionally following lights-out, there was another short period of increased activity lasting between one and three hours with an average high of 315 seconds of patrolling per observation period. Following this brief rise, patrolling usually declined rapidly.

After lights-out (1800 hours), aggressive behavior in *T. trichopterus* tanks diminished and the female fish usually came out into the open water for longer and more frequent periods of time, swimming about the tank with less than usual harassment from the male. In *M. opercularis* tanks following lights-out, the female would usually leave the pot shelter but she was quite furtive and would swim cautiously on the opposite side of the tank from the male.

From approximately 1900 hours activity declined, but did not reach a low level until four to five hours after lights-out. A distinct rise in activity occurred approximately three hours before the lights-on period. Patrolling activity of individual fish during the lights-out period varied from 36 to 533 seconds for *T. trichopterus* and 12 to 469 seconds per 10 minutes for *M. opercularis*.

The lowest average duration for patrolling in 12 tanks during the lights-out period was 247 seconds for *T. trichopterus* and 237 seconds per 10 minutes for *M. opercularis*. Low levels of patrolling activity usually occurred between 2300 and 0300 hours for both species.

The duration of individual patrols increase and decrease during the day much the same as the total duration of patrolling discussed above. However, following lights-out, at 1900, 2300, and 0300 hours, the duration per trip for *T. trichopterus* patrols in 12 tanks increased slightly averaging 13.3, 15.3, and 16.4 seconds, respectively, while total patrolling duration decreased averaging 332, 291, and 247 seconds, respectively. Similar results were obtained from 12 tanks of *M. opercularis* in which the duration per patrolling trip averaged 10.6, 11.3, and 12.9 seconds, respectively, and total patrolling duration averaged 298, 237, and 245 seconds, respectively (Figure 9). Therefore, while total patrolling duration generally declines following lights-out, the length of individual patrols remains fairly stable or increases slightly. This could mean that individual patrols are less likely to be interrupted by the reduced agonistic activity of other fish during the lights-out period.

Individual *T. trichopterus* patrols average approximately 15 to 20% longer than *M. opercularis* patrols and total patrolling duration per 10 minutes for *T. trichopterus* is also usually longer. However, *M. opercularis* average 10 to 15% higher patrolling frequencies than *T. trichopterus* per 10-minute period (Figure 7). *T. trichopterus* and *M. opercularis* averaged 48.35% and 45.71%, respectively, of an observation period (600 seconds) in patrolling activity over 24 hours (Table XXXVIII, Appendix).

Inspiration

Two forms of inspiration were noted, surface inspiration and dashes to the surface. Surface inspiration for individual male *T. trichopterus* varied from one to 130 seconds for one inspiration and from one to nine seconds for *M. opercularis*. Dashes to the surface were usually accomplished in one to two seconds by both species. No attempt was made to distinguish between the two types of inspiration when recording.

Frequently, upon leaving a shelter, harassed females of both species make dashes to the surface. Both males and females exhibited this form of inspiration which was usually restricted to the lights-on period. A more casual approach to the surface during the lights-on period was apparently possible because visual contact between the male and female was considerably reduced.

The frequency of inspiration throughout a 24-hour period varied from 0 to 25 per 10 minutes for individual fish of both species and the average number of inspirations in 12 tanks for _T_. _trichopterus_ was 6.9 and 10.0 for _M_. _opercularis_. During the lights-out period, the frequency of inspiration fluctuated only slightly within a narrow range, (5-10 inspirations per 10 minutes) with an average of 6.7 and 8.5 for _T_. _trichopterus_ and _M_. _opercularis_, respectively. Inspiration by both species appeared to be most frequent one hour before lights-out, one hour before lights-on, and three to five hours after the lights-on period (Figure 7). Frequency during lights-on varied from five to 10 (average 7.0) and 6 to 14 (average 10.6) for _T_. _trichopterus_ and _M_. _opercularis_, respectively. This higher rate of inspiration during lights-on reflects the increased activity at this time.

The two species exhibit similar fluctuations in inspiration per 10 minutes, during the 24-hour period, but _M_. _opercularis_ do inspire more frequently. However, _T_. _trichopterus_ exhibit much higher maximum values for total duration of inspiration per 10 minutes than _M_. _opercularis_. For example, the total duration of inspiration varied from 0 to 217 and 0 to 56 seconds per 10 minutes for individual _T_. _trichopterus_ and _M_. _opercularis_, respectively. Total duration of inspiration per 10 minutes in 12 tanks, for _T_. _trichopterus_ averaged 16.9

and 12.4 seconds for *M. opercularis*. Peaks in total duration occurred at approximately the same time as the peaks in frequency. However, the average durations for *M. opercularis* throughout a 24-hour period were relatively constant in comparison to *T. trichopterus* (Figure 8). The high values registered by individual *T. trichopterus* are responsible for the difference in average durations between the two species. For this reason, the frequencies were also analyzed. At this time, it is not certain whether these differences are typical of the species or just individual variation. From observational notes it would appear that extended periods of inspiration are more common in *T. trichopterus* than in *M. opercularis*. This could be advantageous for *T. trichopterus* since they inspire less frequently than *M. opercularis*, which would decrease the chance of damage from hostiles. Also, extended inspiration periods may allow *T. trichopterus* to stay submerged for greater lengths of time while predators are in the vicinity. A recent investigation by Hadley (1965) has shown that *T. trichopterus* can survive without surfacing to gulp air for 173 hours compared to 93 hours for *M. opercularis*.

Apparently, inspiration did not follow the general trend followed by agonistic behaviors. However, it did follow the pattern set by patrolling. In Figure 6 the peak patrolling periods for both species were 1700, 0500 and 0800 to 1100 hours, the same hours in which peak inspiration frequencies and durations were recorded (Figures 7 and 8). But as may also be seen from Figures 7 and 9, when the average duration of an individual patrol decreased, the frequency of inspiration increased and vice versa. Thus, prolonged patrols were accompanied by fewer inspirations and as the duration of individual patrols became shorter the number of inspirations increased. This suggests that prolonged casual patrols, predominant during the lights-out period, were less exerting and required less oxygen than the short daily sorties which included much agonistic activity.

T. trichopterus and _M. opercularis_ averaged 2.81% and 2.07%, respectively, per 10 minutes inspiring during a 24-hour period (Table XXXVIII, Appendix).

Resting

Resting by individual male _T. trichopterus_ varied from one to 128 seconds for a single rest period and from one to 300 seconds for _M. opercularis_. During the lights-on period, (minimum resting) _M. opercularis_ average more than 25% of their time resting while _T. trichopterus_ average only 8 to 10% resting.

The frequency of resting during a 24-hour period varied from 0 to 23 per 10 minutes for individuals of both species and the average number of resting periods in 12 tanks was 4.2 for _T. trichopterus_ and 10.0 for _M. opercularis_. During the lights-out period, the frequency of resting fluctuated between 5-10 resting periods per 10 minutes with an average of 6.0 and 9.0 for _T. trichopterus_ and _M. opercularis_, respectively. Peak frequencies in resting, for both species, ranged from 0500-0900, 1300-1500, and 1700-1900 hours (Figure 7). Resting frequencies during lights-on varied from 2 to 6 (average 3.6) and 3 to 14 (average 10.4) for _T. trichopterus_ and _M. opercularis_, respectively. The higher rate of resting by _M. opercularis_ is noticeable when observing these fish; they appear slightly more lethargic than _T. trichopterus_. For example, interspersed between many behaviors _T. trichopterus_ exhibit patrolling, whereas _M. opercularis_ will frequently stop and rest.

A measure of total resting duration per 10 minutes revealed that in 12 tanks T. trichopterus averaged 102.3 and M. opercularis averaged 199.7 seconds. Total resting duration for individual fish varied from 0 to 508 and 0 to 588 seconds per 10 minutes for T. trichopterus and M. opercularis, respectively. Peaks in total resting duration per 10 minutes usually occurred in the afternoon and evenings for both species ranging from 1300-1500, 1700-1900, and 2300-0300 hours. The longest resting durations per 10 minutes for both species were recorded during the latter period and steadily declined until sometime between 0500-1100 hours (Figure 8).

Individual rest period durations increase and decrease during 24 hours much the same as total resting duration does, per 10 minutes, for both species. The longest single rest period durations, in 12 tanks of T. trichopterus, occurred at 0300, 0900, and 1400 hours, averaging 46.3, 22.3, and 29.2 seconds, respectively. Similar results were obtained at 0300, 1100, and 1600 hours in 12 tanks of M. opercularis in which the rest period durations averaged 36.4, 22.4, and 64.3 seconds, respectively (Figure 9).

As might be expected, resting appears to increase as other activities begin to decline. Both the average duration per resting period and the total resting duration per 10 minutes reach a maximum during the lights-out period, while the frequency of resting usually stabilizes or declines (Figures 7, 8, and 9). T. trichopterus and M. opercularis averaged 17.05% and 33.28% respectively per 10 minutes in resting activity during a 24-hour period (Table XXXVIII, Appendix).

Male Agonistic Activity

Five activities were included under this category. The frequencies and durations for male lateral display, butting and biting, chasing, fleeing, and mouthfighting were summed and averaged to determine the general level of agonistic activity. With few exceptions agonistic activity appeared to increase and decrease with patrolling activity.

General Agonistic Activity

Following lights-out, the frequency of agonistic activity for both species declined from an average of eight at 1900 hours to one per 10 minutes at 0300 hours (Figure 7). During this time, the predominant agonistic activity was lateral display with a few mild to intense chases followed by butting and biting. The decrease in aggressiveness after lights-out may be due to the lack of visual contact between the male and female.

As patrolling began to increase after 0300 hours, the frequency of *T. trichopterus* agonistic activity increased steadily from four at 0500 to 10 at 0700 to 18 at approximately 0900 hours and then decreasing to 15 per 10 minute period at 1100 hours. *M. opercularis* exhibited similar increases from eight at 0500 to 13 at 0700 then decreasing slightly to 11 at 0900 and then rising again to 14 per 10-minute period at 1100 hours (Figure 7).

The level of agonistic activity for both species decreased from an average frequency of 14 at 1100 hours to eight or nine per 10-minute period at 1600 hours. Occasionally, there is a mid-afternoon surge of activity between 1500-1700 hours which then is followed by a steady decline in agonistic activity so typical after lights-out (Figure 7).

The total duration of agonistic activity increases and decreases with the frequency except between 1700-1900 hours. At this time, the total duration increases, from 24 to 32 and 21 to 28 seconds per 10 minutes for T. trichopterus and M. opercularis, respectively, while the frequency for both species declines (Figures 7 and 8).

The average duration of agonistic activity follows the average duration per patrolling trip for each species. For example, following lights-out, both the average patrolling trip and the average duration of agonistic activity increase slightly, and begin to decline only after 2300 and 0300 hours for T. trichopterus and M. opercularis, respectively. The decline in the average duration of agonistic activity continues until an hour before lights-on when it reaches a low between 2.37-3.50 seconds per activity, for M. opercularis and T. trichopterus, respectively. By 0700 hours the average duration of agonistic activity has increased to 3.31-4.50 seconds per activity, for the two species, respectively (Figure 9). During a 24-hour period, T. trichopterus and M. opercularis average 5.42% and 4.96%, respectively, per 10 minutes in agonistic activity (Table XXXVIII, Appendix).

An analysis of the duration of five agonistic activities revealed that on the average more than 92% of this activity is spent in lateral display, chasing, and butting and biting in the order given (Table XXXIX, Appendix).

Lateral Display

The average frequency of lateral display for both species increases from one at 0300 hours to two at 0500 hours to six per 10-minute period at 0900 hours (Figure 10). By 1100 hours, a high of six to seven

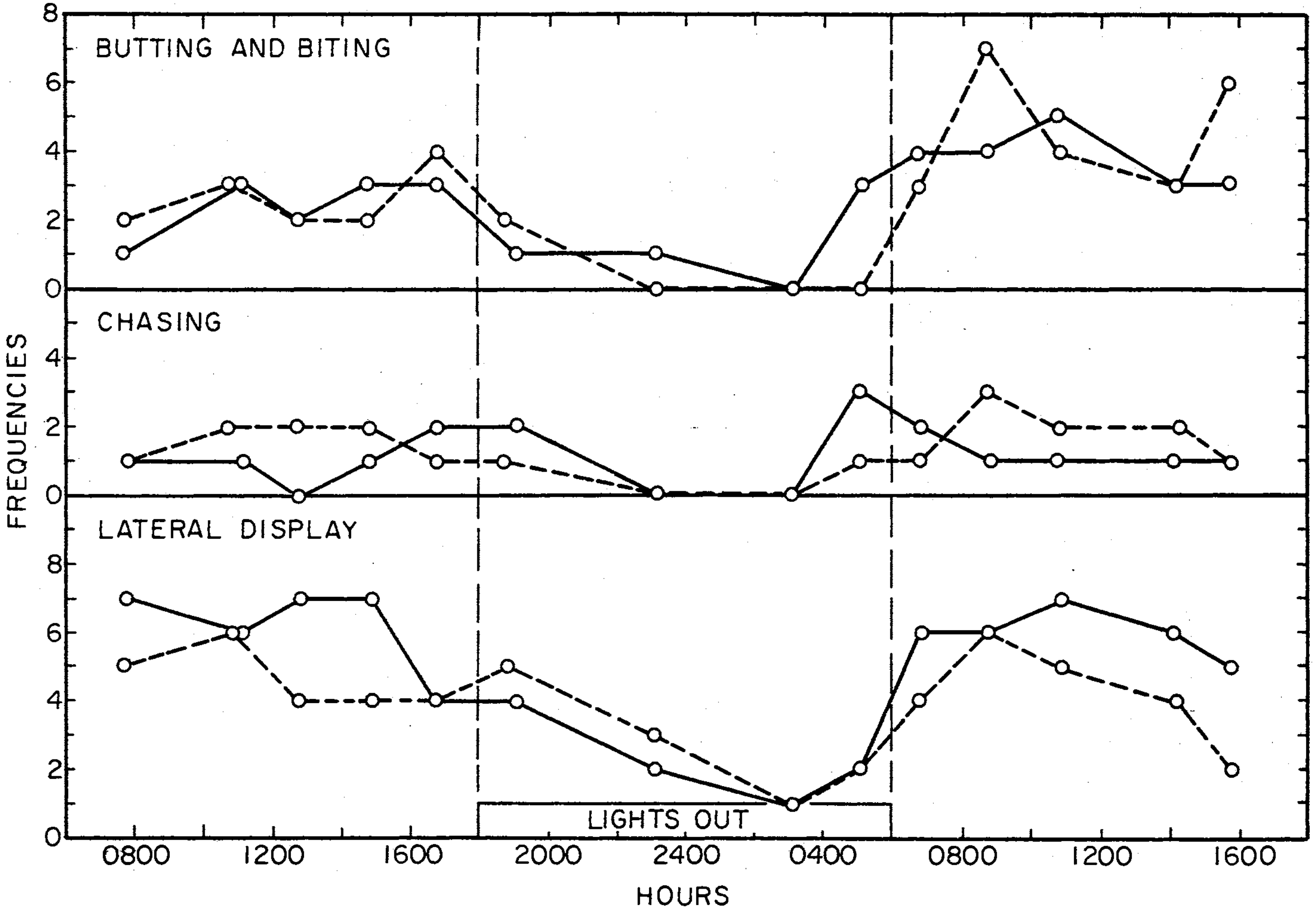

Figure 10. Average Frequencies of Three Male Agonistic Activities Per Ten Minutes Throughout a Thirty-Hour Period in Twelve Tanks Each of *T. trichopterus* (Dashed Line) and *M. opercularis* (Solid Line)

lateral displays per 10 minutes was reached by *M. opercularis*, and *T. trichopterus* initiated a decreasing trend, performing this display an average of five times per 10-minute period. After 1100 hours, *T. trichopterus* usually exhibited fewer lateral displays (averaging four per 10-minute period) until an hour after lights-out when a slight increase to five per 10 minutes is reached. *M. opercularis* frequently showed a rising trend in the number of lateral displays (up to seven per 10 minutes) after 1100 hours extending until mid-afternoon (1500 hours). The average frequency of this display dropped to four per 10 minutes by 1600-1700 hours, and remained at this level until an hour after lights-out. From 1900 hours both species exhibited fewer lateral displays decreasing to two or three per 10 minutes at 2300 hours to the 24 hour low of one lateral display per 10 minutes at 0300 hours (Figure 10). The duration increased and decreased as the frequency except that both species showed definite peaks at 1500, 1900, and 0700 hours averaging 32, 24, and 32 seconds per 10 minutes of lateral display. The longest average duration per lateral display for *T. trichopterus* occurred at 1500 and 0700 hours averaging nine seconds per display. The longest average duration per lateral display for *M. opercularis* occurred at 0300 and 1600 hours averaging nine and seven seconds, respectively, per display. *T. trichopterus* and *M. opercularis* averaged 73.82% and 77.18%, respectively, of the time recorded for agonistic activity, performing lateral displays (Table XXXIX, Appendix).

