AGGRESSIVE BEHAVIOR AMONG MALES OF THE PARADISE FISH, *MACROPODUS OPERCULARIS*

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AN ABSTRACT

Submitted to the College of Science and Arts, Michigan State University, in partial fulfillment of the requirements for the degree of

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Approved James C. Braddock

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ABSTRACT

It is generally known that the male Paradise fish, *Macropodus opercularis*, exhibits aggressive behavior. This study was intended as an analysis of the activities involved. It was discovered that certain sets of pair-mates fought, while others established a dominance-subordination relationship without fighting, and a comparison was made between them.

The fish studied in these observations were obtained from a dealer. All laboratory work was done in the Natural Science Building of Michigan State University during the spring and summer of 1957. Fifty-nine sets of observations were recorded and fighting was observed in twenty-five. Thirty-three fish were used.

In those observations in which fighting occurred three distinct stages were noted. Aggressive behavior was first noted prior to fighting and was characterized by activities involving the pair-mates and reactions of the fish to their surroundings. In those observations where no fighting occurred, this was replaced by a period

prior to the establishment of dominance. The period was terminated by the first retreat by one of the pair-mates.

Periods of actual fighting involved the greatest amount of activity. Mutual exchanges of bites and locking of jaws were characteristic only of this stage, and actual physical contact between the pair-mates occurred with greatly increased frequency as compared with the preceding period. Fighting ended with a retreat by one of the pair-mates.

Following surrender or the establishment of dominance, similar activities were noted, and it was assumed that these stages were equivalent to each other. Certain obvious differences were observed, however, when winners were compared with losers. The winners and dominant fish were more aggressive while the losers and subordinates remained motionless, reacting only when approached by an aggressor.

A brief and generalized comparison was made with the behavior of the Siamese fighting fish, Betta splendens (Braddock and Braddock, 1955). It was found that the behavior of the Bettas resembled that of the Paradise fish in many of its details

LITERATURE CITED

Braddock, J. C. and Zora I. 1955. Aggressive behavior among females of the Siamese fighting fish, Betta splendens. Physiol. Zool., 28: 152-72.

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I. INTRODUCTION

It has been known for some time that the Paradise fish, Macropodus opercularis exhibits aggressive behavior, but this is the first formal study to be undertaken. Several papers have been published concerning the aggressive behavior of other species of fish. Braddock and Braddock (1955) reported that the female Betta splendens displays elaborate fighting behavior. Another study (Braddock 1945) described the dominance-subordination relationship in homosexual and heterosexual groups of both females and males of Platypoecilus maculatus. Hess (1952) in a slightly different type of study found that by using models representing male Bettas and by varying the temperature of the water, he could cause the duration of the challenge response in male Bettas to vary. In his study of the Green Sunfish, Greenberg (1946) discovered that in these fishes, heirarchy represents distinct levels of aggressiveness while territoriality results from a balance between almost equally aggressive individuals. Newman (1956) found that a relatively complicated dominance-subordination relationship occurred in two species of trout. The dominant individuals of both species were light in color while the subordinates were darker. Also size was an important factor in determining dominance, but sex was not significant.

The purpose of this study was to discover and analyze, as far as possible, the various aggressive behavioral traits characteristic of the Paradise fish. A comparison was then made between those fish that did fight and those that established a dominance-subordination relationship without fighting.

It was also hoped that certain consistent differences in detail would be found to occur between the aggressive patterns of *M. opercularis* and *B. splendens* which could be used as criteria in future experiments involving these two species.

II. METHODS AND MATERIALS

All observations reported in this paper were made in a laboratory located on the second floor of the Natural Science Building at Michigan State University. Three large windows facing south admitted insufficient light. Therefore four desk lamps with 100 watt bulbs were used to compensate for the lack of light from the windows.

The laboratory was heated by thermostatically controlled steam radiators located under the windows and well away from the aquaria. Observations were conducted during the spring and summer when there is normally a wide temperature range. Therefore, the range of 78° - 84° F in water temperature was unavoidable.

