Courtship and Reproductive Behavior of the Siamese Fighting Fish, Betta splendens Regan (Pisces, Belontiidae)[1]

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INTRODUCTION

The Siamese fighting fish, *Betta splendens* Regan, today is one of the most popular aquarium fishes around the world. Yet in spite of the dozens of popular articles and increasing numbers of scientific investigations on this interesting species, accounts dealing with reproductive behavior are noticeably lacking in quantitative description and are sometimes contradictory.

Regan (1909), Weber and de Beaufort (1922), Choola (1930), Lissmann (1932), Mathis (1940), Smith (1937, 1945), Tweedie (1952) and Kuhme (1961) are concerned principally with the systematics, reproductive behavior, or fighting behavior of *Betta*. Goodrich and Taylor (1934) determined optimum spawning temperatures and intervals between spawning sequences, while Braddock and Braddock (1955, 1959) and Braddock et al. (1960) studied nest-building and aggressive behavior. Adler and Hogan (1963), Marrone (1965) and Marrone et al. (1966) also dealt with various aspects of aggressive behavior in the fighting fish.

Several significant studies have been conducted on related species. Forselius (1957) surveyed the systematics, distribution, endocrinology and ecology of anabantoid fishes. His behavioral work 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.

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This study has two aims: to provide a general qualitative and quantitative description of courtship and reproductive behavior to be used for comparison with other anabantoid fishes and to demonstrate behavior pattern differences that may be attributable to differences in experience with sexual behavior. Although the experimental design was not completed because of the death of many fish prior to the last segment of the experiment, the present results are suggestive and may provide some impetus for controlled studies of the effects of experience in modifying presumably "innate" courtship and reproductive patterns in fishes.

MATERIALS AND METHODS

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

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 on the sexually experienced group and 11 on 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 commercial fish foods, and midge larvae *(Tendipes).* Young fry were fed a mixture of dried egg yolk and yeast in addition to infusoria.

Aquaria used for observation and recording purposes ranged in size from 30.5 $\times$ 57 $\times$ 16.5 cm to 30 $\times$ 51 $\times$ 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 fluorescent lamps provided light for all aquaria. The aquarium room was heated by a large gas heater which maintained the water temperature at 74 - 84F (23.3 - 28.9C). Photoperiod, temperature, lighting and aquarium size appeared to have no effects on spawning patterns.

Quantitative data were obtained by use of an Esterline-Angus Event Recorder, Esterline-Angus Tape Reader, graph paper, time-measurement ruler and summary charts.

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

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. During initial phases of the study, significant units of behavior were determined qualitatively, and established as events to be recorded for analysis. Although the Esterline-Angus records contain complete data on such units during entire spawning sequences, the present report considers mainly the organization of behavior into bout patterns. The bout analysis technique is described more thoroughly in Miller (1964), Hall (1965) and Miller and Hall (M.S.). The behavioral units are described briefly below to facilitate understanding of the bout analysis. Although 22 partial or complete spawning sequences were recorded, only 12 recordings, six of each group, were selected for analysis because of their completeness.

UNITS OF ACTIVITY

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

Spawning sequence—The 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 or displays, and which does not contain overt aggressive responses, is termed a sexual bout. Female approaching or circling the male or swimming to beneath the nest are judged to be female sexual responses. Male approach, lateral or frontal displays, and circling in the absence of overt aggression are interpreted as criteria for the presence of active sexual factors in males. This category includes the following seven bout types.

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.

Courtship bout—A bout involving sexual responses by one or both partners and 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.

Male-female-response bout—This category refers to a male-female sexual interaction occurring in an area other than under the nest. It includes leading by the male and 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 and 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 postlarvae.

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 bouts 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 are evident during this phase. The period is arbitrarily terminated when the female remains in hiding for long intervals and when the male is only nest-posting and aggressive.

QUALITATIVE DESCRIPTION OF BEHAVIOR

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 presented below, but its purpose is to describe qualitatively the basic stages of the bout. The units which comprise the ethogram are relatively easy to identify and are presented in order to facilitate description of the patterning of reproductive activities in *B. splendens* and should not be confused with the "acts" of Russell et al. (1954) or any other specific neurobehavioral units.

Discussion of the Ethogram (Table I)

1. *Readiness for spawning*—This stage, variable in duration, 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 stripes alternating with lighter stripes of similar width. In contrast, a ripe and receptive female may be identified by loss of the horizontal stripes, presence of darker coloration, and a series of lighter dorsoventral bars.

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.

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

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 enfolds the female so that his head and caudal fin nearly touch (see Fig. 8, Barlow, 1962). 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 then tightens the clasp.