Chasing

An hour after lights-out the average frequency of chasing for both species declined from one to two chases per 10 minutes to zero at 2300 hours and remained at this level until 0300 hours (Figure 10). Chasing by M. opercularis reached a high (three chases per 10 minutes) at 0500 hours and declined steadily to one chase per 10 minutes at 0900 hours. The frequency of chasing for the same fish remained at this level until late afternoon (1700 hours) when it averaged two chases per 10 minutes until sometime after 1900 hours. Chasing by T. trichopterus increased steadily from one per 10 minutes at 0500 to an average of three every 10 minutes at 0900 hours only to decline to two chases between 1100 and 1400 hours. At 1600 hours, one chase per 10 minutes was typical until sometime after 1900 hours when chasing ceased (Figure 10).

Maximum chase durations for T. trichopterus averaged eight seconds per 10 minutes at 1500 and six seconds at 0900 hours. M. opercularis exhibited maximum chasing one hour before lights-on, averaging nine seconds per 10 minutes and another peak around mid-morning (0900-1100 hours) averaging four to six seconds. Chasing declined substantially (zero to two seconds) after 1100 hours. Chasing duration increased again to three to four seconds per 10 minutes around 1500 hours followed by a slow increase to four to five seconds per 10 minutes until an hour after lights-out, when it declined to zero at 2300 hours.

The longest average durations per chase for T. trichopterus occurred between 1500-1600 hours for four to seven seconds. The longest M. opercularis chase durations were observed between 0900 and 1100 hours for four to five seconds. A second peak in average chase durations occurred between 1400-1500 hours for three to four seconds.

T. trichopterus and M. opercularis males averaged 9.82% and 10.86%, respectively, of the time consumed in agonistic activity, chasing females (Table XXXIX, Appendix).

Butting and Biting

Butting and biting is a more aggressive form among the three predominant agonistic activities.

The frequency of butting and biting for both species declined from 1700 to 1900 hours (Figure 10). After 1900 hours butting and biting was only infrequently observed and by 2300 hours *T. trichopterus* butting declined to zero and remained at this level until 0500 hours. By 0700 butting by *T. trichopterus* averaged three every 10 minutes increasing maximally to seven at 0900 hours. The frequency of butting declined to three to four per 10 minutes by 1100 and continued to fall until 1300 when it remained at two to three per 10-minute period between 1300 and 1500 hours. By 1700 hours *T. trichopterus* butting averaged four to six per 10 minutes, declining to two by 1900 hours (Figure 10).

Butting and biting by *M. opercularis* averaged one per 10-minute period at 1900 and 2300 hours and declined to zero by 0300 hours. From 0300 butting by *M. opercularis* averaged three every 10 minutes at 0500 and four at 0700 and 0900 hours. After 0900, the butting frequency reached a maximum of five at 1100 hours, followed by a decline to three per 10 minutes at 1400 hours. From 1400 to approximately 1700 hours, butting by *M. opercularis* averaged three every 10 minutes dropping to one at 1900 hours (Figure 10).

The average duration of butting and biting for both species was almost identical to the average frequency. A single butt or bite being completed in one second, or multiple butts in as many seconds.

Of the time consumed in agonistic activity, *T. trichopterus* and *M. opercularis* averaged 9.02% and 10.19%, respectively, butting and biting (Table XXXIX, Appendix).

Fleeing

Male fleeing by both species was recorded more frequently than mouthfighting. The females involved showed temporary rises in aggressive tendencies regardless of the relative size of the males involved. For example, one *T. trichopterus* female chased and butted a slightly larger male continuously for 46 seconds. Male fleeing for this species was more frequently recorded between 0700-1100 hours and 1500 hours. Individual fleeing durations ranged from 1-46 seconds with an average of 2.7 seconds during the morning period and 1.7 seconds per chase during the afternoon. The highest fleeing frequencies per 10 minutes were recorded for *T. trichopterus* during the early morning (15) and mid-afternoon (27).

M. opercularis males were infrequently chased from 0600-1100 hours and 1400-1600 hours. Individual fleeing durations averaged 1.7 seconds in the morning and 1.8 seconds during the afternoon. Individual male *M. opercularis* were rarely chased continuously for more than six seconds. The highest fleeing frequencies were recorded in the early morning (0700 hours) at five per 10 minutes.

Fleeing by male *T. trichopterus* averaged 6.21% of the recorded agonistic activity and 1.77% in male *M. opercularis* (Table XXXIX, Appendix).

Mouthfighting

Mouthfighting by *M. opercularis* was quite infrequent and only two instances were recorded during the 30-hour recording sessions. In both cases a large male and small female were mouthfighting for one-second durations during the late afternoon.

In contrast, small *T. trichopterus* males and large females exhibited mouth fighting two to three times during the 30-hour recording sessions. It was recorded from 1430-1800 hours and 0900-1130 hours. Mouthfighting durations averaged 4.3 seconds per occurrence during the former period and 4.6 seconds for the latter period.

Mouthfighting by male *T. trichopterus* averaged 1.13% of all recorded agonistic activity and it was negligible for *M. opercularis* (Table XXXIX, Appendix).

Migratory Behavior

Migratory behavior by *M. opercularis* was quite rare and was usually recorded during the early morning, 0400-0600 hours, for only two of 12 males. The durations for this behavior are typically quite extended, averaging 43.1 seconds and ranging from six to 124 seconds for one *M. opercularis* fluttering session. The frequencies ranged from one to seven per 10-minute period.

In contrast, migratory behavior was frequently recorded for *T. trichopterus* males. Two peaks in frequency and duration were noted, one to two hours after lights-on and one hour after lights-out (Figures 7 and 8). Maximum frequencies for individual *T. trichopterus* reached 20 per 10 minutes in the early morning and maximum total durations were as high as 591 of 600 seconds. The longest single fluttering session was 333 seconds and the shortest three seconds.

The average frequency of migratory behavior declined from three per 10 minutes at 1900 to one at 0300 hours. A rise in frequency occurred after 0500 averaging four per 10 minutes at 0700-0800 hours and declining to one or two between 0900-1300 hours. Between 1400-1700 hours migratory behavior was recorded one to two times per 10 minutes rising to three after lights-out (Figure 7).

The total duration per 10 minutes of migratory behavior paralleled the increases and decreases exhibited by the frequencies with one exception. The durations following lights-out decreased from 68 at 1900 to 43 seconds per 10 minutes at 2300 hours. After 2300 hours, however, T. trichopterus appeared to spend more time in migratory behavior per 10 minutes. The total durations per 10 minutes increased from 50 at 0300 to 75 at 0700 hours (Figure 8). This can be partially explained by the fact that only a few males were responsible for most of the migratory behavior during this period.

The average duration per migratory trip followed closely the increases and decreases in total duration with one notable exception. As mentioned above, after 2300 hours the total amount of migratory behavior increased slightly to 7.16, 8.33, and 11.83% of a 10-minute period at 2300, 0300, and 0500 hours, respectively, while the average duration per trip increased sharply to 50.00, 100.00, and 100.00% of the total duration of migratory behavior for the same hours. This increased trip rate resulted from the decreased frequency of fluttering behavior during these early morning hours. These sharp rises in average duration per trip are followed by equally sharp drops by 0700 hours to 25.00% of the total duration (18.75 seconds per 10 minutes). Thus, while total migratory behavior temporarily increases after lights-on the average duration per trip declines rapidly. The peak in average duration per migratory trip occurred at 0500 hours for 71 seconds (Figure 9).

Migratory behavior by T. trichopterus averaged 7.46% of an observation period (Table XXXVIII, Appendix).

Courtship

Courtship activity includes male lateral display, female approach, and female butting. The frequencies and durations for these activities were summed and averaged to determine the general level of courtship activity during spawning intervals.

General Courtship Activity

The average frequency of courtship activity increased from five at 0500 hours to seven per 10 minutes at 0700, for *T. trichopterus* (Figure 7). Courtship for these same fish continued to increase, rising to 11-14 per 10 minutes between 0900 and 1100 hours. After 1100 hours, this activity dropped to four to seven per 10 minutes by 1600-1700 hours. An increase in courtship was recorded at 1900 hours (11 per 10 minutes), followed by a sharp reduction to six at 2300, and two per 10 minutes by 0300 hours.

Courtship activity during the lights-out period consisted almost entirely of female approach and male lateral display. Only two instances of female butting by the same fish were observed after lights-out, at 2200 hours. It was rarely observed any earlier than 0630 hours.

The frequency of courtship activity by *M. opercularis* rose to a morning high of 11-15 per 10 minutes one to two hours after lights-on, followed by a slight decline by 0900-1100 hours (Figure 7). By mid-afternoon, courtship activity exhibited a second rise averaging 12-16 per 10 minutes followed by a steady decline to 8-10 at 1600-1700 hours and continuing to decline after lights-out to three and then two per 10 minutes at 2300 and 0300 hours, respectively. Courtship activity increased steadily after 0300 hours rising to four at 0500 and reaching the morning high by 0700-0800 hours.

Only one instance of female butting was observed after lights-out, at 1945 hours. Thus, female approach and male lateral display were the two major courtship activities during the dark period.

The total duration of courtship activities per observation period were quite similar for both species. Peak durations (over 40 seconds per 10 minutes) were recorded at 0700, 1100, and 1500 hours (Figure 8). Both species showed temporary increases in the total duration of courtship activity following lights-out. By 2300 hours, courtship activity declined and remained at a low level (10 seconds per 10 minutes at 0300 hours) until an hour before lights-on when it began to increase sharply (50 seconds per 10 minutes at 0700 hours). Courtship activity averaged 5.94% and 6.16% of the recorded activity for *T. trichopterus* and *M. opercularis*, respectively (Table XXXVIII, Appendix).

The average duration of courtship displays ranged between 3.1-7.0 for *T. trichopterus* and 2.7-6.2 seconds for *M. opercularis*. Male lateral display averaged over 62% of the courtship activity (Table XL, Appendix). For this reason over-all courtship activity values increase and decrease with lateral display (Figures 9 and 10). Female approach averaged over 33% of the courtship activity for both species whereas female butting averaged only 3.35% and 1.53% for *T. trichopterus* and *M. opercularis*, respectively (Table XL, Appendix).

Peak durations in courtship activity occurred at 0700 and 1500 hours averaging 7.0 seconds per 10 minutes for *T. trichopterus*. *M. opercularis* exhibited peak durations at 0300, 0700, and 1600 hours averaging 6.0, 4.5, and 6.2 seconds per courtship activity, respectively (Figure 9).

Female Activity

Female activity includes approach, chasing, butting, and mouth-fighting by the females of both species. The frequencies and durations for these behaviors were summed and averaged to determine the general level of female activity.

General Agonistic Activity

During the hour after lights-out, *T. trichopterus* females increased their activity slightly, averaging seven per 10 minutes. Activity steadily decreased after 1900, averaging three and one per 10 minutes at 2300 and 0300 hours, respectively (Figure 7). After 0300 hours, female activity steadily increased averaging four and five per 10 minutes at 0500 and 0700 hours, respectively. By 0900, this activity averaged 10 per 10 minutes and reached a maximum of 13 per 10 minutes at 1100 hours. After 1100, activity decreased by as much as 50% until mid-afternoon (1500 hours) when occasionally a slight increase is noted followed by still further reductions. Between 1700-1900 hours, female activity once again begins to increase followed by the usual reductions.

Following lights-out, activity by *M. opercularis* females declined steadily averaging four activities per 10 minutes at 1900 hours, and decreasing to one per 10 minutes from 2300-0300 hours (Figure 7). After 0300, female activity increased slightly to two per 10 minutes at 0500 hours, reaching the morning maximums of six to eight per 10 minutes at 0700-0800 hours. A morning slump (0900-1100 hours) usually followed, averaging five to six activities per 10 minutes. After 1100, female activity began to rise reaching the daily high between 1300-1400 hours and averaging 8-10 per 10 minutes. Following these maximum frequencies, female activity steadily declined averaging three to seven per 10 minutes at 1600-1700 hours, followed by the usual reductions in lights-out activity.

The total duration of female activity per 10 minutes increased and decreased as did the frequency, for both species. Peak durations (over 20 seconds per 10 minutes) were recorded at 0800-0900, 1100, 1500, and 1900 hours for _T. trichopterus_ females. Relatively high durations (over 15 seconds per 10 minutes) were recorded for _M. opercularis_ females at 0700-0800, 1100, and 1300-1400 hours (Figure 8). Only _T. trichopterus_ showed an increase in female activity following lights-out.

The average duration of female activity ranged from 1.5-5.5 for _T. trichopterus_ and 2.2-4.3 seconds for _M. opercularis_. Peak durations for _T. trichopterus_ occurred between 0700-0900, 1500-1600 and 2300 hours averaging 3.4, 4.0-5.5, and 4.3 seconds, respectively, per female activity. _M. opercularis_ exhibited peak durations at 0700, 1600, and 2300 hours averaging 3.7, 4.3, and 4.0 seconds per female activity, respectively (Figure 9). Female activity averaged slightly more than 2% of the recorded time for both species (Table XXXVIII, Appendix).

Approach

An analysis of female behavior revealed that approach averaged 80.73% and 93.07% of the recorded time for this category by female _T. trichopterus_ and _M. opercularis_, respectively (Table XLI, Appendix).

The frequency of female approach follows very closely the increases and decreases of all female activity. This is not surprising since this activity contributes so heavily to this group of behaviors (Figure 7 and Table XLI, Appendix). Increases in the frequency of female approach occurred between 0800-1100 and 1900 hours averaging four and six activities per 10 minutes, respectively, for T. trichopterus. M. opercularis exhibited peaks in the frequency of female approach between 0700-0800 and 1300-1400 hours averaging between five to seven and six to eight activities per 10 minutes, respectively.

Female T. trichopterus averaged 11.29%, 5.62%, and 2.36%, of the time recorded in agonistic activity, for chasing, butting and mouthfighting, respectively, while M. opercularis females averaged 2.94% and 3.99% for chasing and butting, respectively (Table XLI, Appendix). No average values were obtained for M. opercularis mouthfighting.

Total Male Activity

The frequencies and durations of all male activity except resting were summed and averaged to determine the general activity level. Of the two species, M. opercularis are usually less active. Laboratory observations consistently show these fish perform most activities more frequently but for shorter durations than do T. trichopterus. The data support these observations (Figures 7 and 8).

Peak frequencies (above 70 per 10 minutes) in T. trichopterus male activity occurred between 0900-1100 and 1700 hours (Figure 7). The total duration of T. trichopterus activity per 10 minutes averaged over 500 seconds from 0700-1500 hours (Figure 8). Peak activity during lights-on reflected the low resting durations during this period, usually less than 50 seconds per 10 minutes until after 1300 hours when it increased slightly.

Similar results were recorded for M. opercularis, in which the frequency of total activity averaged over 80 per 10 minutes during the morning, dropping slightly to 70 by mid-afternoon, 1400-1500 hours (Figure 7). The total duration of male activity was usually over 400 seconds per 10 minutes during lights-on, decreasing rapidly after 2000 hours (Figure 8). Resting duration steadily increased (over 100 seconds per 10 minutes) during the lights-on period, as total activity decreased.

A large part of the daily activity (over 40%) was recorded as patrolling, for both species, so that the pattern of increases and decreases in total male activity closely followed those of patrolling activity (Figures 7, 8, and 9).