Tap water from the building was used after it had been aerated for several days.

The fish were housed in clear-glass, gallon jugs that had been cut off near the top to provide a wider opening. Approximately 5 inches of water were kept in these containers at all times. No gravel or plants were present. Waste products were siphoned out every seven days. During observation periods the fish were placed in an aquarium whose dimensions were as follows: 30.5 x 26.5 x 26.5 cm. This was filled to a depth of 10 inches. No snails, plants or gravel were put in this aquarium.

Small pieces of finely ground, uncooked shrimp were given to each fish every morning. This diet was supplemented with live vestigial Drosophila once a week.

The fish observed were all adult males obtained from a dealer. Their exact ages were not known. When individuals were paired, their relative sizes were noted prior to each observation and an attempt was made to match them according to size. Thirty-three individuals were used in this study, and fifty-nine pairings were made.

Before the fish were placed together for observation, the jars containing them were placed near the observation aquarium, and the water temperatures were equalized by the room temperature. The fish were then gently netted one after the other, as quickly as possible, and placed in the aquarium. This never required more than twenty seconds. Observations lasted a minimum of thirty minutes and, if longer, were terminated only when mutual behavior ceased.

A record of all observed activities was kept for each observation period. This was accomplished by the use of symbols representing different activities.

At the end of each observation period the fish were placed in their respective containers. A small amount of salt was added to the water in cases where a fish was injured. No individual was paired again before its wounds were completely healed.

For convenience in reporting, the sequence of events in each pairing was divided into the following sections:

1. Activities prior to fighting or the establishment of dominance without fighting. This period included all activities that occurred from the time both fish were placed in the aquarium until actual fighting began or until a definite dominance-subordination relationship was established in its absence. In those instances in which no actual fight took place, this period was judged to end with the first definite retreat by one of the pair-mates.

2. Activities during fighting. This period began with the first exchange of bites before dominance was established, and terminated with the first definite retreat by one of the pair-mates.

3. Activities subsequent to fighting or the establishment of dominance without fighting. This period began with the first definite retreat by one of the pair-mates whether or not a fight had taken place and ended when mutual aggressive activities ceased.

III. RESULTS

1. Activities prior to the establishment of dominance without fighting. A dominance-subordination relationship is not established immediately after two male Paradise fish are placed together in an aquarium. First the fish react in various ways to each other and to their surroundings. These social reactions result in fighting or the establishment of a dominance-subordination relationship without fighting. The following concerns the nature of this phase in those instances where no fighting eventuated. The period varied in duration (Table 1).

TABLE 1

Durations of Periods Prior to the Establishment of Dominance Without Fighting (34 Pairings)

Time (Min.)	No. of Pairings
0-2	13
2-4	9
4-6	3
6-8	2
8-10	0
10-12	2
12-14	2
14-16	1
16-18	1
18-20	0
20-22	1

Among the pairings the longest such period lasted 21 minutes, the shortest 0.25 minutes, and the mean was 5.2 minutes. In 22 of the 34 observations the duration was 4 minutes or less. On the basis of the frequency classes employed in Table 1 the mode was 0-2 minutes.

In 29 of the 34 observations, the first social reaction occurred within 0.5 minutes, and in 19, one or both fish reacted socially as soon as the second fish was placed in the aquarium. In the other 15 observations the maximum time before the first reaction was 4.2 minutes, the minimum 0.25 minutes, and the mean, 0.9 minutes (Table 2). On the basis of the frequency classes employed in Table 2 the mode was 0.0 - 0.25 minutes. The maximum time of 4.2 minutes was exhibited by one extremely passive pair. Not including those fish that showed immediate reactions, the greatest number of pairs (8) showed initial reactions at 0.25 - 0.50 minutes. The other 5 pair-mates explored or remained motionless prior to their first social reactions.