6. *Roll, quiver and gamete release*—The roll occurs simultaneously with the firm clasp, placing the female in an upside down position with her urogenital pore close to the nest. The male's position changes from horizontal to an inverted U-shape over the female with his head pointed downward. This places the male in a position to see the eggs as they sink through the water. Quivering of the body and fins follows immediately or occurs simultaneously with the roll. Egg release usually occurs concurrently with and immediately after the roll although eggs are occasionally released after the clasp terminates, 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. In a few cases, however, pairs sank slowly during the spawning act.

7. *Loosening of clasp and swimming inhibition*—Swimming inhibition occurs in both fish following spawning and pseudo-spawning bouts. Forselius (1957) described swimming inhibition as an "abnormal" position assumed by both fish. They 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, his head points downward and is in a position to view the eggs as they fall beneath him.

8. *Egg retrieval and placement in nest*—The eggs of *B. splendens* 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% 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, though 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 swims toward the bottom. After picking up bottom materials the female swims to beneath the nest beside the male, regardless of whether or not she has found any eggs. She often leaves the nest before encountering the male for another sexual bout. Egg-eating was never observed during the spawning sequence. 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 released and the duration of the male's state of swimming inhibition. Sexually experienced males generally attempt more egg retrievals than inexperienced males (see below). 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 surfacing 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 phase 2. 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.

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.

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 min longer in the sexually experienced fish but total duration in bouts (lines 3, 4) was remarkably similar in the two groups. The total interval time between bouts for the experienced fish per recorded sequence was 61.8 min as compared to only 42.5 min 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 per sequence (84.5% of the spawning sequence bouts), and an average of 88.8 bouts per sequence (81.4%) of the spawning sequence bouts) were carried out by the sexually naive pairs. Intervals between bouts and bout durations were similar during the spawning period. Total bout duration was only slightly longer than total 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 in 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%, two times greater than during the prespawning period and three times that of the spawning period. The younger fish often initiated more sexual bouts between the final successful spawning bout and the onset of male aggression than did the experienced fish. Interval duration between bouts was greatest during this period, especially in experienced fish, primarily because of the female's hesitancy to return to the nest and initiate sexual activities.

Bout categories are analyzed in Table III. The total number of bouts executed during the spawning sequence was similar in the two groups. 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 speudospawning bouts performed by the experienced fish during the spawning sequence was mainly attributable to one pair, which executed 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. The same pair performed only 13 pseudospawning bouts during the spawning period, which equalled the average number of 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. A similar ratio also occurred 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. This is not true in other anabantoids investigated by Miller.

The number of courtship bouts in sexually experienced fish was considerably lower than in 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 in older fish was almost equal to the number of spawning bouts, whereas sexually inexperienced fish executed almost twice as many courtship bouts as spawning bouts during the spawning sequences. Poorer synchronization of the younger fish appears to be a major factor contributing to these gross differences.

Male aggressive bouts comprised the lowest number of bouts during the spawning period and spawning sequence. The greatest number of aggressive bouts in experienced males occurred during the postspawning period. Inexperienced fish performed one-half of their aggressive bouts during the spawning period. These bouts usually occurred after several unsuccessful mounting attempts and were not evident during any particular phase of the spawning 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. The female thus appears to be responsible for the termination of spawning bouts and the subsequent increase in male aggressiveness.

The striking importance of the role that the female plays in courtship and reproduction is evident. Females initiated a majority of bouts of all types except male aggressive bouts. Females initiated 93.7 and 86.9% of the total bouts during spawning sequences for experienced and inexperienced females, respectively. This trend was shown in the prespawning period, and was even higher, 96.5 and 89.9%, 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. It also tended to be slightly longer in both groups during circling bouts. This may indicate that when circling for an attempt to mount continues for a certain length of time, the fish cease the activity and reorient themselves before initiating a new bout. There may be a limit on the length of time circling may occur in a given bout.

TABLE II. GENERAL QUANTITATIVE COMPARISONS OF BOUT ORGANIZATION IN SIX EXPERIENCED AND SIX INEXPERIENCED PAIRS OF *B. splendens*.

	Complete sequence		Prespawning period		Spawning period		Postspawning period	
	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced	Sexually Experienced	Sexually Inexperienced
Mean Duration of Sequences								
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
Mean Total Time in 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
Mean Total Time In 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

TABLE II. Continued

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

*Significant difference between experienced and inexperienced, chi square, 0.05.

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 Aggressive Bouts	12	15	1*	8*
Percent of total bouts	1.8	2.3	0.1	1.5
Mean Duration of Male Aggressive Bout (seconds)	6.9	7.1	3.0	6.8

*Significant difference between experienced and inexperienced, chi square 0.05.