Total male activity averaged 82.95% and 66.72% of the recorded activity for T. trichopterus and M. opercularis, respectively, with the balance being made up of resting activity. Miscellaneous male activities including feeding, approaching, bubble blowing, yawning, chafing, and flexing averaged 18.91% and 13.98% for T. trichopterus and M. opercularis, respectively, (Table XXXVIII, Appendix).

Discussion

The likelihood of diurnal rhythms prompted this segment of the study. The need to understand and describe these activity cycles seemed obvious, since it was necessary to know if extended recordings (over 64 days) taken at approximately the same time every day would give a reliable measurement of fluctuations in pre- and post-spawning behavior.

In addition, it was important to know if fluctuations in pre- and post-spawning behavior could be distinguished from the normal fluctuations in daily behavior.

The data do seem to indicate a definite cycling of fish activities (Figures 6, 7, 8, 9, and 10). Thus it seemed reasonable to expect that changes in pre- and post-spawning behavior could be compared if one first understood the nature of the daily fluctuations in behavior between spawnings. The average values for various behaviors have been analyzed and their cycles described. The changes in the pre- and post-spawning behaviors are described in the next chapter.

The data utilized in describing activity cycles were obtained by observing and recording the daily behavior. However, no definitive explanation could be given for the causal factors underlying these behavior cycles since no experimental work was conducted.

An analysis of non-agonistic activity revealed that the males of both species spend more than 40% of their time in patrolling activity. Peaks in the frequency of patrolling coincided with peaks in inspiration and resting (Figure 7). This suggests that as the number of individual patrols increased the need for more oxygen increased and resting became more frequent. Usually agonistic activity and patrolling increased and decreased together. This correlation could be explained by the fact that with increased movement more encounters occur, resulting in increased agonistic activity although other explanations are possible. However, this explanation does not always hold true, especially during the increase in patrolling duration after lights-out at which time the total duration of butts and bites declines. This also does not explain the apparent lag between peaks in patrolling and agonistic activity. Another point requiring clarification is the rapid increase in agonistic activity prior to lights-on, followed by a sharp decline, while patrolling continues to increase. The early increase in aggressiveness, prior to lights-on, is perhaps due to the reestablishment of a territory (nest-site) and/or the reassertion of male dominance as he moves about the tank.

During the lights-out period, an inverse relationship exists between total patrolling duration and resting. That is, as patrolling declines total resting durations increase. However, individual patrols and rest periods appear to increase together during the lights-out period (Figures 8 and 9). Apparently during this period longer rests are possible due to a decrease in agonistic activity and fewer patrols. However, when a patrol is initiated it lasts for a longer period of time than usual, perhaps due to a lack of visual contact with the female, which results in fewer agonistic encounters.

Like patrolling activity, migratory behavior seems to coincide with agonistic activity and probably for the same reason. That is, increased fluttering activity by _T. trichopterus_ males seems to attract the female and frequently this contact is followed by agonistic activity. The longest migratory trips occurred just prior to lights-on and declined shortly afterward (Figures 8 and 9).

Courtship and female behavior followed a similar pattern simply because they included some behaviors common to both categories. Certain differences did exist: for example, after 0900 male lateral display by _M. opercularis_ increased sharply thereby increasing the degree of courtship activity compared to a slow rise in female activity (Figures 8 and 10).

Major differences between the two species seemed to be higher frequencies and lower durations for most behaviors in *M. opercularis* as compared with *T. trichopterus*. However, *M. opercularis* did exhibit higher resting durations and frequencies compared to *T. trichopterus* (Figures 7, 8, and 9).

CHAPTER VIII

PRE- AND POST-SPAWNING BEHAVIOR CHANGES

Descriptions of behavioral changes during the spawning cycles of fish have been reported by Forselius (1957), Pal and Southwick (1966), Ward (1966), Hall and Miller (1968), and Wimmer (1970).

More quantitative approaches to the analysis of behavioral changes during spawning sequences were published by Barlow (1964), Greenberg, Zijlstra and Baerends (1965), Miller and Hall (1968).

During this study, a quantitative approach was used to detect differences and similarities in trends, primarily between male _T. trichopterus_ and _M. opercularis_ behavior patterns, during the spawning cycle.

Of thirty-eight different behavior patterns monitored during this study, twenty male activities and three female activities are analyzed. The remaining activities are omitted because of infrequent occurrences.

The data used in the analysis of pre- and post-spawning behaviors are based on four tanks of each species, each tank containing one male and one female. Seven _T. trichopterus_ and eight _M. opercularis_ spawnings were recorded in these tanks and the data derived from 20 minutes of daily observation (total of morning and afternoon observation periods) are used to determine the fluctuations in the daily activity. The duration of each behavior in seconds is averaged to provide mean daily figures. The cumulative daily totals for the four pairs of fish are averaged for each activity.

Following an extended series of pre- and post-spawning observations, an 11-day period was selected as a reasonable length of time to determine trends for most behaviors. Figure 11 illustrates the pre- and post-spawning fluctuations for the duration of patrolling per 20 minutes over a 43-day period. All other daily activities are graphed from five days before spawning (D-5) to five days after spawning (D+5) with the spawning day designated as (Do).

The various behavior patterns analyzed were clustered in six presumably functional classes of fish activity to show the pre- and post-spawning fluctuations: Non-agonistic activity, agonistic activity, migratory behavior, courtship, parental behavior, and maintenance behavior.

Non-Agonistic Activity

Under this category, the duration of patrolling is used as an index of non-agonistic activity.

Total Patrolling Duration

During non-reproductive periods, the duration of patrolling averages more than 600 seconds (>50%) per 20 minutes for both species. During reproductive periods, T. trichopterus patrolling is reduced by 45%, averaging 345 seconds per 20 minutes. Wimmer (1970) reports smaller reductions (18.4%) in patrolling at the onset of spawning behavior by T. microlepis. Patrolling by M. opercularis on the spawning day may actually increase slightly but it is still 10-15% lower than

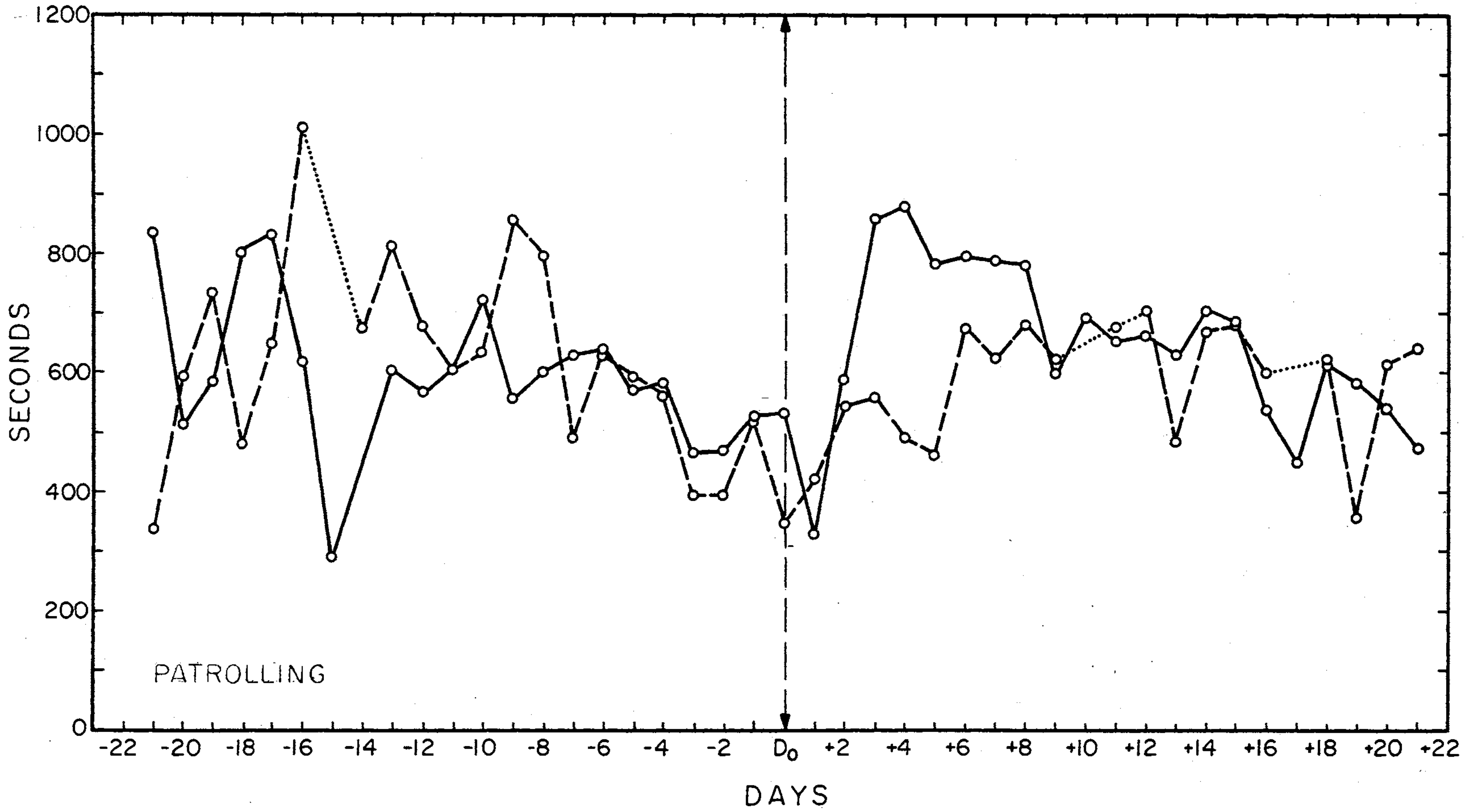

Figure 11. Average Total Patrolling Durations of Males Per Twenty-Minute Period, From Twenty-One Days Before (D-21) Until Twenty-One Days After (D+21) Spawning. *T. trichopterus* (Dashed Line) Four Pairs With Seven Spawnings and *M. opercularis* (Solid Line) Four Pairs With Eight Spawnings. Data Not Recorded (Dotted Line). D_0 = Spawning Day.

nonreproductive patrolling, averaging 535 seconds per 20 minutes (Figure 11).

Maximum patrolling durations for T. trichopterus reached 1013 seconds per 20 minutes 16 days before spawning; whereas, maximum patrolling duration for M. opercularis reached 882 seconds four days after spawning. Noticeable reductions in T. trichopterus patrolling, following a series of highs, occurred on the spawning day, averaging 345 seconds per 20 minutes, but M. opercularis did not exhibit similar reductions in patrolling until one day after spawning averaging 333 seconds per 20 minutes (Figure 11). Following these lows, the duration of patrolling began to increase rapidly for both species, averaging well over 500 seconds per 20 minutes two days after spawning.

Pre-spawning patrolling durations decreased from 1013 seconds 16 days before spawning to 345 seconds per 20 minutes on the spawning day for T. trichopterus and for M. opercularis from 605 seconds 13 days before spawning to 333 seconds per 20 minutes one day after spawning. This decreasing trend is then reversed after spawning, rising rapidly to postspawning peaks. T. trichopterus patrolling durations continue to increase from the spawning day to 12 days after spawning reaching 707 seconds per 20 minutes followed by a declining trend 19 days after spawning averaging 358 seconds per 20 minutes. M. opercularis patrolling durations begin to increase one day after spawning reaching a peak three days later (D+4) averaging 882 seconds per 20 minutes followed by a steady decline to 471 seconds 21 days after spawning (Figure 11).

Duration of Individual Patrols

Like total patrolling duration, single patrol durations were shorter during reproductive periods than in nonreproductive periods averaging 7.32 and 10.53 seconds, respectively, for *T. trichopterus* and 8.38 and 8.90 seconds per 20 minutes, respectively, for *M. opercularis*. Thus, a reduction in total patrolling is accompanied by a proportional reduction in patrolling frequency resulting in shorter individual patrols. Wimmer (1970) found that single patrol durations were longer in reproductive rather than nonreproductive periods when studying *T. microlepis*.

Agonistic Activity

Agonistic activities by both sexes occur during the spawning sequences as well as between them. As spawning time approaches, a general increase in the duration of agonistic activities occurs (Figures 12 and 13).

Approach, Lateral Displays, and Opercle Spreads

In tanks of nonreproductive *T. trichopterus*, the total duration of male approach and lateral display averaged 52 and 45 seconds per 20 minutes, respectively. Two days before spawning, males exhibited increased durations of these behaviors, averaging 60 and 47 seconds per 20 minutes, respectively. Substantial reductions in the duration of approach and lateral display (averaging 22 and 31 seconds per 20 minutes, respectively) occurred on the spawning day. One day after spawning, the total duration of male approach increased to 45 seconds per 20 minutes and the total duration of lateral display decreased to

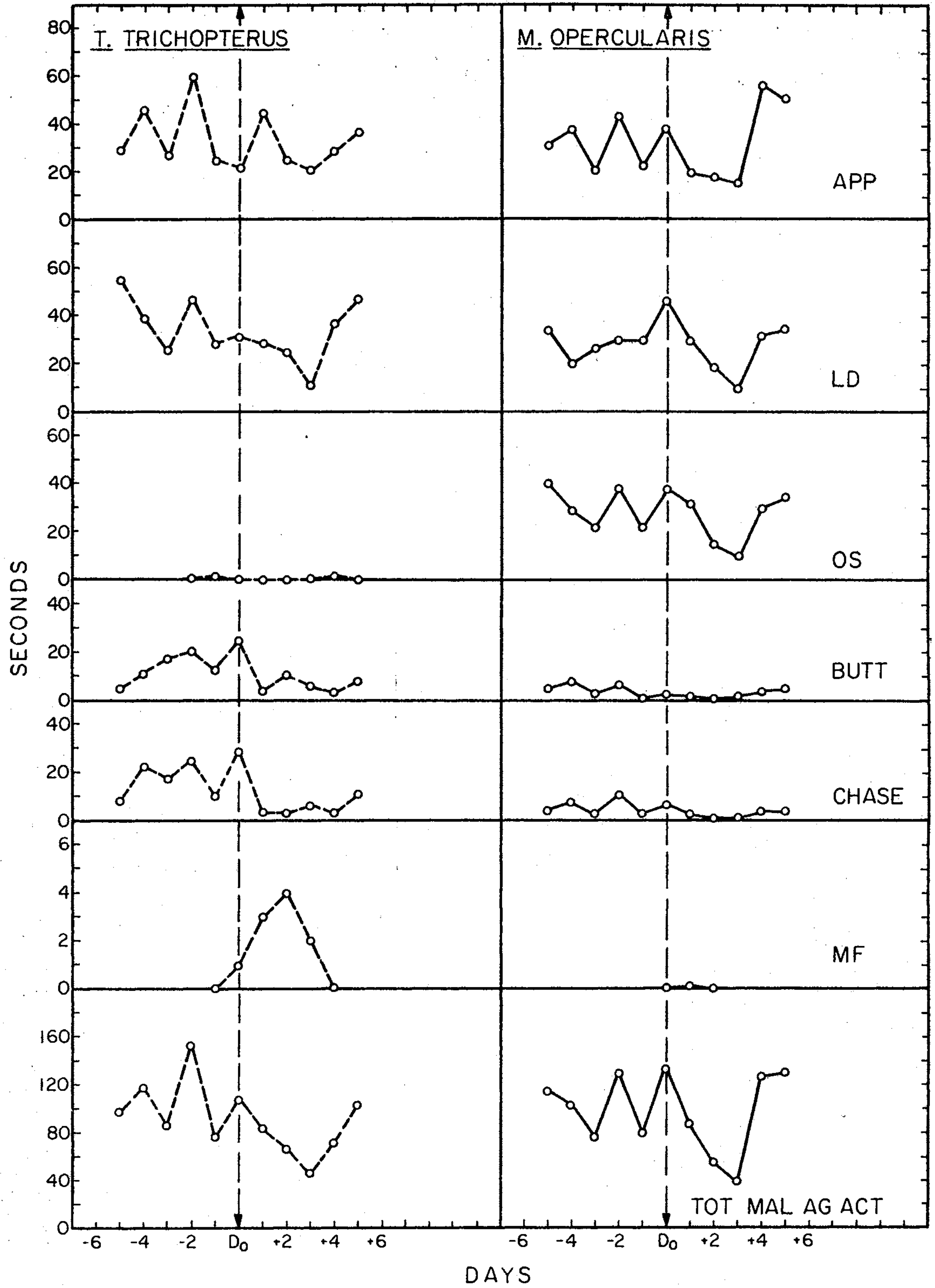

Figure 12. Average Total Durations of Male Agonistic Activities Per Twenty-Minute Period, From Five Days Before (D-5) Until Five Days After (D+5) Spawning. Tot Mal Ag Act is the Sum of all Averages, to Show the Amount of Time Spent in Total Male Agonistic Activity. APP = Approach; LD = Lateral Display; OS = Opercle Spread; Butt = Butting; Chase = Chasing; MF = Mouthfighting; Do = Spawning Day

