COURTSHIP AND REPRODUCTIVE BEHAVIOR OF THE SIAMESE FIGHTING FISH, *BETTA SPLENDENS* REGAN (PISCES, BELONTIIDAE)

By

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CHAPTER I

INTRODUCTION

The Siamese fighting fish, Betta splendens Regan (Belontiidae, Perciformes, Anabantoidei), has been a popular aquarium fish in Europe and the United States for at least 40 years (Smith, 1945). Literature concerning reproductive behavior, however, is meager and sometimes contradictory. Most of the following accounts are concerned with fighting behavior or with description of reproductive behavior: Regan (1909), Weber and de Beaufort (1922), Choola (1930), Mathis (1940), Smith (1945), and Tweedie (1952). Lissman (1932) gave significant information concerning stimulus-response systems, but devoted little space to reproductive behavior.

B. splendens is an excellent fish for laboratory study. It is hardy, readily available, and easily bred. Sexual maturity is reached as early as 75 days (Mathis, 1940) and nest building by the male may begin as early as 53 days (Braddock and Braddock, 1959). Optimum spawning temperature and the duration between spawning sequences of B. splendens were established by Goodrich and Taylor (1934). Braddock and Braddock (1959) described development of nest behavior of B. splendens males and females. Frequency, size, and duration of nests were reported for fish of different ages. Braddock et al. (1960) attempted to determine whether B. splendens could discriminate nest

size by floating paper disks of various sizes on the surface of the water. Braddock and Braddock (1955) described in detail aggressive behavior in B. splendens females and their corresponding color changes.

Several significant studies have been conducted on related species. Forselius (1957) made a detailed study of the systematics, distribution, endocrinology, and ecology of anabantoid fishes. His work on behavior was concerned principally with the genus Colisa. Osteology and phylogeny of anabantoid fishes were studied by Liem (1963), who included a review of the systematics of the group and some ecological factors thought to be involved in the evolution of the group. Picciolo (1964) described nest and sex discrimination in several anabantoid fishes. Miller (1964) described the social behavior of Trichogaster trichopterus and included quantitative data on motor patterns, nest building, and reproductive behavior. Hall (1965) dealt primarily with the comparative ethology of three anabantoid fishes and included quantitative data on their reproductive and courtship behaviors.

This study of the Siamese fighting fish primarily deals with courtship and reproductive behavior of breeding pairs in aquaria. The objectives of the study were: (1) to describe and quantify courtship and reproductive behavior and (2) to attempt to show the behavioral differences and similarities among sexually experienced and inexperienced pairs of B. splendens.

Discrete observable behavioral activities, body postures and movements were defined to facilitate the description and quantification of behavior. Identical behavioral units were used to record behavioral patterns of both sexually experienced and inexperienced pairs of B. splendens.

CHAPTER II

MATERIALS AND METHODS

The study was conducted from January to July, 1965, at the Oklahoma State University Aquatic Biology Laboratory, Stillwater, Oklahoma.

Materials

Eight sexually experienced males and 12 sexually experienced females were maintained during the study. These were obtained from aquarium dealers in Stillwater and Oklahoma City. Ten pairs, offspring of the sexually experienced pairs, were raised in the laboratory and their reproductive behavior was studied during their first spawning sequences. Twenty-two recordings of the reproductive and courtship behavior patterns were made, 11 of the sexually experienced group and 11 of the sexually inexperienced group. Males and females of near equal size were paired for observation and recording purposes, but mates were changed so that one male did not continually spawn with the same female. Females were introduced periodically and were removed after completion of a spawning sequence. Only males were permanent residents of each aquarium.

Fish were fed Daphnia, dried foods, and tendipedid larvae. Young fry were fed a mixture of dried egg yolk and yeast in addition to infusoria.

Seven aquaria were used for observation and recording purposes. They ranged in size from 30.5 x 57 x 16.5 cm to 30 x 51 x 30.5 cm with volumes of 28.6 to 46.6 liters.

Each aquarium bottom was covered to a depth of approximately two cm with small gravel and was planted with Vallisneria and Ceratophyllum. Artificial plants and broken clay pots placed in the aquaria provided some protection for the females.

Natural daylight from two southern exposure windows and overhead florescent lamps provided light for all aquaria. The photoperiod was not rigidly controlled. The aquarium room was heated by a large gas heater which maintained the water temperature at 74-84°F (23.3-28.9°C). Photoperiod, temperature, lighting, and aquarium size appeared to have no effects on spawning patterns.

Quantitative data were obtained by the use of an Esterline-Angus Event Recorder, Esterline-Angus Tape Reader, graph paper, time-measurement ruler, and summary charts. The equipment aided in obtaining, transforming, and analyzing the data.

Photographic analysis, helpful in the qualitative aspect of the study, was made by a Pentax 35 mm camera, Bolex 16mm movie camera with electric motor, and Bell and Howell Time Analysis 16mm movie projector.

Methods

Daily observations of each aquarium were made to determine the spawning readiness of the pair. Coloration, general behavior of one or both fish, and form and structural features of the bubble-nest (if present) were useful in determining their physiological and psychological states.

The procedures used in obtaining the quantitative data were discussed by Hall (1965). Behavior patterns for both male and female were recorded concurrently on the Esterline-Angus Event Recorder at a chart speed of 1 1/2 inch per minute. The keyboard was coded for the various patterns and arranged in the usual sequence of occurrence to facilitate manipulation of keys as the patterns developed. Although 22 partial or complete spawning sequences were recorded, only 12 recordings, six of each group, were analyzed. These were selected because of the completeness of the spawning sequences.