Clasp duration appears to determine the extent of success of the bout (i.e., whether the bout is terminated during the clasp, or after pseudospawning or spawning occur). 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 clasp

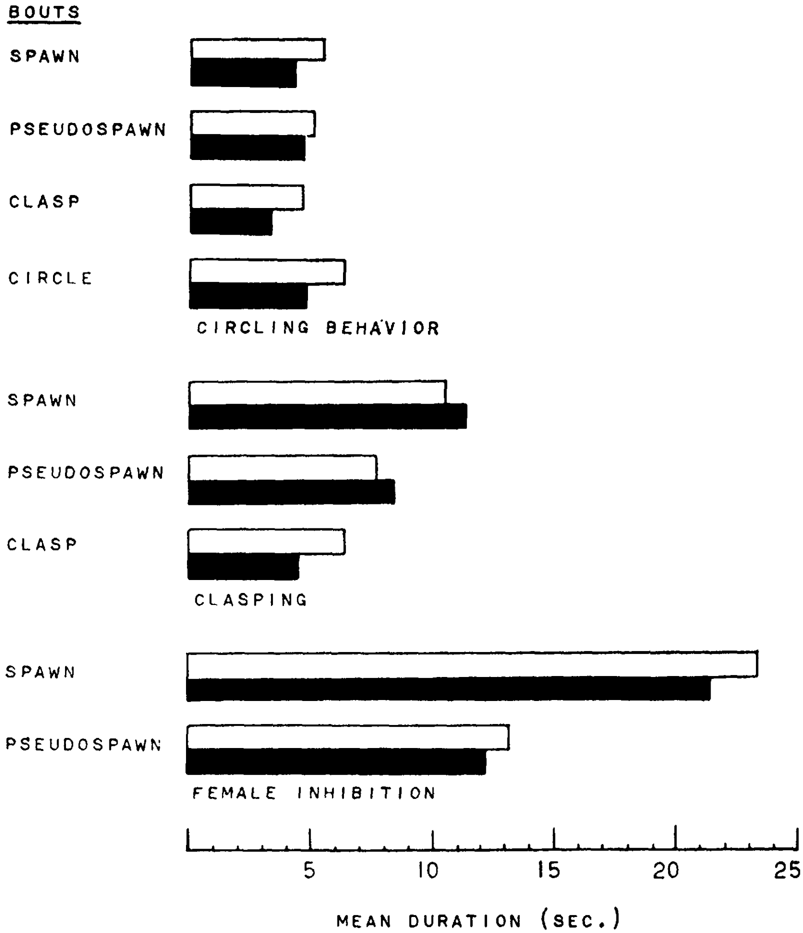

Figure 1. Relationships of Bouts to Duration of the Bout Activities in Sexually Inexperienced (□) and Sexually Experienced (■) Pairs of *B. splendens*.

duration three seconds lower than the clasp duration for the successful spawning bout. Shorter clasp durations of 6.5 sec for the inexperienced pairs and 4.5 sec 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. Miller (1964) showed that a critical period existed in the blue gourami so that once a clasp was maintained beyond a certain length of time (30-35 sec) it was continued to completion and swimming inhibition, regardless of whether or not the female remained in the clasp. We have observed similar occurrences in *Betta*, but do not have quite enough data to clearly delimit this period.

The duration of female swimming inhibition during spawning bouts average 9 to 10 sec longer than in 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 seconds 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 contain similar motor patterns during the first stages of the approach, although approach in the aggressive bout was generally more rapid than in the sexual bout. The duration and complexity of the bout was often determined by the female's response to the approach. When the female fled upon male approach, male aggression usually resulted, and the bout was judged 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. However, if the male chased the female immediately following the display, it was also judged as an agressive bout. This classification differs somewhat from that used by Miller (1964) and Miller and Hall (M.S.) for other anabantoids.

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

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

Egg Retrieval—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% 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, which she had picked up from the bottom, into the nest.

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 numbers of eggs emitted by the female are not strictly reflected in these proportions since the young males attempted egg retrieval in only 87.2% of the spawning bouts, while experienced males made retrieval attempts in 99.6% of their spawning bouts. 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.

The larger, older females appeared to produce more eggs. This agrees with the observations of Forselius (1957).