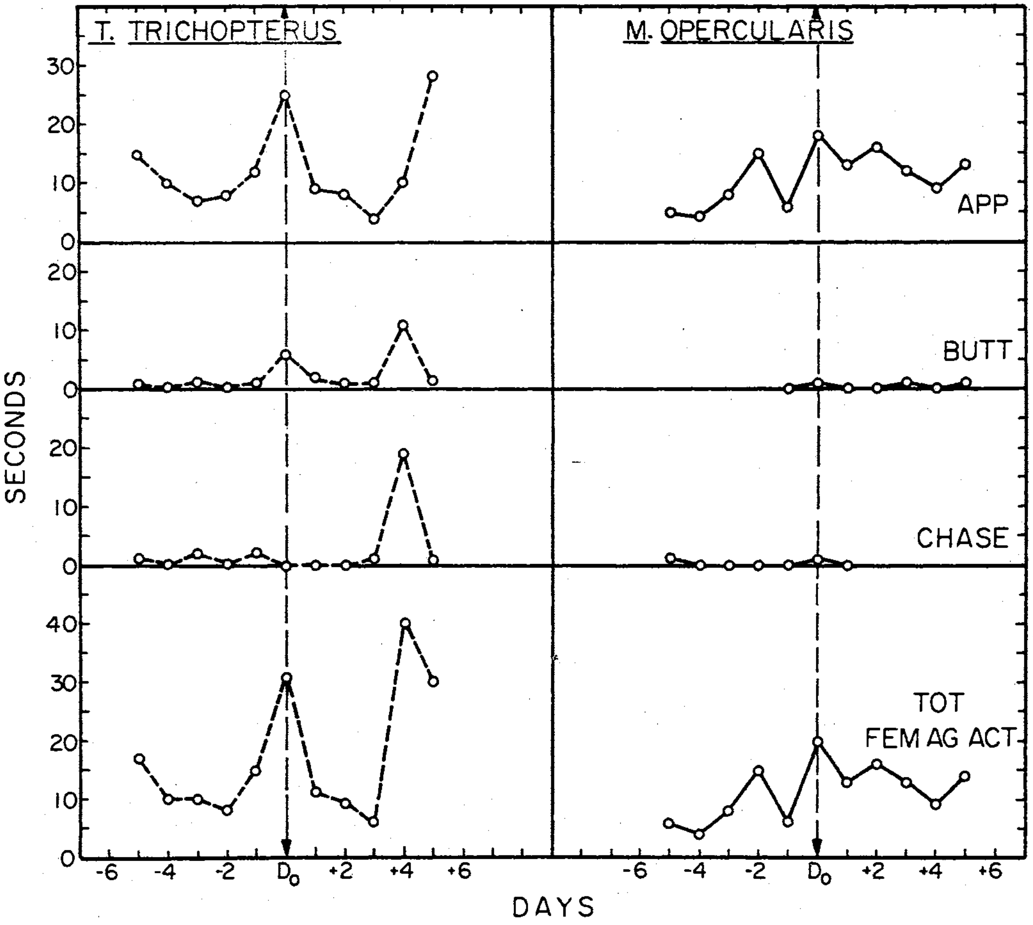

Figure 13. Average Total Durations of Female Agonistic Activities Per Twenty-Minute Period, From Five Days Before (D-5) Until Five Days After (D+5) Spawning. Tot Fem Ag Act is the Sum of All Averages, to Show the Amount of Time Spent in Total Female Agonistic Activity. APP = Approach; Butt = Butting; Chase = Chasing; Do = Spawning Day

29 seconds followed by sharp decreases in both behaviors during the next two days. By the fourth and fifth days after spawning, the durations of approach and lateral display increased rapidly averaging 37 and 47 seconds per 20 minutes, respectively (Figure 12).

In contrast, female _T. trichopterus_ exhibit sharp increases in the duration of approach on the spawning day averaging 25 seconds per 20 minutes. During the four days preceding and following spawning, female approach was reduced by more than 50% averaging 9.25 and 7.75 seconds per 20 minutes, respectively. Increased durations for female approach occurred five days after spawning averaging 28 seconds per 20 minutes (Figure 13).

Little or no opercle spread was recorded during the observation periods for _T. trichopterus_.

In tanks of nonreproductive _M. opercularis_, the total duration of male approach and lateral display was 77 and 60 seconds per 20 minutes, respectively. During the 11-day period selected, the total durations of approach and lateral display were considerably reduced from the nonreproductive levels. For example, two days before spawning the total duration of male approach averaged 44 seconds per observation period and declined sharply on the following day to 23 seconds only to rise again on the spawning day, averaging 39 seconds per 20 minutes. After spawning, male approach rapidly declined, averaging 16 seconds per 20 minutes on the third day. By the fifth day the trend had reversed and the total duration of male approach averaged 51 seconds per 20 minutes (Figure 12).

The total duration of male lateral display averaged 30 seconds per observation period one day before spawning. On the spawning day, a maximum for the 11-day period of 47 seconds of lateral display per 20 minutes was recorded. After spawning, the duration of lateral display declined, reaching a low of 10 seconds per 20 minutes on the third day and rising to 35 seconds per observation period on the fifth day (Figure 12). Six days after spawning M. opercularis exhibited the nonreproductive levels of male approach and lateral display.

A notable increase in the total duration of male opercle spread occurred two days before spawning and on the spawning day averaging 38 seconds per 20 minutes on both days. After spawning a steady decline for three days, followed by a rise in the total duration of opercle spreading was noted, almost identical in duration to lateral display (Figure 12). This is not surprising since male M. opercularis frequently exhibit both lateral display and opercle spread when approaching a female, especially on the spawning day.

Maximum durations for female approach occur on the spawning day, averaging 18 seconds per 20 minutes. During the five days preceding and following spawning, female approach averaged 7.60 and 12.60 seconds per 20 minutes, respectively (Figure 13). Peaks in the duration of approach by male and female M. opercularis occurred on the spawning day, but the total durations for both sexes were quite different. Males averaged 39 seconds and females 18 seconds of approach per 20 minutes (Figures 12 and 13).

Butting and Chasing

In tanks of nonreproductive T. trichopterus, the total duration of male butting and male chasing averaged nine seconds per 20 minutes for each activity. The total duration of butting and chasing increased from nonreproductive levels, five days before spawning, to maximum durations averaging 25 and 29 seconds per 20 minutes, respectively, on the spawning day. One day after spawning, the total butting and chasing durations averaged four and three seconds per 20 minutes, respectively, and reached nonreproductive levels five days after spawning (Figure 12).

Female butting increased on the spawning day, averaging six seconds per 20 minutes compared to one second one day before spawning. After spawning, butting durations again declined and did not rise again until four days later, averaging 11 seconds per 20 minutes (Figure 13). Usually, female T. trichopterus do show a marked increase in butting on the spawning day, especially during an actual spawning sequence. However, this increase could only be measured during a spawning and would not show up in the daily records.

Low levels of female chasing occurred during the five days preceding spawning, averaging one to two seconds per 20 minutes of daily observation. On the spawning day and the two following days, no female chasing was recorded. However, by the third day after spawning, female chasing resumed and a maximum duration of 19 seconds per 20 minutes was reached on the fourth day (Figure 13).

During nonreproductive behavior, M. opercularis males averaged nine and six seconds per 20 minutes, respectively, butting and chasing females. Two days before spawning, these two behaviors averaged seven and 11 seconds per 20 minutes, respectively, and declined on the spawning day to three and seven seconds of butting and chasing per observation period. After spawning, both activities remained at low levels slowly rising and only reaching nonreproductive levels six days later (Figure 12).

Female M. opercularis exhibit lower levels of butting and chasing on the spawning day than males, averaging one second per 20 minutes for each activity, respectively. During the entire 11-day period, very little female butting and chasing ensued (Figure 13). Both sexes of T. trichopterus show distinctly higher durations of butting and chasing when compared to M. opercularis (Figures 12 and 13).

Mouthfighting

Mouthfighting was more pronounced between male and female T. trichopterus than in M. opercularis, which rarely exhibited this behavior. During nonreproductive periods, T. trichopterus averaged one second of mouthfighting per 20 minutes. Little or no mouthfighting was recorded during the five days preceding spawning. The maximum duration for T. trichopterus mouthfighting was reached two days after spawning averaging four seconds per 20 minutes followed by a rapid decline (Figure 12).

Total Agonistic Activity

Agonistic activity by nonreproductive male and female T. trichopterus averaged 124 and 41 seconds per 20 minutes, respectively. Maximum male agonistic activity occurred two days before spawning, averaging 152 seconds per 20 minutes followed by a 50% reduction in this activity (76 seconds) the day before spawning. On the spawning day, male agonistic activity increased to 108 seconds per 20 minutes. After spawning, agonistic activity began to decline reaching a low of 47 seconds per 20 minutes three days later. By the fifth day, it was evident that male agonistic activity was again increasing and the total duration per 20 minutes was 103 seconds (Figure 12).

Agonistic activity by female _T. trichopterus_ averaged 12 and 21 seconds per 20 minutes during the five days preceding and following spawning, respectively. On the spawning day, it increased to 32 seconds per 20 minutes followed by a steady decline, reaching a low of eight seconds per 20 minutes three days later. On the fourth day (D+4), agonistic activity increased sharply, averaging 40 seconds per 20 minutes (Figure 13).

The total duration of agonistic activity by nonreproductive _M. opercularis_, male and female fish, averaged 203 and 31 seconds per 20 minutes, respectively. Maximum durations of agonistic activity during the 11-day period were recorded on the spawning day for both males and females, averaging 134 and 20 seconds per 20 minutes, respectively. Three days after spawning, male agonistic activity had declined to a low of 39 seconds per 20 minutes and agonistic activity by females declined to nine seconds on the fourth day (D+4). Agonistic activity by male and female fish increased sharply five days after spawning, averaging 130 and 14 seconds per 20 minutes, respectively (Figures 12 and 13).

Since female lateral display and opercle spread were not monitored in either species, the total duration of female agonistic activity could be somewhat misleading. Therefore, comparisons of total agonistic activity between males and females should not be made. However, comparisons of pre- and post-spawning changes in agonistic activity for either sex are considered valid. For example, changes in total female agonistic activity before and after spawning can be compared because the same behaviors were monitored: approach, butting and chasing.

Migratory Behavior

In nonreproductive male *T. trichopterus*, migratory behavior averaged 52 seconds per 20 minutes; whereas, in non-reproductive *M. opercularis* males, migratory behavior occurred too infrequently to be measured. One day before spawning, migratory behavior by *T. trichopterus* males increased sharply averaging 47 seconds per 20 minutes of observation. In one case, a male (B-17) exhibited migratory behavior on this day (D-1) for 282 seconds per 20 minutes; in other cases, no migratory behavior was observed. On the spawning day, migratory behavior declined to only eight seconds per 20 minutes. After spawning, the behavior was erratic, averaging 32 seconds per 20 minutes four days later (D+4) and declining to zero on the fifth day (D+5) (Figure 14).

Three to five days before spawning, *M. opercularis* males exhibited traces of migratory behavior averaging only one second per 20 minutes. No further display of this behavior was observed during the 11-day period (Figure 14). This difference in the amount of migratory behavior between the males of the two species was confirmed during long-term laboratory observations. *T. trichopterus* exhibited this activity much more frequently and for longer durations than *M. opercularis*.

No migratory behavior was ever observed in the females of either species, probably because of male dominance which restricted female movement in the tank.

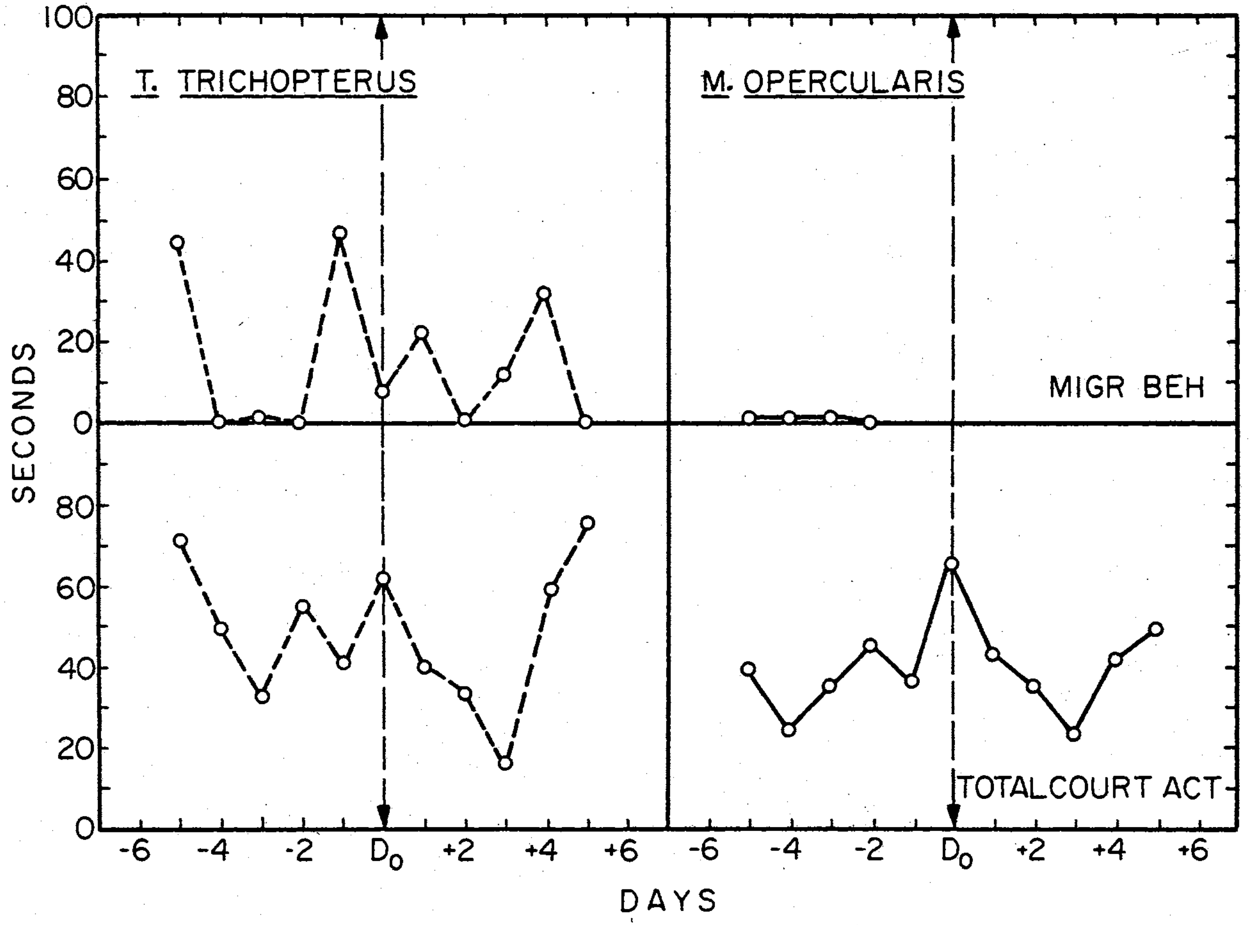

Figure 14. Average Total Durations of Migratory Behavior and Courtship Activity Per Twenty-Minute Period, From Five Days Before (D-5) Until Five Days After (D+5) Spawning. Tot Court Act is the Sum of Male Lateral Display, Female Approach and Female Butting to Show the Amount of Time Spent in Total Courtship Activity. Migr Beh = Migratory Behavior by Males; Do = Spawning Day

Courtship

The duration of male lateral display, female approach and female butting, is used as an index of courtship activity. Other courtship activities occurred too infrequently to be included. In non-reproductive *T. trichopterus* and *M. opercularis*, courtship activity averaged 77 and 89 seconds per 20 minutes, respectively.