CHAPTER III

TAXONOMY

In its native Thailand, B. splendens inhabits ponds, ditches, drains, and sluggish waters; it does not appear to have been indigenous to any other country (Smith, 1945). Forselius (1957) noted that it has been domesticated there for more than a hundred years.

Liem (1963) listed seven genera in the family Belontiidae and proposed that the genera Betta, Macropodus, Malpulatta, Parasphromenus, and Trichopsis be included in the subfamily Macropodinae. Weber and de Beaufort (1922) and Liem (1963) recognized five species of Betta, but Tweedie (1952) was of the opinion there were only two.

Characteristics of Belontiidae

Most members of the family Belontiidae share certain unifying traits: (1) the presence of a labyrinth, (2) the deposition of eggs in a bubble-nest, and (3) the employment of a nuptial clasp.

The labyrinth is an accessory respiratory organ which enables the fish to obtain atmospheric oxygen. It is composed of lamellae, covered over with highly vascularized tissue, and lies on both sides of the gill chamber in an upward-directed diverticulum. Atmospheric air taken in through the mouth is forced into the labyrinth where gaseous exchange takes place. The labyrinth developes in the young in two to three weeks after hatching (Peters, 1947; Sterba, 1962).

A bubble-nest consists of a mass of bubbles deposited by the male at the air-water interface. Nesting activity usually precedes or accompanies male nuptial coloration, increased aggressiveness, and establishment of a territory. B. splendens males ordinarily inspire only once and blow out one bubble at a time. The air bubble is taken into the mouth, enclosed in mucus, and deposited on the surface of the water (Braddock and Braddock, 1959). Repeated bubble blowing results in a floating mass of mucus-covered bubbles, which is generally formed around floating plant material and the sides or corners of the aquarium. The objects in contact with the bubble-nest usually determine its shape.

The shape or "critical size" of the nest (6 cm in diameter) which was considered important by Braddock and Braddock (1959) was not found to be related to spawning success in this study. Several pairs which had nests of smaller size spawned successfully, and spawning occasionally preceded nest construction in others.

The male remains near the nest during the expiration of the bubbles. The nest usually increases in diameter and depth during and immediately following a spawning sequence. Reproductive activities under the nest sometimes cause the bubbles to burst. If the disturbance dislodges eggs from the nest, courtship ceases momentarily and the eggs are replaced by both fish and the nest is repaired by the male.

The third characteristic common to Belontiidae, the clasp, is discussed in Chapter V.

CHAPTER IV

MOTOR PATTERNS AND UNITS OF ACTIVITIES

Motor Patterns

Fin erection. Erection of the median and pelvic fins occurs principally in the frontal and lateral displays. These are most often seen when a male approaches a female or when he is defending his territory. Males show fin erections while stationary or during a slow movement toward a female. Forselius (1957) stated that fin erection is most probably caused by a conflict between drives, usually aggressive or fleeing, or by thwarting of a fleeing drive through the attraction to an oestrus female approaching a nest. During prespawning courtship phases, fin erection is often followed by chasing and biting. Miller (1964) and Hall (1965), in dealing with other anabantoid fishes, indicated that fin erection signified intensity of courtship and aggressive behavior. Slight fin erection indicated the lowest intensity, maximal fin spread indicated higher intensity and maximal fin spread with the body curved laterally into a sigmoid shape indicated maximal intensity. Fin erection in B. splendens appears to reflect similar intensity patterns. Median fins of the "Veiltail" variety of B. splendens are conspicuously enlarged, accentuating any erection and causing considerable increase in apparent outline of the body.

Gill cover erection. Gill cover erection occurs simultaneously with the lateral and frontal displays and seems to enhance their effectiveness. It is most distinct in the final phase of the approach. When viewed from the front, the erected gill covers appear to enlarge the head. Forselius (1957) contends that gill cover erection has secondarily acquired a threatening function.

Tail beating. Tail beating occurs rarely, but it is sometimes executed by the female during early courtship phases. It consists of undulating movements of the caudal peduncle and caudal fin. Tail beating was observed only after unsuccessful mounting attempts. Tail beating coincided with female butting behavior under similar circumstances.

Biting and butting. Biting was observed only in males and only during aggressive situations of the pre- and postspawning periods. The male attacks the female with his mouth open and grasps a fin or part of her body. Butting is a thrust of the head to the body region of the other fish. Butting occurs in both sexes following several unsuccessful female mounting attempts. It is also present during aggressive bouts, but is performed only by the male.

Chasing. Chasing involves male pursuit of a fleeing female. Chases of longer duration occur after termination of spawning bouts when the female fails to return to the nest, and during aggressive pre- and postspawning periods. Chasing stops when the female is hidden from the male after completion of the spawning period. Lower intensity chases occur during prespawning and spawning periods, but they usually terminate with a lateral or frontal display.

Motor patterns other than those described above are included in the ethogram discussion of Chapter V. These are: (1) leading-to-the-nest, (2) circling, (3) mounting, (4) clasping or nuptial embrace and roll, (5) swimming inhibition, and (6) egg retrieval.

Units of Activity

Bout. A social interaction, which may include any activities noted above, or subsequently is called a bout.

Spawning sequence. A total of all male-female interactions (bouts) and intervals between bouts which occur during the prespawning, spawning, and postspawning periods is termed a spawning sequence. This sequence corresponds to the "mating cycle" of Forselius (1957).

Sexual bout. A male-female interaction which contains sexual responses is termed a sexual bout. Female approaching or circling the male or swimming to beneath the nest are judged as female responsiveness. Male approach, lateral or frontal displays, and circling serve as criteria for the sexual activity in males.