SUMMARY

Development 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

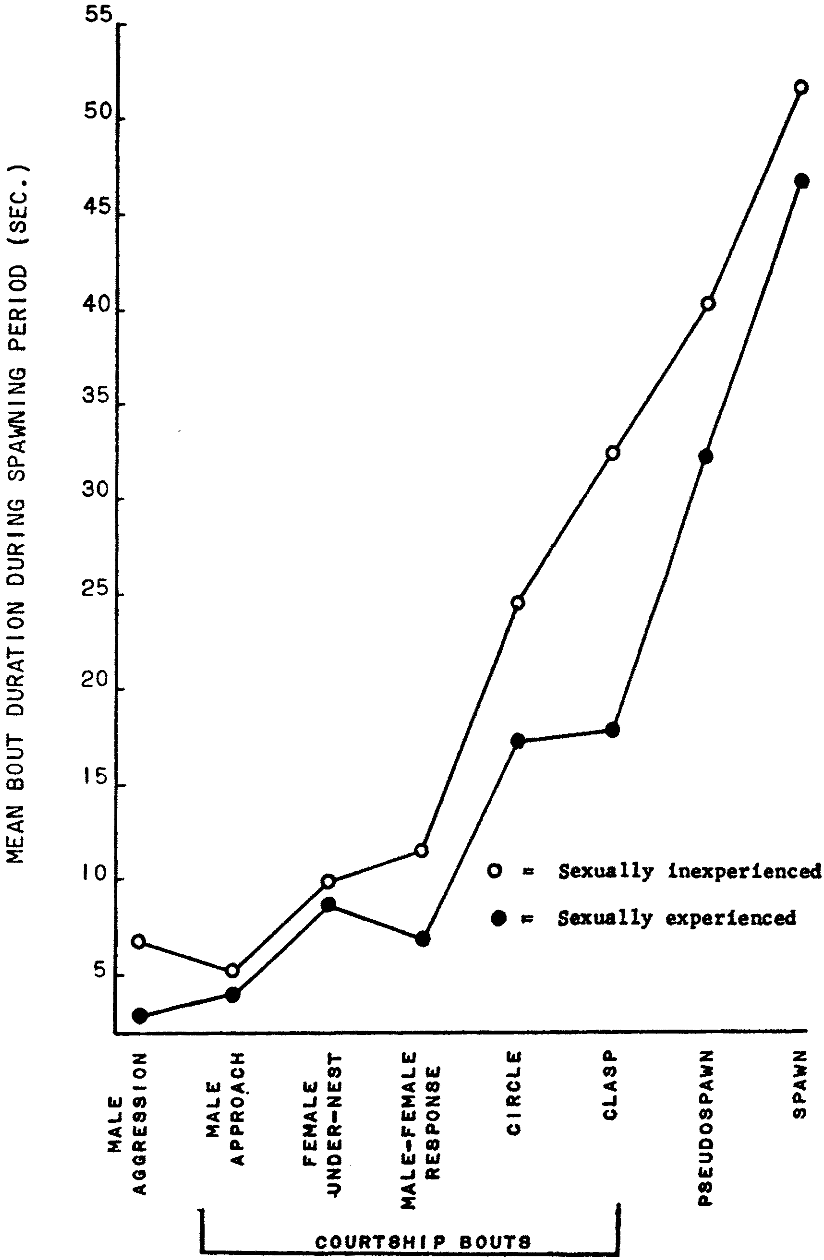

Figure 2. Comparison of Mean Durations of Bouts.

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

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 again conspicuous 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 may be primarily responsible for termination of the spawning period, probably because of her hesitancy to initiate sexual activities or return to the nest, with resulting increased male aggressiveness.

The low number of clasp bouts occurring in spawning sequences suggests that once the clasp posture is attained the fish usually proceed to the swimming inhibition stage. Clasp duration was longest in spawning bouts and 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. Group differences could therefore be attributed to factors other than sexual experience, per se. Since our young fish were lost prior to completion of the design, we cannot with any certainty establish the critical factor or factors responsible for these differences. Comparison of data from the first and third spawning periods of one pair of young fish do reflect, however, the same general patterns and trends exhibited by the sexually experienced and sexually inexperienced fish. This might suggest that experience rather than increased age or size results in a greater overall reproductive efficiency and better mutual synchronization of motor patterns. Based on these limited data, however, a firm conclusion cannot be drawn. Older sexually inexperienced pairs must be investigated before we can precisely identify causal relationships involved.

On the basis of this study some general statements can be made which reflect quantitative differences between the two groups.

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 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. More spawning bouts and fewer courtship bouts were performed by the sexually experienced pairs throughout the spawning sequence.
5. The sexually experienced females appeared to release more eggs and the sexually experienced males attempted a higher percent of egg retrievals. Thus, the number of eggs placed in the nest was considerably greater in experienced fish.

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