During the five days preceding spawning, courtship activity averaged 50 and 36 seconds per 20 minutes for *T. trichopterus* and *M. opercularis*, respectively. On the spawning day, courtship activity increased for both species, averaging 62 and 66 seconds per 20 minutes for *T. trichopterus* and *M. opercularis*, respectively. After spawning, courtship activity declined rapidly and by the third day (D+3) averaged only 16 and 23 seconds per 20 minutes for *T. trichopterus* and *M. opercularis*, respectively. Five days after spawning, the total courtship duration reached a maximum of 76 seconds for *T. trichopterus* and only 49 seconds per 20 minutes for *M. opercularis* (Figure 14).

Parental Behavior

A strict definition of parental behavior would include the care and protection given the eggs and fry by the adult fish following the first spawning bout. However, fluctuations in nestbuilding both preceding and following a spawning sequence can also be compared, and are herein considered as part of the functional complex of parental activities.

Bubble Blowing

During nonreproductive periods, surface bubble blowing by *T. trichopterus* males ranges from one to 304 seconds with an average duration of 120 seconds per 20 minutes of observation. During the five days preceding spawning, surface bubble blowing declines, averaging 140 seconds five days before spawning to 64 seconds two days later (D-3) followed by a sharp increase to 427 seconds per 20 minutes on the spawning day. Surface bubble blowing reaches maximum duration two days after spawning, averaging 465 seconds, followed by a steady decline reaching a low of 86 seconds per 20 minutes five days after spawning (Figure 15). Only male *T. trichopterus* exhibit surface bubble blowing.

Subsurface bubble blowing is performed by the males of both species and female *M. opercularis*. During nonreproductive periods, the duration of this behavior ranges from zero to 249 seconds (averaging 125 seconds) for *T. trichopterus* and from zero to 165 seconds (averaging 60 seconds) per 20 minutes for male *M. opercularis*. As spawning approaches males of both species exhibit increasing durations of subsurface bubble blowing. Maximum durations for this activity average 476 seconds on the spawning day by *T. trichopterus* and 411 seconds per 20 minutes one day after spawning by *M. opercularis*. *T. trichopterus* bubble blowing steadily declines after spawning, averaging only 148 seconds on D+2, but then begins to increase, averaging 280 seconds per 20 minutes five days after spawning. *M. opercularis* exhibit a similar decreasing trend of bubble blowing, reaching a low of only three seconds per 20 minutes four days after spawning, followed by a slight increase the next day (D+5) (Figure 15).

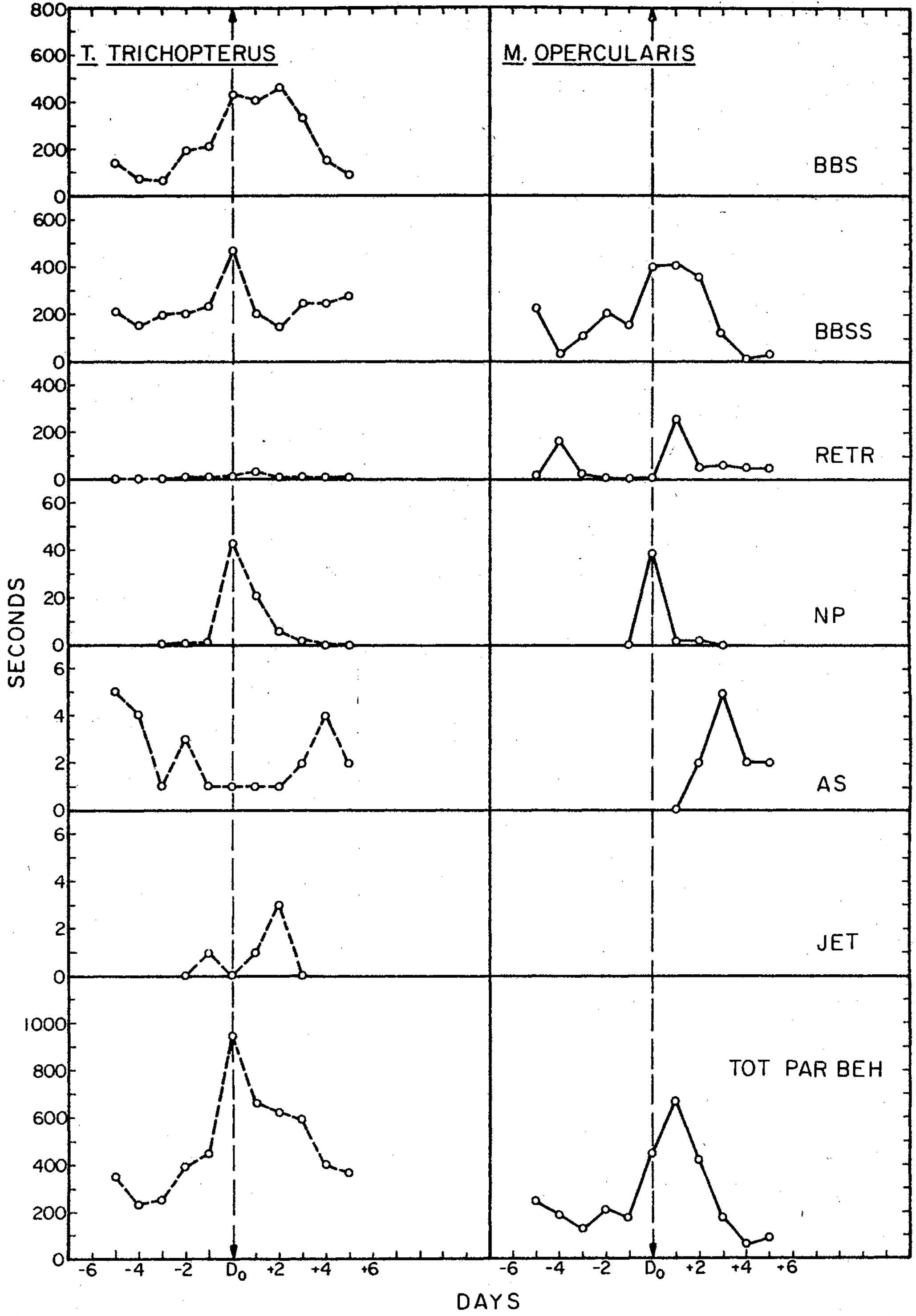

Figure 15. Average Total Durations of Parental Behavior of Males Per Twenty-Minute Period, From Five Days Before (D-5) Until Five Days After (D+5) Spawning. Tot Par Beh is the Sum of All Averages, to Show the Amount of Time Spent in Total Parental Behavior. BBS = Surface Bubble Blowing; BBSS = Subsurface Bubble Blowing; Retr = Retrieve Eggs and Fry; NP = Nestpushing; AS = Attacking Snails; Jet = Jetting; D_o = Day of Spawning.

Retrieving

Male retrieving was sometimes recorded before spawning either because fry may have been present in the tank from a previous spawning or displacement retrieving occurred. In this case, there is no difference in the motor pattern from an actual retrieve. For this reason, retrieving is considered to begin on the spawning day for both species.

Retrieving on the spawning day averaged seven and four seconds per 20 minutes by *T. trichopterus* and *M. opercularis*, respectively. Maximum durations for retrieving occurred one day after spawning, averaging 31 and 258 seconds per 20 minutes by *T. trichopterus* and *M. opercularis*, respectively. Retrieving by *T. trichopterus* declined sharply during the next four days (D+2 to D+5), averaging only three seconds per 20 minutes. *M. opercularis* also exhibited reduced durations of retrieving during the same period averaging 58 seconds per 20 minutes of observation (Figure 15).

Nestpushing

Nestpushing is performed by the males of both species. Maximum duration occurred on the spawning day, averaging 43 seconds by *T. trichopterus* and 39 seconds per 20 minutes by *M. opercularis*. One day after spawning, nestpushing is greatly reduced, averaging 21 seconds and two seconds per 20 minutes by *T. trichopterus* and *M. opercularis*, respectively. Three days later (D+4), nestpushing is discontinued by both species. One difference between the two species is that *T. trichopterus* begin nestpushing one day sooner (D-1) and end one day later (D+3) than *M. opercularis* (Figure 15).

Attacking Snails

Nonreproductive males of both species attacked snails for one to two seconds per 20 minutes of observation. *T. trichopterus* exhibited more consistent snail attacks throughout the 11-day period than *M. opercularis*, who exhibited this behavior for only four days after spawning (D+2 to D+5). Maximum durations averaged five seconds per 20 minutes for both species. However, the peak in snail attacks by *T. trichopterus* occurred five days before spawning; whereas, *M. opercularis* exhibited a similar peak three days after spawning (Figure 15).

Jetting

Only *T. trichopterus* males exhibited jetting during the recording sessions, but *M. opercularis* males were observed jetting at other times. Jetting by *T. trichopterus* infrequently occurred both before and after spawning. But maximum durations occurred two days after spawning, averaging three seconds per 20 minutes (Figure 15).

Total Parental Behavior

T. trichopterus males spend more time performing parental activities during the spawning day, than on the days that follow. From a low of 229 seconds four days before spawning to a maximum of 954 seconds per 20 minutes on the spawning day, *T. trichopterus* exhibit a sharp increase in parental activity. After spawning, the duration of parental activity declines rather slowly, averaging as much as 371 seconds five days later (D+5) (Figure 15).

M. opercularis males exhibit a slightly different pattern of parental activity than *T. trichopterus*, since maximum durations do not occur until one day after spawning, averaging 671 seconds per 20 minutes. A very rapid decline in the duration of parental activity follows averaging only 62 seconds per 20 minutes four days after spawning (Figure 15).

Nest Size

The nests of *T. trichopterus* and *M. opercularis*, in aquaria, are usually constructed entirely of bubbles, but occasionally floating debris, plant fragments, etc., do become incorporated into the nest.

Nest size can vary considerably from one spawning to the next. In fact, spawnings by both species have been observed in which no nest was present. In some cases maximum nest size was not always attained on the spawning day. During the spawning day and on the days that follow, the nest was constantly being attended and frequently reached maximum size one to two days after spawning. Five *T. trichopterus* nests ranged in diameter, on the spawning day, from 8 mm to 67 mm, with an average of 19.8 mm. Five *M. opercularis* nests ranged from 8 mm to 119 mm on the spawning day, and averaged 49.4 mm in diameter. The average nest size reached a maximum diameter on D+2, averaging 29.2 and 67.8 mm for *T. trichopterus* and *M. opercularis*, respectively (Table XIII).

The age or past experience of a male in nest construction appeared to have little or no effect on the size of the nest. For example, male P-7 spawned three times during the study and, in the order constructed, built the following nests on the spawning day: 119 mm, 62 mm, and 45 mm in diameter (Table XIII).

The size of the fish in relation to nest size shows some correlations. Larger fish tend to construct larger nests, but occasionally the

TABLE XIII

FISH SIZE AND PREVIOUS NESTING EXPERIENCE IN RELATIONSHIP TO NEST SIZE

Fish	Standard Length (mm)	Daily Nest Size Diameter (mm)				Spawning Number	Avg. Diam. (mm)
T. trichopterus		D_o	D+1	D+2	D+3		
B-10	53.6	8	36	88	62	2	48.5
B-2	59.5	8	62	8	8	2	21.5
		8	8	8	8	4	8.0
B-17	63.3	8	22	8	8	2	11.5
		67	8	34	45	3	38.5
Average		19.8	27.2	29.2	26.2		25.6
M. opercularis							
P-4	37.6	22	22	62	8	2	28.5
P-7	55.8	119	8	88	80	1	73.7
		62	8	8	8	2	21.5
P-14	59.0	36	67	130	124	1	89.25
		8	8	51	36	2	25.7
Average		49.4	22.6	67.8	51.2		47.73

larger fish construct some of the smallest nests and three small males constructed nests above average size (Table XIII).

Maintenance Behavior

Maintenance activity and comfort movements are behavior patterns concerned with sustenance and body care of the individual fish, rather than social contact. In some instances, they may also act as social signals. The maintenance behaviors monitored were inspiration, feeding, and resting. Comfort movements included yawning, chafing, and flexing. These activities were grouped together since they apparently have similar functions.

Generally, there is a reduction in the amount of maintenance activity and comfort movements on the spawning day. This reduction is accompanied by a sharp increase in parental, agonistic, and courtship activities.

Inspiration

Inspiration during nonreproductive periods averaged 47 and 26 seconds per 20 minutes by *T. trichopterus* and *M. opercularis*, respectively. Maximum durations of *T. trichopterus* inspiration occurred one day before spawning averaging 112 seconds per 20 minutes. Inspiration then decreased on the spawning day by as much as 81% (averaging 21 seconds per 20 minutes). One day after spawning, *T. trichopterus* inspiration averaged 99 seconds per 20 minutes and rapidly declined during the following days averaging only 15 seconds five days later (D+5) (Figure 16).

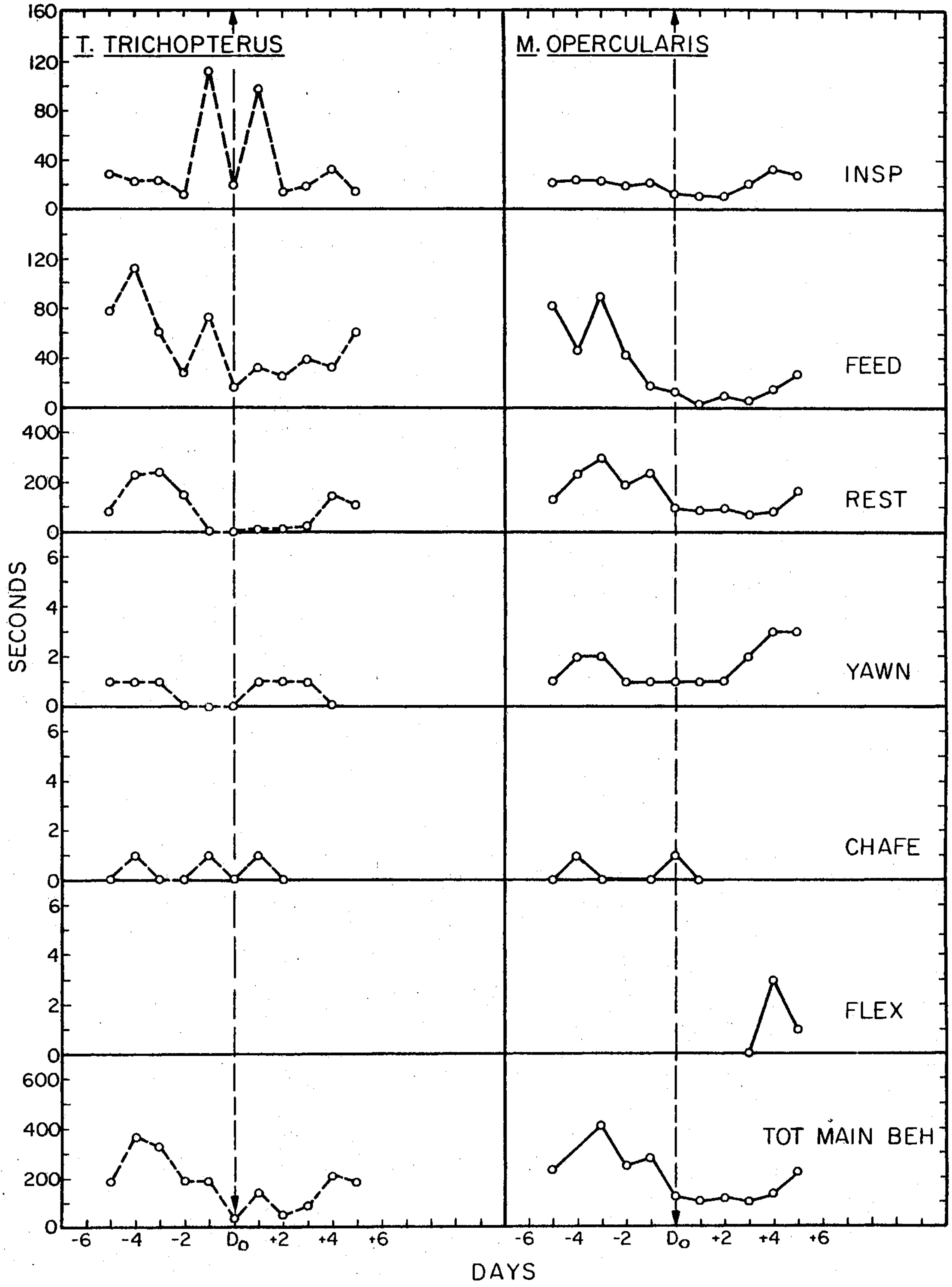

Figure 16. Average Total Durations of Maintenance Behavior of Males Per Twenty-Minute Period, From Five Days Before (D-5) Until Five Days After (D+5) Spawning. Tot Main Beh is the Sum of All Averages, to Show the Amount of Time Spent in Total Maintenance Behavior. INSP = Inspiration; Do = Spawning Day

M. opercularis exhibited a small increase in inspiration one day before spawning averaging 22 seconds followed by a decline on the spawning day averaging only 12 seconds per 20 minutes. Nonreproductive levels of inspiration were reached five days after spawning, averaging 28 seconds per 20 minutes (Figure 16).