Spawning bout. This refers only to those sexual bouts in which gametes are released by male and female. It includes all movements and activities associated with the release of sex products and is equivalent to a "spawning cycle" of Forselius (1957).

Pseudospawning bout. The pseudospawning bout is a sexual bout identical to a spawning bout except that no eggs and possibly no sperm are released. Swimming inhibition is exhibited in one or both sexes.

Clasp bout. A bout which progresses only to a clasp is termed a clasp bout. Swimming inhibition and emission of sex products fail to occur. It includes other movements leading to the clasp position.

Courtship bout. A bout involving sexual responses by one or both partners that does not reach the clasp stage is a courtship bout. The following three categories represent three types of courtship bouts.

Circle bout. A circle bout progresses only to circling or adjustment of the pair in preparation for the male mounting the female. It is an advanced type of courtship bout.

Female-under-the-nest bout. This term refers to the female appearing under the nest without a response by the male. It is preceded by male-leading-to-the-nest, female approach or female placing of eggs into the nest. It is another kind of courtship bout.

Male-female-response bout. This type of courtship bout refers to a male-female sexual interaction occurring in an area other than under the nest. It includes leading by the male and the female following or sexual displays by either fish.

Male aggressive bout. Any bout involving only male aggressiveness is a male aggressive bout. This usually includes male approach, chasing, and/or biting by the male with the female fleeing.

Nest posting. Nest posting comprises all occasions when the male has taken up a position close under the nest, except while he is caring for the eggs or post-larvae.

Prespawning period. The period, characterized by courtship and/or aggressive bouts, that precedes the first successful spawning bout is called the prespawning period.

Spawning period. This denotes the period between the first and last successful spawning bout in the spawning sequence. It includes all bouts occurring during this period.

Postspawning period. The period following the last successful spawning bout is termed the postspawning period. Male aggressiveness and female retreat is evident during this phase. The period is terminated when the female remains in hiding for long intervals and when the male is only nest-posting and aggressive.

CHAPTER V

QUALITATIVE DESCRIPTION OF BEHAVIOR

Schiller (1957) defined the term ethogram as "a broad and detailed description of the normal behavior of a species." The ethogram (Table I) used in this study for the purpose of describing courtship and reproduction is used in accordance with this definition.

Hall (1965) defined an ideal spawning bout as a "sexual bout in which gametes were released with an apparent economy of effort and with little male or female aggression." Few actual spawning bouts follow the exact form of the ethogram, but its purpose is to describe qualitatively the basic stages of the bout. The units which comprise the ethogram are designed to clarify meaningful discussions of the reproductive activities observed in B. splendens and are not to be confused with the "acts" of Russel et al. (1954).

Discussion of the Ethogram (Table I)

1. Readiness for spawning. This stage is a preliminary necesity for both sexes. The duration is variable and occurs at the onset of the prespawning period. Body coloration often indicates the motivational state of the sexual partners. The male's nuptial coloration tends to become homogeneously more brilliant. The nonoestrus female has characteristic markings consisting of two or three blackish horizontal bands alternating with lighter bands of similar width. In

TABLE I

BETTA SPLENDENS SPAWNING SEQUENCE ETHOGRAM

Male	Female
1. Acquires nuptial coloration; establishes territory; initiates nest building; attains physiological readiness to spawn	1. Acquires nuptial coloration; remains away from male in opposite end of aquarium; attains physiological readiness to spawn
2. Intermittent nest building; approaches female; leads to the nest	2. Responds to male by presenting lateral display or following male; approaches nest with or without his leading
3. Circles (invitation posture)	3. Circles; attempts mounting
4. Preliminary clasp	4. Enters invitation posture
5. Firm clasp	5. Sigmoid posture
6. Roll, quiver and ejaculation	6. Roll and egg release (may continue after clasp release)
7. Loosening of clasp; swimming inhibition	7. Swimming inhibition
8. Egg retrieval; places eggs in nest; nest care	8. Searches on bottom; picks up similar sized material from bottom; returns to nest with or without eggs
9. Nest-posting	9. Avoids male

contrast, a ripe and receptive female may be identified by loss of the horizontal bands and a darker coloration with a series of lighter dorso-ventral stripes.

2. Male-leading-to-the-nest and female approach. Throughout this phase, the male intermittently builds the nest and approaches the female while presenting lateral and frontal displays. The swimming motions of the approach are slow, with undulations of the caudal region and fin. The female follows if she is receptive. The male becomes aggressive if the female responds with flight. During the prespawning period aggressive behavior becomes very prominent when the female is unreceptive. The male approach and leading may occur in stages, consisting of brief halts and movements toward the female or returning to the point of origin. Forselius (1957) observed that during the prespawning period the number of halts in a male approach and the number of halts during leading were inversely proportional to each other. Fewer halts in the approach resulted in more halts during leading and vice versa. A possible explanation may be that when the male approaches with few halts, he is highly aggressive toward the female and continues to be so as he leads to the nest.

Lissman (1932) showed experimentally that when a Betta male began to lead an oestrus female to the nest, she would follow. If she were taken away and replaced by a strange aggressive male, the first male continued leading until he discovered that the following fish displayed another behavior (generally aggressive pursuit instead of sexual following) which resulted in the first male reverting to aggressive behavior.

During the later prespawning phase, the female approaches the nest without male presentation of sexual displays. The female approach is

slow and deliberate. The male stops nest-building and folds the dorsal fin during or subsequent to the female approach.