The difference in the maximum duration of inspiration for the two species (112 versus 34 seconds per 20 minutes), resulted from T. trichopterus typically spending longer periods of time inspiring than M. opercularis, especially during periods of nestbuilding.

Feeding

Feeding behavior was monitored several hours before or after food was placed in the aquaria. Pronounced fluctuations in the duration of feeding occurred before spawning, resulting in a decrease in this activity as the spawning day approaches. The lowest feeding durations of the entire 11-day period were recorded on the spawning day.

Nonreproductive T. trichopterus feed for an average of 113 seconds and M. opercularis average 56 seconds per 20 minutes. The maximum T. trichopterus feeding durations during the 11-day period occurred four days before spawning, averaging 113 seconds per 20 minutes. Feeding on the spawning day decreased to only 17 seconds per 20 minutes. After spawning, T. trichopterus feeding durations increased steadily, averaging 61 seconds per 20 minutes on D+5 (Figure 16).

M. opercularis exhibited maximum feeding durations three days before spawning, averaging 90 seconds per 20 minutes. On the spawning day, feeding averaged 13 seconds followed by a decline averaging only three seconds per 20 minutes one day later. A slow increase in

M. opercularis feeding durations occurred during the next four days averaging 28 seconds per 20 minutes on D+5 (Figure 16).

Resting

Resting is a frequent activity of both species, but both show substantial reductions in rest duration on the spawning day. Nonreproductive T. trichopterus and M. opercularis average 124 and 359 seconds per 20 minutes resting, respectively. As spawning time approaches a peak in T. trichopterus and M. opercularis, resting durations occur three days before spawning, averaging 244 and 300 seconds per 20 minutes, respectively. On the spawning day, resting durations average one and 96 seconds per 20 minutes for T. trichopterus and M. opercularis, respectively. After spawning, resting increases slowly and on D+5 averages 109 and 162 seconds per 20 minutes for T. trichopterus and M. opercularis, respectively (Figure 16).

One explanation for the difference in resting durations on the spawning day is that T. trichopterus spend more time nestbuilding on this day than do M. opercularis. Another reason is simply that M. opercularis usually spend more time resting than do T. trichopterus, as evidenced by the average figures for nonreproductive fish (359 versus 124 seconds per 20 minutes, respectively).

Yawning, Chafing and Flexing

During nonreproductive periods, yawning and chafing by T. trichopterus occurred infrequently, ranging from zero to one second per 20 minutes. In nonreproductive M. opercularis, yawning was frequently observed for one to two seconds per 20 minutes, whereas chafing was rare. Flexing by either species during nonreproductive periods was also rare.

Both yawning and chafing appear with low frequencies before spawning by the two species. Usually, each yawn or chafe consumes about one second. T. trichopterus exhibited no yawning or chafing on the spawning day, during the 20-minute observation period. Both behaviors did occur once on the following day (Figure 16).

M. opercularis differ slightly since they exhibit yawning continuously throughout the 11-day period. Generally, yawning occurred for one to two seconds per 20 minutes until two to three days after spawning. Four to five days after spawning, yawning durations for M. opercularis increased, averaging three seconds per 20 minutes. Chafing by M. opercularis occurred once during the observation period on the spawning day (Figure 16).

Flexing is usually observed several days before or after a spawning in both species. However, T. trichopterus did not exhibit a sufficient amount of flexing for comparison. Flexing by M. opercularis was observed on the fourth and fifth day after spawning, averaging three and one seconds per 20 minutes, respectively (Figure 16).

Total Maintenance Behavior

The total duration of maintenance behavior declines steadily as the spawning day approaches. This is followed by a slow recovery which never quite reaches pre-spawning levels by D+5.

A peak in T. trichopterus maintenance activity occurred four days before spawning, averaging 370 seconds, and declined to 39 seconds per

20 minutes on the spawning day. After spawning, T. trichopterus exhibit a fluctuating trend with an over-all increase in maintenance activity which averaged 185 seconds per 20 minutes five days after spawning.

Maximum maintenance activity, by M. opercularis, occurred three days before spawning, averaging 415 seconds and declining to 123 seconds per 20 minutes on the spawning day. The decline in maintenance activity continued until three days after spawning, reaching a low of 100 seconds per 20 minutes. Two days later (D+5), maintenance activity by M. opercularis averaged 222 seconds per 20 minutes (Figure 16).

Certain differences regarding maintenance activity exist between the two species. The maximum duration of maintenance activity occurs one day sooner for T. trichopterus (D-4) than for M. opercularis (D-3). Resting durations for both species are an exception, since each reach maximum values on the same day (D-3). Another difference is the relative amount of maintenance activity on the spawning day. M. opercularis spent almost 32% more time in maintenance activities on the spawning day than T. trichopterus. One contributing factor was the large amount of time M. opercularis spent in resting.

Fluctuations in Pre- and Post-Spawning Activities

One of the objectives of this study is to compare the rates of increase and decrease of several functional classes of behavior during the spawning cycle. As spawning approaches, the relative fluctuations in activity levels can also be determined. However, the maximum duration of activity, per 20 minutes, varies considerably with each class of behavior. This makes it difficult to compare the relative differences and similarities that may exist in Figures 11-16. For this reason, in Figure 17, the average values for each major activity are expressed as percentages of the maximum duration reached by that activity during the 11-day period. Six functional classes of behavior are compared: Patrolling, migratory, maintenance, male and female agonistic, courtship, and parental activities. In Figure 17, the percent of maximum duration for each activity is shown on the day it occurred with respect to spawning.

Four T. trichopterus activities reached maximum duration before spawning: patrolling (D-5), maintenance (D-4), male agonistic (D-2), and migratory behavior (D-1); and three activities were submaximum (above 90% of maximum duration): courtship and migratory behavior (D-5), and patrolling (D-4). Two activities reached maximum duration after spawning, female agonistic (D+4) and courtship (D+5), and one activity was submaximum, patrolling (D+2 and D+3). On the spawning day, fish activity can be classified as to whether it is increasing or decreasing with respect to the durations on D-1 and D+1. Three T. trichopterus activities showed a definite decrease in duration on the spawning day; patrolling was 40% below maximum duration, maintenance activity declined by 90%, and migratory behavior decreased 80%. Three activities increased on the spawning day, male and female agonistic activity was 75% of maximum, courtship was 85% of maximum, and parental behavior was maximum (100%) (Figure 17).

Only two M. opercularis activities reached maximum duration before spawning: migratory behavior (D-5 to D-3) and maintenance behavior (D-3), and male agonistic activity was just below maximum duration on D-2. After spawning, parental behavior reached maximum duration on D+1

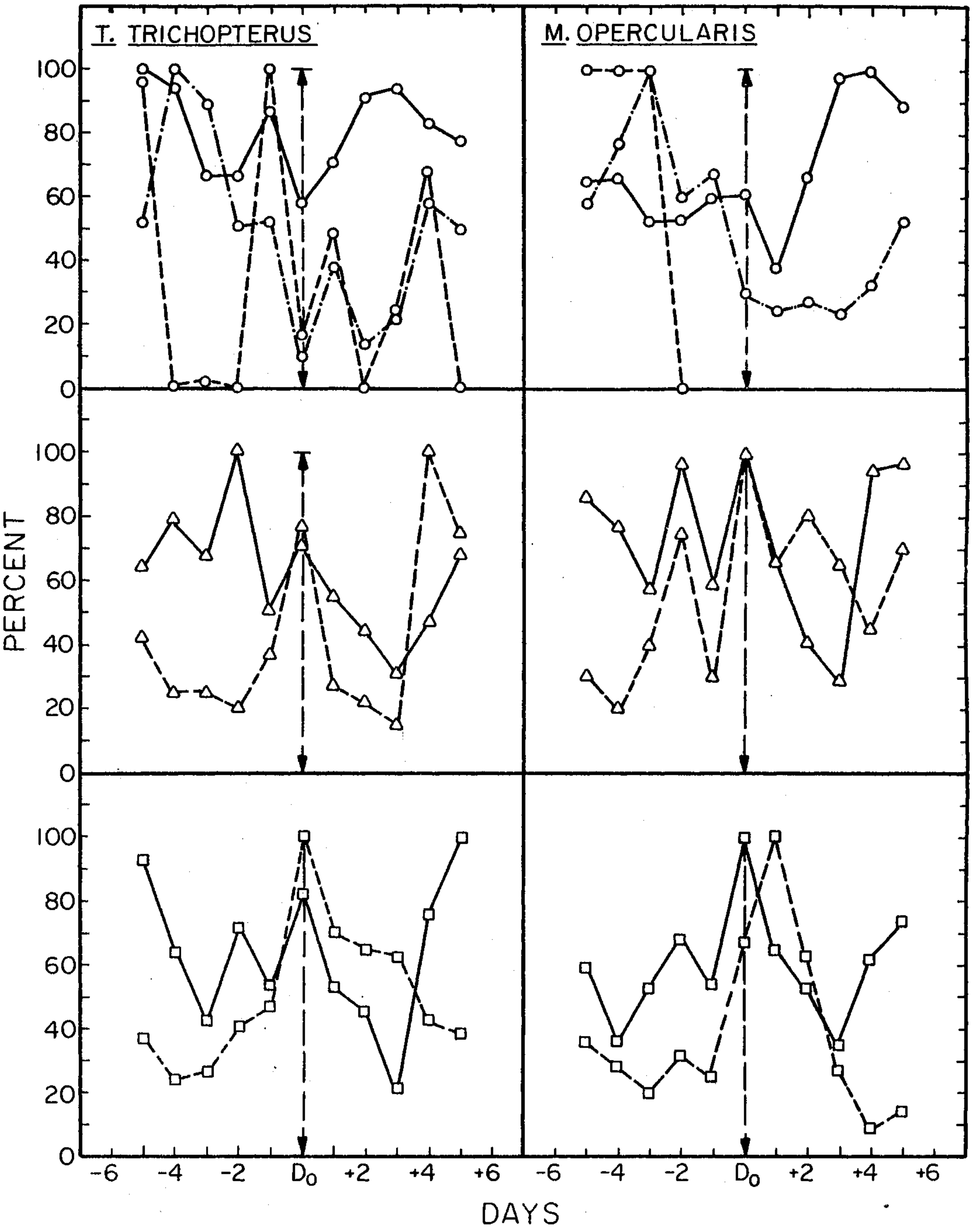

Figure 17. Average Total Durations of Pre- and Post-Spawning Activities as Presented in Figures 11-16, But Now Expressed as Percentages of the Maximum Value Attained by Each Activity During the Eleven-Day Observation Period. Patrolling (Circle With Solid Line); Migratory Behavior (Circle With Dashed Line); Maintenance Behavior (Circle With Dot and Dashed Line); Male Agonistic Activity (Triangle With Solid Line); Female Agonistic Activity (Triangle With Dashed Line); Courtship (Square With Solid Line); Parental Behavior (Square With Dashed Line).

and patrolling on D+4 with submaximum durations recorded for patrolling (D+3) and male agonistic activity (D+4 and D+5). On the spawning day, maintenance activity was 70% below maximum, migratory behavior was not observed since D-3, and patrolling actually increased, slightly less than 1%, but was still 40% below maximum and on D+1 patrolling decreased another 20% (60% below maximum). Two M. opercularis activities increased to maximum duration on the spawning day: male and female agonistic activity and courtship (Figure 17).

Both T. trichopterus and M. opercularis showed relatively high levels of courtship and agonistic activity both before spawning (D-2) and on the spawning day; whereas, the level of migratory behavior and maintenance activity was very low on Do. But the maximum duration for T. trichopterus migratory behavior occurred just one day before spawning and was not observed in M. opercularis. Patrolling by T. trichopterus was almost 33% less on Do than on D-1 (42% below maximum duration); whereas, M. opercularis do not show a similar decrease in patrolling behavior until D+1. Also T. trichopterus spent almost twice as much time in parental behavior on the spawning day than M. opercularis. However, on the next day (D+1), parental behavior by M. opercularis does increase by 33% (671 seconds, maximum duration) but is still almost 30% below the maximum duration (954 seconds) of parental behavior by T. trichopterus (Figures 15 and 17).

Nonreproductive and Reproductive Periods

During this study the fish were considered to be in the nonreproductive phase during spawning intervals and in the reproductive phase on the spawning day. Presumably, when spawning is not imminent, the fish are not in reproductive condition, but males appear to be ready to spawn most of the time. Usually when the female of either species is not in reproductive condition, she will exhibit little or no courtship activity, and spends a good deal of her time in hiding. However, when she becomes swollen with eggs her behavior begins to change, which in turn affects male behavior. This implies that some behaviors are more appropriate than others in initiating a spawning. For this reason, behaviors are analyzed to determine the changes in behavioral levels (percent occurrence) during nonreproductive and reproductive periods. Figures 11-17 support the hypothesis that the relative levels of certain behaviors change as a fish passes through the nonreproductive to the reproductive phase and Table XIV summarizes these changes.

Almost all behaviors monitored on the spawning day were lower in duration than those same behaviors during nonreproductive periods, except parental behavior which increased sharply. One reason for this over-all decrease could be that the 20-minute observation periods on the spawning day may not include pre-spawning activities where many new behaviors make their appearance and others show increased durations (e.g., female approach and female butting). The two predominant activities during nonreproductive periods, by both species, were patrolling and maintenance activities, which together consumed more than 75% of the 20-minute observation period. On the spawning day, patrolling by _T. trichopterus_ declined to 28.75% and maintenance activity to only 3.25%, whereas _M. opercularis_ patrolling on Do was still the predominant activity but declined slightly to 44.58% and maintenance activity to 10.25% of the observation period. The two activities which accounted for the

TABLE XIV

RELATIVE CHANGES IN OCCURRENCE* OF BEHAVIORS FROM NONREPRODUCTIVE TO REPRODUCTIVE PERIODS

	T. trichopterus				*M. opercularis*			
	Nonreproductive Phase**		Reproductive Phase**		Nonreproductive Phase		Reproductive Phase	
	Seconds***	Percent	Seconds***	Percent	Seconds	Percent	Seconds	Percent
Male Behavior								
Patrolling	640	53.33	345	28.75	627	52.25	535	44.58
Agonistic	124	10.33	108	9.00	203	16.92	134	11.17
Migratory	52	4.33	8	0.67	0	0.00	0	0.00
Parental	252	21.00	954	79.50	70	5.83	447	37.25
Maintenance	284	23.67	39	3.25	442	36.83	123	10.25
Resting	124	10.33	1	0.08	359	29.92	96	8.00
Inspiration	47	3.92	21	1.75	26	2.17	12	1.00
Female Behavior								
Agonistic	41	3.42	32	2.67	31	2.58	20	1.67
Courtship	76	6.33	62	5.16	89	7.42	66	5.50
Male Lateral Display	45	3.75	31	2.58	60	5.00	47	3.92
Female Approach	25	2.08	25	2.08	27	2.25	18	1.50
Female Butting	6	0.50	6	0.50	2	0.17	1	0.08

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[*] Percent of observation period (average values for 1200 seconds) consumed by each class of behavior.