3. Male and female circling. Circling involves a curving of the male's body while swimming around the female. During the prespawning period, the frequency of circling by both sexes is greater than during the spawning period. In well synchronized pairs, the female does very little circling, but rather is stationary with her body tilted upward and she mounts as the male presents the horizontal U-shaped invitation posture. The highest synchronization level is generally attained during the latter phase of the spawning period. Circling duration is usually 2-4 seconds. If the mount is unsuccessful, circling ceases and a brief pause of 2-4 seconds follows before another attempt is made. If unsuccessful mounting attempts are prolonged, the female usually moves away from the nest and courtship bouts cease for a longer duration. Prolonged incomplete bouts in Trichogaster trichopterus cause the female to lose orientation to the male and result in the male ceasing to behave sexually and to begin to chase the female (Miller, 1964).

4. Female mounting and male preliminary clasp. When the fish have adjusted their bodies into the appropriate position, the female moves from beneath the male up into the horizontal U-shaped invitation posture formed by the male. The male bends around the female so that his head and caudal fin nearly touch. The female's abdomen is touched on one side by the male's operculum and her other side is touched by his posterior body region. The clasp results in proximity of the genital pores.

5. Female sigmoid curve and male firm clasp. After mounting, the female bends her body into a sigmoid posture. The male flexes his body, thus tightening the clasp.

6. Roll, quiver and gamete release. The roll occurs simultaneously with the firm clasp. The roll places the female in an upside down position with her urogenital pore toward the surface and close to the nest. The male's position changes from a horizontal to an inverted U-shape on top of the female with his head pointed downward. This places the male in a position to see the eggs as they fall through the water and he may orientate himself this way for egg retrieval. Quivering of the body and fins immediately follows or occurs simultaneously with the roll. Egg release usually occurs concurrently and immediately following the roll. However, female oviposition is not necessarily accomplished by pressure on the female's abdomen by the clasping male, since eggs are occasionally released after the clasp release, and some were observed to be discharged without a nuptial embrace.

The moment of ejaculation was not observed. Forselius (1957) suggested that ejaculation occurs while the fish are in the clasp position. In the blue gourami (Miller, 1964) milt is forced out in a small cloud just prior to egg release. The spawning act usually occurs directly beneath and close to the bubble-nest. However, occasionally the pair sank slowly during the spawning act. The demersal eggs sink toward the bottom or momentarily rest on the male's caudal or anal fin.

7. Loosening of clasp and swimming inhibition. Swimming inhibition occurs in both male and female following spawning and pseudo-spawning bouts. Forselius (1957) described swimming inhibition as an

"abnormal" position assumed by both fish. Both members retain their clasp postures temporarily, but the female then floats to the surface of the water in a sigmoid position and lies there resembling a dead fish for 12-24 seconds. The male remains in the inverted U-position under the nest or sinks slowly. When the male revives from this state, he is orientated with his head downward and in a position to view the eggs as they fall beneath him.

8. Egg retrieval and placement in nest. The eggs of B. splendens are demersal and slowly sink to the bottom or are trapped by the curved body of the male. Since the male revives from the swimming inhibition state in 4-8 seconds, he is able to catch approximately 90 percent of the eggs in his mouth before they reach the bottom. The eggs are 0.8 to 0.9 mm in diameter (Choola, 1930) and blend with the gravel bottom, making detection of eggs difficult. Thus, eggs reaching the bottom are seldom found by either sex, but the female occasionally picks up one or two eggs while sorting through materials on the bottom. The male usually is in the process of swimming to the nest to deposit collected eggs while the female is swimming toward the bottom. After picking up bottom materials the female swims to beneath the nest beside the male, regardless of whether she has found any eggs. The female often leaves the nest before encountering the male for another sexual bout. Eating of eggs by either sex during the spawning sequence was never observed. However, the female occasionally retrieved an egg which was not immediately placed in the nest. The number of eggs retrieved and placed in the nest depends upon the number of eggs released and the duration of the male's state of swimming inhibition. Sexually experienced males

generally attempt more egg retrievals than inexperienced males. The male resumes nest-building and egg-care following the bout.

9. Male nest posting and female avoidance. After deposition of the eggs in the nest and repair or further construction of the nest, the male takes up a horizontal posture beneath the nest and leaves this position only for "air-gulping" or if the female approaches. The female avoids interaction with the male and usually remains in the area of the aquarium farthest from the nest.

In summary, five phases are recognized in the B. splendens ethogram. These are:

1. Prespawning preparatory phase (1)
2. Courtship phase (2, 3, and 4)
3. Clasp (5 and 6)
4. Swimming inhibition (7)
5. Postspawning phase (8 and 9)

Reproductive behavior is often interrupted because of inappropriate responses by one or both fish. Such interruptions may occur during any phase but most frequently occur during phases 2-4. Lack of synchronization appears to be responsible for incipient spawning bouts. As the spawning sequence nears termination, intervals between bouts become longer, the female shows few sexual movements, and the male generally becomes aggressive. Thus reproductive behavior and the spawning sequence end.

CHAPTER VI

QUANTITATIVE DESCRIPTION OF COURTSHIP AND REPRODUCTION

Data were obtained from 12 spawning sequences of B. splendens involving six sexually experienced pairs and six inexperienced pairs. These sequences included a total of 678 bouts for the experienced pairs and 574 for the inexperienced pairs. Major differences and similarities in prespawning, spawning and postspawning periods are compared. Causal analysis has not been attempted.

Differentiation between sexually experienced and sexually inexperienced fish occurred in numbers and durations of bouts, in intervals between bouts, and in complexity and extent of completion of sexual bouts.

General quantitative comparisons of periods are presented in Table II. Mean duration of complete spawning sequences was almost 30 minutes longer in the sexually experienced fish, but bout duration was remarkably similar in the two groups. The mean interval between bouts for the experienced fish during the entire recorded sequence was 61.8 minutes as compared to only 42.5 minutes for the inexperienced pairs. The majority of the bouts were executed during the spawning period for both groups. During this period the experienced fish performed an average of 95.7 bouts (84.5% of the spawning sequence bouts), and an average of 88.8 bouts (81.4% of the spawning sequence bouts) were

TABLE II

GENERAL QUANTITATIVE COMPARISONS OF PERIODS

	Total		Prespawn		Spawn		Postspawn	
	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced
MEAN DURATIONS								
Recorded								
Seconds	7283	5625	1031	409	5549	4671	721	545
Minutes	121.4	93.8	16.9	6.8	92.5	77.9	12.0	9.1
Bouts								
Seconds	3574	3073	559	132	2882	2699	133	242
Minutes	59.6	51.2	9.3	2.2	48.1	45.0	2.2	4.0
Intervals								
Seconds	3709	2552	454	277	2667	1972	588	303
Minutes	61.8	42.5	7.6	4.6	44.4	32.9	10.2	5.1
MEAN NUMBER OF BOUTS								
Recorded	113.0	109.2	36.5	11.8	95.7	88.8	5.2	12.6
Male Initiated	7.2	14.3	3.0	2.0	3.3	9.0	2.9	4.4
Female Initiated	105.8	94.9	33.5	9.8	92.4	79.8	2.3	8.2
PERCENTAGE OF BOUTS INITIATED BY MALE OR FEMALE								
Male Initiated	6.3	13.1	8.2	16.9	3.5	10.1	54.8	34.9
Female Initiated	93.7	86.9	91.8	83.1	96.5	89.9	45.1	65.1
PERCENTAGE OF TOTAL DURATION SPENT IN BOUTS OR INTERVALS								
Recorded	100	100	10.9	9.0	84.5	81.4	4.6	9.6
Bouts	49.1	54.6	54.2	32.3	51.9	57.8	18.4	44.4
Intervals	50.9	45.4	45.8	67.7	48.1	42.2	81.6	55.6

carried out by the sexually naive pairs. Intervals between bouts and bout durations were similar during the spawning period. Bout duration was only slightly longer than interval time for both groups.

The postspawning period was quantitatively different from the other two periods in several ways. The most evident difference occurs in the older group and is due to a more abrupt shift from male sexual behavior to aggressive behavior. Bouts were shorter and fewer than those of the inexperienced partners. Only during this period did the experienced male initiate a higher percent of bouts than did the female. Bouts initiated by the inexperienced male increased to 34.9 percent, two times greater than during the prespawning period and three times that of the spawning period. The younger fish often attempted more sexual bouts following the final successful spawning bout before the onset of male aggression than did the experienced fish. Interval duration between bouts was greatest during this period, especially in experienced fish. This is due primarily to the female's hesitancy to return to the nest and failure to initiate sexual activities.

Bout categories are analyzed in Table III. The total number of bouts executed during the spawning sequence was similar. There were 678 and 655 for the sexually experienced and inexperienced fish, respectively. However, the older fish performed 262 successful spawning bouts (45.6% of the spawning period bouts) compared to only 151 spawning bouts (28.3% of the spawning period bouts) for the naive pairs.

Pseudospawning bouts occurred primarily during the spawning period. Each group had 79 pseudospawning bouts during this period. The greater number of pseudospawning bouts performed by the experienced fish during the spawning sequence was mainly attributed to one pair, which executed

TABLE III

BOUT CATEGORY ANALYSIS

	Spawning Sequence		Spawning Period	
	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced
TOTAL NUMBER OF BOUTS	678	655	574	533
TOTAL NUMBER OF SPAWNING BOUTS	262	151	262	151
Male initiated	3	13	3	13
Female initiated	259	138	259	138
(Male and female) percent of total bouts	38.6	23.1	45.6	28.3
MEAN DURATION OF SPAWNING BOUTS (seconds)	46.8	52.9	46.8	52.9
TOTAL NUMBER OF PSEUDOSPAWNING BOUTS	118	86	79	79
Male initiated	4	4	3	3
Female initiated	114	82	76	76
(Male and female) percent of total bouts	17.4	13.2	13.4	14.8
MEAN DURATION OF PSEUDOSPAWNING BOUT (seconds)	30.9	40.4	32.2	40.4
Male initiated	31.7	51.5	34.7	53.3
Female initiated	30.9	39.9	31.8	39.8
TOTAL NUMBER OF CLASP BOUTS	24	33	14	19
Male initiated	3	5	0	2
Female initiated	21	28	14	17
(Male and female) percent of total bouts	3.5	5.0	2.4	3.5
MEAN DURATION OF CLASP BOUT (seconds)	16.2	29.6	17.9	29.9
Male initiated	10.0	30.4	--	9.5
Female initiated	17.1	29.4	17.9	32.4
TOTAL NUMBER OF COURTSHIP BOUTS	262	370	211	276
Male initiated	21	49	13	28
Female initiated	241	321	198	248
(Male and female) percent of total bouts	38.6	56.4	31.2	51.8
MEAN DURATION OF COURTSHIP BOUTS (seconds)	10.9	14.9	10.8	16.0
Male initiated	5.0	15.0	5.2	20.6
Female initiated	11.4	14.9	11.2	15.5
TOTAL NUMBER OF MALE AGGRESSION BOUTS	12	15	1	8
Percent of total bouts	1.8	2.3	0.1	1.5
MEAN DURATION OF MALE AGGRESSION BOUT (seconds)	6.9	7.1	3.0	6.8

31 pseudospawning bouts during the prespawning period. This appears to be an unusually large number of pseudospawning bouts and is atypical when compared to other members of the same group. However, the same pair performed only 13 pseudospawning bouts during the spawning period, which was the average number for both groups.