[**] Nonreproductive Phase - data collected during spawning intervals (20 minutes of daily observation).
Reproductive Phase - data collected on spawning day during 20 minutes of observation, morning and afternoon.

[***] Average duration in seconds recorded for each activity during observation period.

least amount of time consumed, by each species during both periods, were migratory behavior and female agonistic activity. During nonreproductive periods, *T. trichopterus* migratory behavior and female agonistic activity averaged a little over 7% but declined to just over 3% of the 1200 seconds, observed on Do. No migratory behavior was observed in *M. opercularis* during the recording sessions of either the nonreproductive or reproductive periods. Female agonistic activity averaged approximately 2.50% during nonreproductive periods and declined to 1.50% of the observation period on Do (Table XIV).

Both species showed the expected increases in parental activity on the spawning day from nonreproductive levels. These increases were quite noticeable to the observer on Do. *T. trichopterus* spent 21% of the observation period in parental activities (primarily bubble blowing) during nonreproductive periods and increased this to almost 80% on Do. Nonreproductive *M. opercularis* consumed only 5.83% of the time in parental activity (primarily bubble blowing) but increased this to 37.25% of the observation period on Do. This actually represents an increase of 84% more time spent in parental activities, on the spawning day. During the reproductive phase parental activity was predominant in *T. trichopterus*; whereas, in *M. opercularis*, patrolling was the predominant activity.

Two activities showed unexpected low durations on the spawning day when compared to nonreproductive levels: male agonistic activity and courtship. During non-experimental laboratory observations on Do, it seemed that these activities actually increased considerably. But during nonreproductive periods, *T. trichopterus* and *M. opercularis* averaged approximately 10% and 17% of the observation period in agonistic activity, respectively, and these figures declined to 9% and 11%, respectively, on the spawning day.

The duration of T. trichopterus courtship declined slightly (from 6.33 to 5.16% because the males performed less lateral display during the observation periods on the spawning day, than during nonreproductive periods; whereas, the females approached and butted males for equal amounts of time during both periods. Even greater reductions occurred in M. opercularis courtship durations (from 16.92 to 11.17%) because male lateral display, female approach and butting all showed lowered durations on the spawning day when compared to nonreproductive periods (Table XIV).

These decreases in male agonistic activity could be adaptive since it would allow the female to approach the male more often during pre-spawning activities. However, male agonistic activity and courtship actually do increase (30 to 40%) on the spawning day when compared to the duration of these same activities on D-1 and D+1 (Figures 12, 13, 14, and 17). But in comparison with nonreproductive levels agonistic behaviors do carry lower durations. Miller (1964) states that with the onset of the reproductive phase in male T. trichopterus this period is usually marked by increased aggressiveness, territoriality, and bubble blowing. The short term data from this study agree with his conclusions. However, no quantitative comparisons were made during his study between nonreproductive and reproductive levels of agonistic activity before spawning. This study attempts to provide this information.

Discussion

A change in fish behavior as spawning time approaches is an a priori assumption, and quite apparent even to the casual observer. However, in order to adequately measure the duration and composition of behavioral changes both before and after spawning, quantitative techniques were necessary. As a result, three different comparisons can be made. The average duration of nonreproductive behaviors can be compared to the average behavioral durations on the spawning day; the maximum duration of various behaviors during an 11-day period (D-5 to D+5) can be compared to the durations of behavior on the spawning day, and the level of activity on the spawning day can be compared to the duration of behaviors one day before and one day after spawning. A fourth method would be to compare the changes in behavior during the spawning day. This has been reported on to some extent by: Barlow (1962) in _Badis badis_; Miller (1964) in _T. trichopterus_; Greenberg et al. (1965) in _Aequidens portalegrensis_; Hall (1966a) in _T. leeri_, _T. trichopterus_ and _M. opercularis_; Hall and Miller (1968) in _T. leeri_; Miller and Hall (1968) in _T. leeri_; Rainwater (1968) in _Betta splendens_; and Wimmer (1970) in _T. microlepis_.

In reporting behavioral changes, the term maximum duration is used only to indicate the highest duration per 20 minutes of a behavior or group of activities during a particular period, for example, D-5 to D+5. The occurrence of maximum durations for some behaviors just before or after a spawning, and for others on the spawning day could mean that certain behaviors are more or less efficient in promoting pre-spawning and spawning behavior. However, this connotation would not necessarily always follow since the maximum duration for some behaviors intimately involved in the success of a spawning were not always registered during the spawning day observations. Nevertheless, certain behaviors such as female approach, do show maximum durations if measured during prespawning or spawning bouts, as shown by Wimmer (1970) in *T. microlepis*. Therefore, if the maximum duration of a behavior were used as the sole criterion in evaluating the relationship of the behavior to spawning activity, a misinterpretation could result. For example, female approach by *T. trichopterus* reached maximum duration on D+5 and not on Do (Figure 13). This could be interpreted to mean that this behavior was not particularly essential to spawning, but Miller and Hall (1968) stressed its close relationship to successful spawning bouts. Of course, maximum duration is a useful measure when it fits in with other quantitative data as well as laboratory observations. For this reason, all three methods of comparison between behavioral changes are used to assess their effectiveness in measuring relative changes in the spawning cycle.

Another aspect of the study required the identification of nonreproductive and reproductive fish. A sharp distinction between the two periods was difficult to determine beforehand, especially as spawning time approached. For this reason, the fish were considered to be in the reproductive phase on the spawning day when appropriate behaviors were usually observed. This does not exclude the possibility that the reproductive phase may also extend throughout the entire 11-day period (D-5 to D+5) or longer, or for only a few days. But the behavior observed on the spawning day was sufficiently different from the behaviors observed between spawnings (spawning intervals) to confidently make these comparisons.

Nonreproductive fish usually do not show any consistent territorial defense. They are usually pale and typically swim about the tank slowly (high patrolling durations), searching for food, or merely hover for extended periods of time. If bubble blowing occurs at this time, it is sporadic and the nests rapidly deteriorate. Agonistic activity is usually somewhat higher during nonreproductive periods, with occasional female chases. Maintenance activities occur frequently and total resting durations are relatively long.

With the onset of the reproductive phase, territorial defense by the males was quite apparent as was general fish activity (low resting durations). The females generally possessed swollen abdomens. Spawning activity was usually preceded by intense nestbuilding. Most of this activity occurred within five days of spawning. However, there were occasional bursts of nestbuilding by males during spawning intervals. No bubble blowing was ever recorded for *T. trichopterus* females and only sporadic attempts were made by *M. opercularis* females, but male bubble blowing increased considerably and was especially vigorous on the spawning day. The males' reluctance to leave the nest was evident since he would quickly return after each foray in search of the female. Perhaps *M. opercularis* males have learned to spend less time away from the nest since female *M. opercularis* frequently approach the nest and do show token help with nestbuilding and retrieving. This kind of "cooperation" could lead to a reduction in physical aggression and an increase in displays by *M. opercularis* males in contrast to the increased butting and chasing by the *T. trichopterus* males. During this period, the males of both species become darkly colored and the females assume varying shades of darkness depending on the size and dominance of the male.

The low durations of non-agonistic activity, as gauged by patrolling on the spawning day, may perhaps be explained as the result of increased territoriality and bubble blowing. This is also accompanied by a sharp reduction in the durations of migratory behavior and maintenance activities (Figure 17). Agonistic activities show increased durations on the spawning day for both species, but differences do exist. _T. trichopterus_ males exhibit lower durations for male approach and higher durations for butting and chasing than _M. opercularis_ males who spend more time displaying. _T. trichopterus_ females approach and butt males for longer periods on the spawning day than _M. opercularis_ females, which could reduce the need for male _T. trichopterus_ to leave the nest site. After arriving under the nest, a _T. trichopterus_ female usually butts the male which inhibits attack. If she is not quite ready to spawn the male responds by increased butting and chasing.

After spawning, _T. trichopterus_ males do not allow the females under the nest. In fact, both partners exhibit more butting and chasing. In contrast, _M. opercularis_ females are tolerated near the nest edge for a few days after spawning and then increased male butting and chasing develops (Figure 12). In both species, there does appear to be a reduction in sexual responsiveness of the postspawning male as evidenced by the increase in male butting and chasing. This could be explained as the result of competing tendencies (in the statistical sense of Hinde; 1970:360) for maintaining a nest, retrieving eggs or fry, and sexual responses. Miller and Hall (1968) give another explanation -- that the more aggressive post-spawning male is simply responding to an unresponsive female. However, four days after spawning there is an increase in butting and chasing by *T. trichopterus* females as well as an increase in male approach and lateral display. This would seem to indicate a resumption of agonistic activity, perhaps because of an unresponsive male (Figures 12 and 13). Usually when an aggressive male is either the same size or larger than the female, she is inhibited by frequent male attacks and remains in hiding. However, if the female is larger or the male is not aggressive and approximately the same size as the female, many agonistic encounters ensue leading to increased male and female approach, lateral display, and mouthfighting.

M. opercularis males appear to be somewhat "less aggressive" than *T. trichopterus* males. While approaching the females for longer durations on the spawning day, they display more and butt and chase much less than *T. trichopterus* males. The *M. opercularis* females may approach males on the spawning day only slightly less than *T. trichopterus* females but exhibit very little butting and chasing. The increase in male lateral display and opercle spread in response to increased female approach with little butting may actually decrease the need for male butting and chasing (Figures 12 and 13). Miller and Hall (1968) suggest that there might be an imperfect relationship between the female butting rate and lateral display. In this case there is very little butting by *M. opercularis* females and yet a high level of male lateral display. Perhaps in *M. opercularis*, a species which exhibits reduced female butting during spawning bouts, a relationship exists between male lateral display and male and female approach. Usually when a female *M. opercularis* approaches a male he gives a lateral display, but so do *T. trichopterus* males under similar circumstances. However,

T. trichopterus males would also respond to female approach by butting and chasing her especially if she did not butt him first; whereas, M. opercularis males would usually continue to display.

Miller and Hall (1968) suggest that learning processes may be intimately involved in the development of the lateral spread. Perhaps M. opercularis males have learned at an early age the utility of a lateral display as opposed to butting and chasing the female. This would at least allow the males to remain under the nest for longer periods, instead of leaving it unguarded to chase the female. It is very tempting to suggest that with the relatively high rate that M. opercularis females approach males, it is both advantageous and energy conserving for males to perform lateral display than to butt and chase the females, and this could be learned.

During the course of the study, consideration was given to the possibility that one parameter might be more useful than another in distinguishing differences in pre- and post-spawning behaviors. Upon reflection, it appears that each of the parameters compared was useful. Changes in nonreproductive and reproductive behaviors reflect long term gradual changes (trends); whereas, a comparison of behavioral changes during the 11-day period (D-5 to D+5) appear to show intermediate changes. However, when comparing the level of activity on the spawning day to the duration of behavior on D-1 and D+1, it appears to give a clearer picture of the relatively short term changes in behavior that apparently precede and follow spawning activity. These short term quantitative changes (Figures 11-17) seem to agree with the over-all general impression of pre- and post-spawning behavioral changes that were observed.

CHAPTER IX

SUMMARY

This paper provides qualitative descriptions of T. trichopterus and M. opercularis behaviors during nonreproductive and reproductive periods. It also includes a quantitative description and analysis of various factors associated with spawning. The principal objectives are: to evaluate the influence of precipitation, barometric pressure, and water temperature on spawning activities; to determine the existence and nature of activity cycles; and to compare behavioral changes during the spawning cycle.

The data were obtained by observing tanks containing one male and one female during 10-minute observations, twice daily, for extended periods. During the nonreproductive phase 10-minute intermittent observations were conducted for periods up to 30 hours. Quantitative data collected during the nonreproductive and reproductive periods were compared. The data were divided into agonistic and nonagonistic activities.

Both species appeared to have the capability to spawn every few days. However, an alternating pattern of spawning intervals was observed. "Long" intervals were followed by relatively "shorter" intervals and vice versa. After several successive spawnings, a female seemed to require an even longer interval than usual.

The greatest number of *T. trichopterus* spawnings per three-hour period occurred between 1600-1900 hours, and most *M. opercularis* spawnings occurred between 1900-2200 hours. The number of spawnings in progress per hourly interval declined sharply for both species after 1900 and 2200 hours, respectively. Typically, *M. opercularis* spawned later in the day than *T. trichopterus*. The average duration of a *T. trichopterus* spawning sequence was slightly longer than a *M. opercularis* sequence.

Precipitation did not prove to be a reliable factor in predicting future nestbuilding by *T. trichopterus* or *M. opercularis* in aquaria. The mere rise or fall in barometric pressure also did not appear to influence nestbuilding by either species. However, the data tend to weakly support the hypothesis that barometric pressures below 29.00 inches of mercury may have stimulated *T. trichopterus* to build nests, and acted as a permissive factor at this level for *M. opercularis*. Water temperatures between 80° to 84°F appeared to enhance nestbuilding by *T. trichopterus*, but *M. opercularis* built nests at temperatures between 75° and 85°F. *M. opercularis* appeared to have wider tolerance limits to water temperature and barometric pressure than *T. trichopterus*, particularly when nestbuilding.

Precipitation did not prove to be statistically significant in association with the onset of spawning by *T. trichopterus* and *M. opercularis* in the laboratory. Falling barometric pressure, however, did seem suspect in influencing spawning activity in these two species. No particular range of pressure was essential in influencing spawning, but *T. trichopterus* did spawn more frequently at the lower pressure ranges, i.e., below 29.00 inches of mercury. *M. opercularis* appeared less specialized, spawning at pressure ranges between 28.55 to 29.39 inches of mercury. In conclusion, both species appeared to spawn more frequently when the barometric pressure was either falling or below 29.00 inches of mercury. Both species spawned more frequently when the water temperature was between 80° to 86°F. Also, most spawnings (80%) occurred when daily water temperature was either constant or rising. *M. opercularis* seemed capable of spawning during extreme fluctuations of barometric pressure and water temperatures; whereas, *T. trichopterus* did not spawn under these same conditions. This seemed to reflect the more specialized nature of *T. trichopterus*.

Cycling of fish activities seemed to occur in both species. Males spent more than 40% of their time in patrolling, a nonagonistic activity. Peaks in patrolling occurred during the early morning for *M. opercularis* and during the late morning for *T. trichopterus*. The lowest levels of patrolling occurred during the lights-out period, between 1900 and 0400 hours. Although total patrolling duration generally declined following lights-out, the length of individual patrols remained fairly stable and in some cases even increased slightly. Individual *T. trichopterus* patrols may be 15 to 20% longer than *M. opercularis* patrols, but *M. opercularis* exhibited higher patrolling frequencies. Peaks in patrolling coincided with peaks in inspiration, resting, and agonistic activity during the daylight hours. During the lights-out period, as patrolling declined, total resting durations increased. *M. opercularis* spent almost twice as much time resting as did *T. trichopterus*. Peak resting durations occurred between 2300 to 0300 hours.

Agonistic activity frequently increased with patrolling activity, probably because increased movement resulted in more male-female encounters. However, after lights-out patrolling activity remained at a fairly high level while agonistic activity decreased, probably because of a lack of visual contact between the male and female. More than 92% of the time consumed in agonistic activity was spent in lateral display, chasing, and butting and biting in the order given.

Migratory behavior appeared to increase and decrease with agonistic activity because the fluttering male seemed to attract the female and this meeting was frequently followed by butting and chasing. Peak periods in courtship activity by both species occurred at 0700, 1100, and 1500 hours. In general, M. opercularis exhibited higher frequencies and lower durations for most behaviors than T. trichopterus. However, much higher resting frequencies and durations were registered by M. opercularis when compared to T. trichopterus.

As the spawning day approached, patrolling durations decreased for both species. After spawning, patrolling durations once again began to increase. Single patrols were also shorter during reproductive periods than in nonreproductive periods. The decrease in patrolling was followed by an increase in territoriality and nestbuilding. Both species showed sharp reductions in the duration of maintenance activities and migratory behavior on the spawning day. However, agonistic activities increased at this time. T. trichopterus males exhibited more butting and chasing than M. opercularis males who spent more time displaying. T. trichopterus females approached and butted males for longer periods on the spawning day than M. opercularis females, who showed very little butting.