The experienced fish performed only 24 clasp bouts (3.5%) and the inexperienced fish performed 33 clasp bouts (5.0%) during the spawning sequence. The same ratio was also noted in the spawning period. The relatively few clasp bouts seem to indicate that when the pair attain the clasp position they will usually proceed to the swimming inhibition stage. The sigmoid curvature of the female's body associated with the clasp seems to induce the swimming inhibition state.

The number of courtship bouts for sexually experienced fish was considerably lower than for inexperienced fish (262 vs 370 during the spawning sequence and 211 vs 276 during the spawning period for the experienced and inexperienced fish, respectively). The number of courtship bouts of the older fish was almost equal to the number of spawning bouts. However, the sexually inexperienced fish executed almost twice as many courtship bouts than spawning bouts during the spawning sequence. Poorer synchronization of the younger fish appears to be a major factor contributing to these gross differences.

Male aggression bouts comprised the lowest number of bouts during the spawning period and spawning sequence. The greatest number of aggressive bouts of the experienced males occurred during the post-spawning period, but the inexperienced performed one-half of the aggression bouts during the spawning period. These bouts usually occurred after several unsuccessful mounting attempts and were not

evident during any one particular phase of the period. Male aggression was most evident during the postspawning period and became the dominant activity when the female failed to return to the nest and sought an area of the aquarium away from the male. It appears that the female is responsible for the termination of the spawning bouts and cessation of these activities stimulates the increase in male aggressiveness at one time.

Females initiated a higher number of all type of bouts except the male aggression only bouts. The striking importance of the role that the female plays in courtship and reproduction is evident. Females initiated 93.7 and 86.9 percent of the total bouts during the spawning sequence for experienced and inexperienced females, respectively. This trend was shown in the prespawning period and was even higher, 96.5 and 89.9 percent, during the spawning period.

Sexual bout components are shown in Figure 1. Circling duration was relatively constant in all bouts in which it occurred. It was only 1.3 to 1.5 seconds longer among the inexperienced fish and slightly longer in both groups during the bouts which progressed only to circling. This may indicate that when circling for an attempt to mount reaches a critical time, the fish cease the activity and reorient themselves before initiating a new bout.

Clasp duration appears to determine the extent of success of the bout (i.e. whether the bout is terminated after the clasp, pseudo-spawning, or spawning bout). Egg release may depend, in part, on the clasp duration since clasps of the greatest duration resulted in the release of gametes for both fish. Pseudospawning bouts had an average

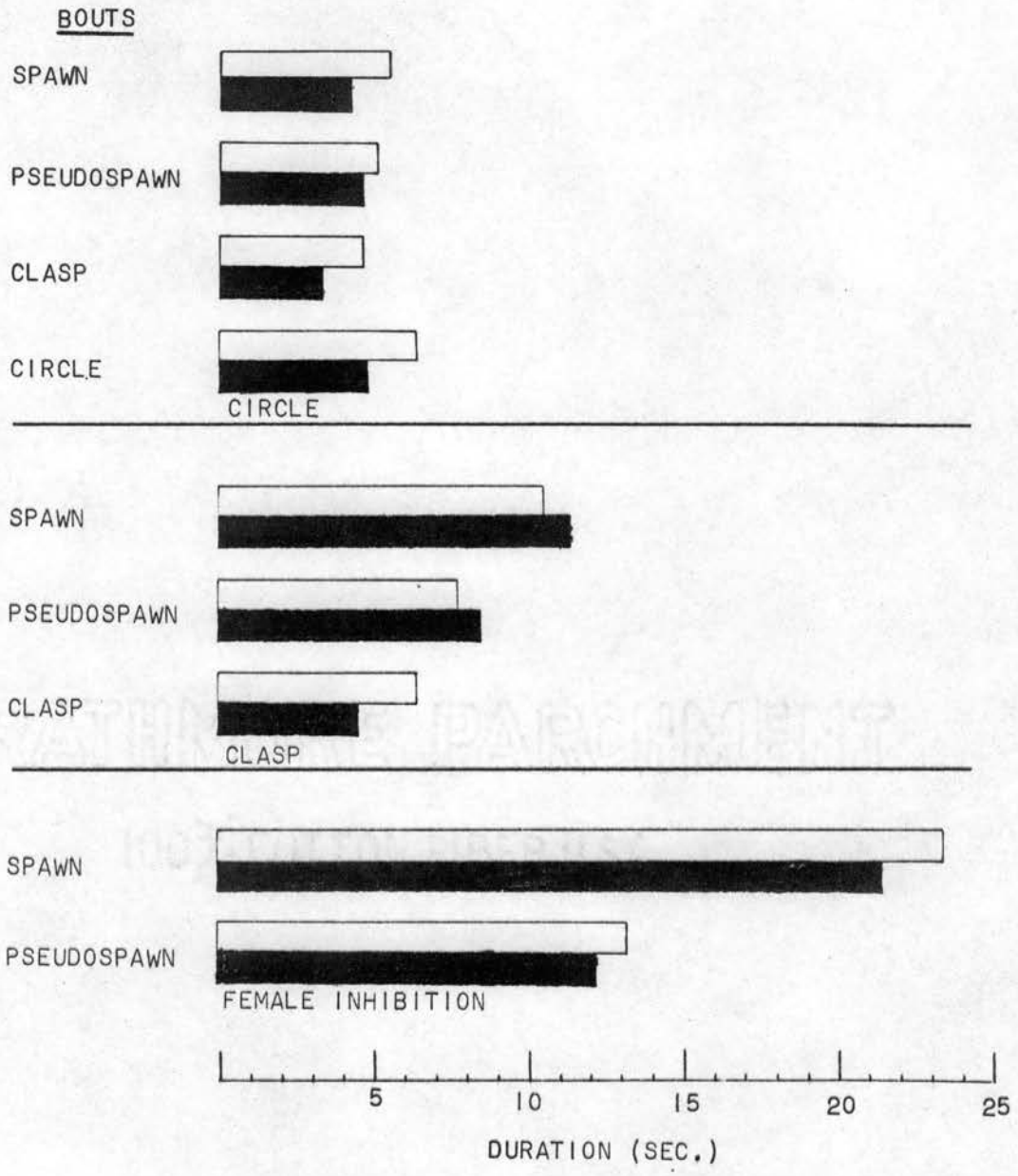

Figure 1. Relationships of Bouts to Duration of the Bout Activities in Sexually Inexperienced (□) and Sexually Experienced (■) Pairs of B. splendens

clasp duration three seconds lower than the clasp duration for the successful spawning bout. Shorter clasp durations of 6.5 seconds for the inexperienced pairs and 4.5 seconds for the experienced fish occurred in bouts terminated at the clasp stage. This suggests that the firm clasp must occur and possibly be maintained for a certain length of time before one or both partners enter the swimming inhibition stage.

The duration of female swimming inhibition during the spawning bouts averaged 9 to 10 seconds longer than the pseudospawning bouts. Egg release appears to cause the female to remain in a state of swimming inhibition longer. The eggs were usually emitted immediately following the firm clasp and the roll, and during the first few seconds of the swimming inhibition stage. Eggs were released during the final stage of swimming inhibition on relatively few occasions.

Comparison of mean durations of bouts during the spawning period is illustrated in Figure 2. Male aggression and male approach bouts exhibited similar motor patterns during the first stages of the approach. The approach of the aggressive bout was generally more rapid than the sexual approach, but the extent of the bout was often determined by the female's response to the approach. A bout in which the female fled when the male approached usually resulted in an aggressive bout. Nonfleeing females appeared to cause the male to halt and present a lateral or frontal display. Such occurrences were judged as courtship bouts. If the male pursued the female immediately following the display, it was judged as an aggression bout. The duration of these bouts is largely determined by the female response to the male approach.

Durations of other incipient spawning bouts tended to increase in the order of female-under-the-nest, male-female-response, circle and