After spawning, pairs of *T. trichopterus* exhibited more butting and chasing than pairs of *M. opercularis* who appeared more "cooperative" for a few days longer. Female *M. opercularis* attempted to help with nest-building and retrieving eggs or fry in contrast to female *T. trichopterus* who were not tolerated near the nest. *T. trichopterus* males spent almost twice as much time in parental behavior on the spawning day than *M. opercularis* males, primarily because of the time consumed in bubble blowing.

A comparison of nonreproductive and reproductive behaviors revealed that patrolling and maintenance activities were the two predominant activities for both species during the spawning intervals. On the spawning day maintenance activities were reduced substantially, but patrolling, although reduced, remained the predominant activity for *M. opercularis*. Migratory behavior and female agonistic activity accounted for the least amount of time consumed by either species during the nonreproductive and reproductive periods. Both species showed substantial increases in parental activity on the spawning day from nonreproductive levels. But male agonistic activity and courtship carried lower durations on the spawning day than during nonreproductive periods. Decreases of this nature could be adaptive in allowing the female to approach the male more frequently and perhaps reduce the possibility of injury during prespawning activities. However, male agonistic activity and courtship actually increased 30 to 40% on the spawning day when compared to the level of these activities one day before and one day after spawning. These data then reflect the short term changes in behavior as spawning approached: usually characterized by increased aggressiveness, territoriality, and bubble blowing.

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APPENDIX

TABLE XV

SPAWNING INTERVALS TIME (DAYS) BETWEEN SPAWNING SEQUENCES IN *T. TRICHOPTERUS* RESIDENT FEMALES

Tank	Interval - Days	Average Interval Days
B 2	2, 26, 8	9
B 10	4	4
B 11	11, 41	26
B 16	37, 22, 17, 24	25
B 17	64, 21	42
B 37	one spawning sequence	-
B 46	one spawning sequence	-

Mean Average Interval 21.2 days
Number of Spawning Sequences = 19

TABLE XVI

NUMBER OF SPAWNING SEQUENCES PER MONTH IN *T. TRICHOPTERUS* (n = 8 PAIRS)

May	0
June	2
July	8
August	6
September	3
October	0
November	0
Total	19

TABLE XVII

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

Tank	Interval - Days	Average Interval Days
P 4	5, 25, 21, 81	33
P 7	29, 21	25
P 8	55, 44, 28	42
P 14	26	26
P 27	one spawning sequence	-
P 28	75, 9	42
P 29	6, 18, 7	10
P 31	4, 64, 35	34
P 33	one spawning sequence	-
P 34	9 - resident female	9
	one spawning sequence new female	-

Mean Average Interval 27.6 days
Number of Spawning Sequences = 30

TABLE XVIII

NUMBER OF SPAWNING SEQUENCES PER MONTH IN M. OPERCULARIS (n = 10 PAIRS)

May	1
June	3
July	9
August	4
September	3
October	5
November	5
Total	30

TABLE XIX

2 X 2 CONTINGENCY TABLE FOR ALL T. TRICHOPTERUS NESTS PRESENT OR ABSENT DURING PERIODS OF PRECIPITATION

	Precipitation	No Precipitation	Total
Nests Present	68 (66)*	261 (263)	329
Nests Absent	148 (150)	602 (600)	750
Total No. Observations	216	863	1079**

*(Expected values).

**$\chi^2 = 0.110$ with one degree of freedom, $0.80 > P > 0.70$.

TABLE XX

2 X 2 CONTINGENCY TABLE FOR ALL M. OPERCULARIS NESTS PRESENT OR ABSENT DURING PERIODS OF PRECIPITATION

	Precipitation	No Precipitation	Total
Nests Present	95 (75)*	317 (337)	412
Nests Absent	108 (128)	591 (571)	699
Total No. Observations	203	908	1111**

*(Expected values).

**$\chi^2 = 10.345$ with one degree of freedom, $0.005 > P > 0.001$.

TABLE XXI

THE NUMBER OF NESTS PRESENT ON WET AND DRY DAYS ABOVE AND BELOW 29.00 INCHES OF MERCURY

	Mean Barometric Pressure				
	Below 29.00 Inches of Mercury		29.00 Inches of Mercury and Above		
	Wet Days	Dry Days	Wet Days	Dry Days	Total
Days	36 (17.06%)	79 (37.44%)	13 (6.16%)	83 (39.34%)	211 days
	54.50%		45.50%		
Nests Present					
T. trichopterus	53 (16.11%)	155 (47.12%)	15 (4.56%)	106 (32.21%)	329 nests
	63.22%		36.78%		
M. opercularis	70 (16.99%)	162 (39.32%)	25 (6.07%)	155 (37.62%)	412 nests
	56.31%		43.69%		

TABLE XXII

THE NUMBER OF *T. TRICHOPTERUS* NESTS PRESENT DURING A RISE OR FALL IN THE DAILY MEAN BAROMETRIC PRESSURE (M.B.P.)

M.B.P.	Rise		Fall		No Change		
Nests	Present	Absent	Present	Absent	Present	Absent	Total
Frequency	154	357	162	365	13	28	1079
Percent Total Observations	14.27	33.08	15.01	33.82	1.20	2.59	100%
Percent Nests Present	46.80		49.24		3.95		100%

TABLE XXIII

THE NUMBER OF *M. OPERCULARIS* NESTS PRESENT DURING A RISE OR FALL IN THE DAILY MEAN BAROMETRIC PRESSURE (M.B.P.)

M.B.P.	Rise		Fall		No Change		
Nests	Present	Absent	Present	Absent	Present	Absent	Total
Frequency	201	316	192	362	19	21	1111
Percent Total Observations	18.09	28.44	17.28	32.58	1.71	1.89	100%
Percent Nests Present	48.78		46.60		4.61		100%

TABLE XXIV

THE NUMBER OF T. TRICHOPTERUS NESTS PRESENT DURING DAILY FLUCTUATIONS IN WATER TEMPERATURE

Fluctuations in Water Temperature*	Rise		Fall		No Change		
	Nest Present	Nest Absent	Nest Present	Nest Absent	Nest Present	Nest Absent	Total
Number of Observations	120	264	122	278	86	201	1071
Total No. Observations	384		400		287		1071
Percent of Total Observations	35.85		37.35		26.80		100%
Percent of Nests Present	36.58		37.20		26.22		100%

*The net difference in day to day water temperatures.

TABLE XXV

THE NUMBER OF M. OPERCULARIS NESTS PRESENT DURING DAILY FLUCTUATIONS IN WATER TEMPERATURE

Fluctuations in Water Temperature*	Rise		Fall		No Change		
	Nest Present	Nest Absent	Nest Present	Nest Absent	Nest Present	Nest Absent	Total
Number of Observations	133	246	145	254	130	193	1101
Total No. Observations	379		399		323		1101
Percent of Total Observations	34.42		36.24		29.34		100%
Percent of Nests Present	32.60		35.54		31.86		100%

*The net difference in day to day water temperatures.

TABLE XXVI

THE NUMBER OF PRECIPITATION-RELATED SPAWNING SEQUENCES (PRS) FOR *T. TRICHOPTERUS* AND *M. OPERCULARIS*

	Precipitation one day before spawning	Precipitation on the spawning day	Precipitation one day after spawning	Total number precipitation-related spawning sequences	Number of spawnings without precipitation	Total number of all spawning sequences
Number of occurrences*	7			7		7
	4	4		4		4
	1	1	1	1		1
	1		1	1		1
		6		6		6
			12	12		12
					18	18
			TOTAL	31	18	49

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*The manner in which precipitation was associated with each spawning sequence.

TABLE XXVII

CONTINGENCY TABLE FOR _T. TRICHOPTERUS_ PRECIPITATION-RELATED SPAWNINGS (PRS)*

	Precipitation Days	Non-Precipitation Days	Total
Spawning Days	12 (9)**	6 (9)	18
Non-Spawning Days	91 (94)	102 (99)	193
Total	103	108	211***

*PRS = Precipitation – day preceding, same day, or following spawning day.

**(Expected values).

***$\chi^2 = 2.19$ with one degree of freedom, $0.20 > P > 0.10$.

TABLE XXVIII

CONTINGENCY TABLE FOR _M. OPERCULARIS_ PRECIPITATION-RELATED SPAWNINGS (PRS)*

	Precipitation Days	Non-Precipitation Days	Total
Spawning Days	16 (13)**	11 (14)	27
Non-Spawning Days	87 (90)	97 (94)	184
Total	103	108	211***

*PRS = Precipitation – day preceding, same day, or following spawning day.

**(Expected values).

***$\chi^2 = 1.52$ with one degree of freedom, $0.30 > P > 0.20$.

TABLE XXIX

CONTINGENCY TABLE FOR *T. TRICHOPTERUS* SPAWNING ON PRECIPITATION DAY ONLY

	Precipitation Days	Non-Precipitation Days	Total
Spawning Days	5 (4)*	13 (14)	18
Non-Spawning Days	44 (45)	149 (148)	193
Total	49	162	211**

*(Expected values).

**$\chi^2 = 0.35$ with one degree of freedom, $0.60 > P > 0.50$.

TABLE XXX

CONTINGENCY TABLE FOR *M. OPERCULARIS* SPAWNING ON PRECIPITATION DAY ONLY

	Precipitation Days	Non-Precipitation Days	Total
Spawning Days	6 (6)*	21 (21)	27
Non-Spawning Days	43 (43)	141 (141)	184
Total	49	162	211**

*(Expected values).

**$\chi^2 = 0.00$ with one degree of freedom, $99.95 \gg P$.

TABLE XXXI

FLUCTUATIONS IN DAILY MEAN BAROMETRIC PRESSURE

Barometric Pressure	Rise	Fall	No Change	Total
Days	102	100	9	211
Percent of total	48.34	47.39	4.27	100%

TABLE XXXII

FREQUENCY OF SPAWNING COMPARED TO TRENDS IN MEAN BAROMETRIC PRESSURE

	T. trichopterus	*M. opercularis*	*T. trichopterus*	*M. opercularis*	*T. trichopterus*	*M. opercularis*	Total
	Rise		Fall		No Change		
Spawning Frequency	9	14	9	14	1	2	49
Totals	23		23		3		49
Percent of Total	47		47		6		100%

TABLE XXXIII

FREQUENCY OF PRECIPITATION COMPARED TO TRENDS IN MEAN BAROMETRIC PRESSURE

Barometric Pressure	Rise	Fall	No Change	Total
Days of Precipitation	25	22	2	49
Percent of Total	51	45	4	100%

TABLE XXXIV

COMPARISON OF SPAWNING FREQUENCY ON DAYS WITH AND WITHOUT PRECIPITATION

	Spawning Frequency on wet days	Spawning Frequency on dry days	Total Spawning Frequency	Frequency Wet Days	Frequency Dry Days	Total Days
	11	38	49	49	162	211
Percent of Total	22	78	100%	23	77	100%

TABLE XXXV

NET CHANGES IN BAROMETRIC PRESSURE (INCHES) DURING 211-DAY PERIOD

Net Change in Inches of Mercury	Net Change in Daily Mean Barometric Pressure for 211 Days (No. Days)	Net Change in Daily Mean Barometric Pressure One Day Preceding Spawning (No. Spawnings)	Net Change between the Barometric Pressure at the Start of Spawning and the Preceding Day's Mean Barometric Pressure (No. Spawnings)
.00	9 (4.26)*	3 (6.13)	1 (2.04)
0.01-0.05	79 (37.44)	13 (26.53)	12 (24.49)
0.06-0.10	64 (30.33)	19 (38.77)	12 (24.49)
0.11-0.15	33 (15.65)	9 (18.37)	13 (26.53)
0.16-0.20	16 (7.58)	4 (8.16)	3 (6.13)
0.21-0.25	9 (4.26)	1 (2.04)	5 (10.20)
0.26-0.30	1 (0.48		2 (4.08)
0.31-0.35			1 (2.04)
Total	211 days	49 spawnings	49 spawnings
Range of Net Change	0.00-0.28	0.00-0.21	0.00-0.35

*(Percent of total).

TABLE XXXVI

NUMBER OF SPAWNING SEQUENCES AT EACH RANGE OF MEAN BAROMETRIC PRESSURE PLUS 28.00 INCHES OF MERCURY, APRIL 21 - NOVEMBER 17, 1965 (211 DAYS)

	0.50-0.59		0.60-0.69		0.70-0.79		0.80-0.89		0.90-0.99		1.00-1.09		1.10-1.19		1.20-1.29		1.30-1.39		Total	
	*T.t.**	*M.o.***	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*	*T.t.*	*M.o.*
Frequency of spawning sequences	-	-		1	1	1	3	5	9	9	6	8	-	1	-	1	-	4	19	30
Percent of total	-	-		3	5	3	16	17	47	30	32	28	-	3	-	3	-	13	100%	100%
Total Frequency	-	-	1		2		8		18		14		1		1		4		49	
Percent of total	-		2		4		16		37		29		2		2		8		100%	

* *T. trichopterus*

** *M. opercularis*

TABLE XXXVII

NUMBER OF DAYS RECORDED AT EACH RANGE OF MEAN BAROMETRIC PRESSURE (INCHES OF MERCURY PLUS 28.00), APRIL 21 - NOVEMBER 17, 1965 (211 DAYS)

	0.50-0.59	0.60-0.69	0.70-0.79	0.80-0.89	0.90-0.99	1.00-1.09	1.10-1.19	1.20-1.29	1.30-1.39	Total
Frequency (Days)	-	2	7	39	67	48	21	18	9	211
Percent of total	-	1	3	18	32	23	10	9	4	100%

TABLE XXXVIII

RELATIVE DURATION* OF SEVEN CLASSES OF BEHAVIOR DURING THIRTY HOURS OF RECORDING**

Male Behavior	*T. trichopterus* (Percent)	*M. opercularis* (Percent)
Patrolling	48.35	45.71
Resting	17.05	33.28
Migratory	7.46	0.00
Agonistic	5.42	4.96
Inspiration	2.81	2.07
Miscellaneous***	18.91	13.98
	100.00	100.00
Courtship	5.94	6.16
Female	2.76	2.43

*Percent of observation period (Average values for 600 seconds) consumed by each class of behavior.

**Based on 12 pairs of fish of each species.

***Including Feeding, Approach, Bubble Blowing, and Comfort Movements.

TABLE XXXIX

RELATIVE DURATION* OF FIVE MALE AGONISTIC ACTIVITIES DURING THIRTY HOURS OF RECORDING**

Behavior	_T. trichopterus_ (Percent)	_M. opercularis_ (Percent)
Lateral Display	73.82	77.18
Chasing	9.82	10.86
Butting and Biting	9.02	10.19
Fleeing	6.21	1.77
Mouthfighting	1.13	0.00***
	100.00	100.00

[*] Percent of total agonistic activity (Average values for 600 seconds) consumed by five behaviors.

[**] Based on 12 pairs of fish of each species.

[***] Mouthfighting by _M. opercularis_ was only rarely recorded and therefore no average values could be calculated.

TABLE XL

RELATIVE DURATION* OF THREE COURTSHIP ACTIVITIES DURING THIRTY HOURS OF RECORDING**

Behavior	*T. trichopterus* (Percent)	*M. opercularis* (Percent)
Male Lateral Display	63.10	62.22
Female Approach	33.55	36.25
Female Butting	3.35	1.53
	100.00	100.00

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[*] Percent of total courtship activity (Average values for 600 seconds) consumed by three behaviors.

[**] Based on 12 pairs of fish of each species.

TABLE XLI

RELATIVE DURATION* OF FOUR FEMALE ACTIVITIES DURING THIRTY HOURS OF RECORDING**

Behavior	*T. trichopterus* (Percent)	*M. opercularis* (Percent)
Approach	80.73	93.07
Chasing	11.29	2.94
Butting	5.62	3.99
Mouthfighting	2.36	0.00***
	100.00	100.00

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*Percent of total female activity (Average values for 600 seconds) consumed by four behaviors.

**Based on 12 pairs of fish of each species.

***Mouthfighting by *M. opercularis* was only rarely recorded and therefore no average values could be calculated.

VITA 2

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