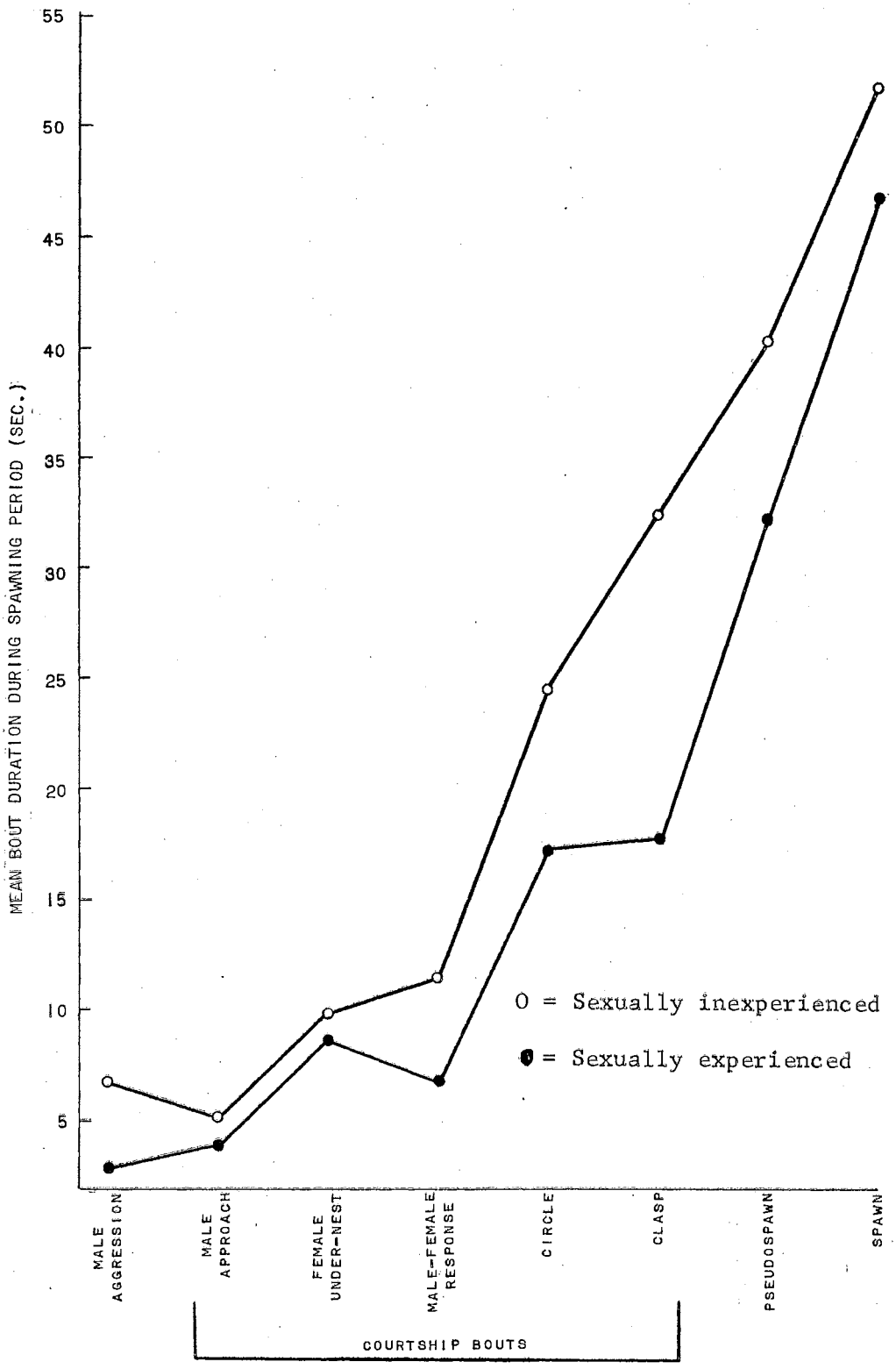

Figure 2. Comparison of Mean Durations of Bouts

clasp bouts as the result of a greater number of motor patterns performed in each of these bouts.

Pseudospawning and spawning bout duration differences were mainly attributed to the longer period of swimming inhibition exhibited by the female in the spawning bout which has been previously discussed.

In all bout categories the mean bout duration for the sexually inexperienced was greater than for the experienced fish. It appears that poorer synchronization in younger fish increases bout duration and reduces the number of spawning bouts within an allotted time, thus reducing the overall efficiency of reproductive behavior.

Comparisons of egg retrieval are listed in Table IV. Egg counts were made as the male retrieved the sinking eggs following each spawning bout. The number of eggs retrieved was approximately 90 percent of the number released by the female. Eggs which sank to the bottom were seldom retrieved by the male and it was difficult to determine when the female picked them up from the bottom. However, the female was occasionally observed placing one or two eggs into the nest which she had picked up from the bottom.

Experienced males retrieved more eggs, on the average, than did the inexperienced males. The older males retrieved an average of 371.3 eggs per spawning sequence (8.5 eggs per spawning bout) compared to only 125 retrieved eggs (5.8 eggs per spawning bout) for the sexually inexperienced males. The actual number of eggs emitted by the female would not be reflected in such proportions since the young males attempted egg retrieval in only 87.2 percent of the spawning bouts, as compared to 99.6 percent of retrieval attempts made by the experienced

males. However, the age and size of the female appeared to have an influence on the number of eggs produced. Larger females appeared to have produced more eggs. This agrees with the observations of Forselius (1957).

The number of eggs retrieved by the experienced males ranged from 185 to 570 compared to the inexperienced male range of 35 to 301 per spawning sequence.

TABLE IV

MALE EGG RETRIEVAL

	Sexually Experienced Males	Sexually Inexperienced Males
TOTAL NUMBER		
Spawning bouts	262	151
Eggs retrieved by males	2228	750
Egg retrieval attempts by males	261	130
MEAN NUMBER		
Eggs retrieved by males/spawning sequence	371.3	125.0
Eggs retrieved by males/spawning bout	8.5	5.8
PERCENT		
Egg retrieval attempts	99.6	87.2

CHAPTER VII

SUMMARY

Acquisition of nuptial coloration and performance of various activities signal the onset of reproductive readiness in B. splendens. The male establishes a territory, begins nest-building, and approaches the female with sexual displays. The female responds to the male approach by fleeing or following the male to the nest. Courtship and male aggressive bouts dominate during the prespawning period. Aggressive behavior diminishes as the female becomes more receptive but male aggression is evident during the postspawning period. Courtship and spawning bouts constitute the majority of bouts during the spawning period.

The role of the female in courtship and reproductive behavior is evident. She initiates a much higher percent of the sexual bouts throughout the spawning sequence than does the male and her response to the approaching male often determines the nature of the bout (i.e. whether it includes courtship, reproductive or male aggressive behavior). The female also is responsible for termination of the spawning period. This is probably due to female hesitancy to initiate sexual activities and return to the nest, which result in increased male aggressiveness.

The low number of clasp bouts which occurred throughout the spawning sequence indicates that when the clasp posture is attained the fish usually proceed to the swimming inhibition stage. Clasp duration was

longest for the spawning bouts. It appears that clasp duration may determine the extent of success of the bout, and in part, whether eggs are released.

Sexually inexperienced fish were also younger and of smaller size than the sexually experienced pairs. Comparison of data from the first and third spawning periods of one pair of young fish reflected the same general differences exhibited by the sexually experienced and sexually inexperienced fish. This suggests that experience rather than age or size results in a greater overall reproductive efficiency and better mutual synchronization of motor patterns. Based on limited data, however, a firm conclusion could not be drawn. Further investigation of older sexually inexperienced pairs should be considered.

On the basis of this study some general statements can be made which reflect quantitative differences between sexually experienced and sexually inexperienced B. splendens.

1. All spawning sequences were longer in the sexually experienced fish. This was due primarily to longer intervals between bouts.
2. In all bout categories the mean bout duration for sexually experienced pairs was less than for the naive pairs, which reflects the poorer synchronization in the younger fish.
3. A more abrupt shift from sexual to male aggressive behavior and a higher percent of male initiated bouts occurred in the sexually experienced fish during the postspawning period.

4. A higher percent of spawning bouts and fewer courtship bouts were performed by the sexually experienced pairs throughout the spawning sequence.
5. The sexually experienced female appeared to release more eggs and the sexually experienced males attempted a higher percent of egg retrievals. Female size may have an influence on the number of eggs released (Forselius, 1957). Thus, the number of eggs placed in the nest was considerably more in the experienced fish.

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