TABLE 2

Time Elapsed Before First Social Reaction Prior to the Establishment of Dominance (34 Pairings)

Time (Min.)	No. of Pairings
0.0-0.25	21
0.25-0.50	8
0.50-0.75	0
0.75-1.00	2
1.00-1.25	0
1.25-1.50	0
1.50-1.75	1
1.75-2.00	1
4.00-4.25	1

In every case the first reaction observed between pair-mates took the form of challenging. In 33 of the 34 pairings the first challenge was individual, while in one instance it was mutual. Individual challenging is a stereotyped reaction. One fish approaches the other,

holds its body in a rigid position, and spreads its caudal fin. The gill covers may or may not be erected. The color of the fins and body usually becomes more fully saturated. Individual challenges may be of either short or long duration, and may or may not occur in a rapid series. The total number of individual challenges for the 34 observations in which no fight occurred was 750, an average of 12 per individual. Both pair mates exhibited individual challenging in 29 pairings, and one only in 5. The maximum number per fish during this period was 55, the minimum 0, and the mean 11. For contact pairs these figures were 104, 1, and 22 respectively (Table 3).

Mutual challenging occurs when two fish challenge at the same time. The two fish approach each other and stop in a head to tail position. Their bodies become rigid, and their tail fins are spread. The gill covers may or may not be erected. Frequently the bodies of both fish vibrate rapidly, and they sink slowly to the bottom of the aquarium. Mutual challenges varied slightly in duration, lasting from approximately 3 seconds to 10 seconds, but unlike individual challenges, they did not occur in rapid succession. Frequently an individual challenge became a mutual challenge if the original challenger maintained his position.

Mutual challenging occurred throughout the period prior to the establishment of dominance without fighting. The total number of mutual challenges was 100, and they occurred in 22 pairings. Considering only those pairings in which this activity was observed, the maximum number per

contact pair was 16, the minimum 1, and the mean 5 (Table 3).

When mutual challenges are considered as individual challenges of each pair-mate, the maximum number of all challenges per individual was 69, the minimum 0, and the mean 14. For contact pairs these figures were 136, 3, and 28 respectively. Some sort of challenging occurred in all experiments with a total of 950 challenges. Only 3 of the 68 pair-mates did not challenge at all.

TABLE 3

Frequencies of Various Activities Prior to the Establishment of Dominance without Fighting (34 Pairings)

	Indiv. Chal.	Mut. Chal.*	All Chal.	Chasing*	Ret.*	Biting*	Explor.*	Dance for Pos.*
Totals for all Pairings	750	100	950	15	11	6	57	100
No.Pair-Mates Involved	63	44	65	2	2	6	20	44
No.Pairings Involved	34	22	34	2	2	5	12	22
Max./Indiv.	55	16	69				11	18
Min./Indiv.	0	1	0				1	1
$\bar{V}$/Indiv.	11	5	14				3	5
Max./Pairing	104	16	136				13	18
Min./Pairing	1	1	3				1	1
$\bar{V}$/Pairing	22	5	28				5	5

*Maximum, minimum, and mean figures apply only to those pairings where activitity occurred.

Chasing is the pursuit, either rapid or slow, of one pair-mate by the other. This occurred in only 2 of the 34

pairings, and only 2 individuals exhibited this behavior giving a total of 15 instances for all pairings.

Retreating occurred only as a response to chasing. It took the form of either rapid or slow movement away from the other fish. Eleven retreats were recorded.

Biting was noted in 5 of the 34 pairings. In one pairing both fish bit, while in four, only one of the pair-mates exhibited this activity. The total number of bites recorded was 6, and all individuals showing this activity bit only once.

Exploring was observed in 12 pairings (Table 3) and involved swimming into various regions of the aquarium, usually picking up bits of algae and other small particles in what appeared to be an attempt to feed. The total number of instances for all pairings was 57 with 20 pair-mates involved. Considering only those individuals that actually explored, the maximum number of instances per individual was 11, the minimum 1, and the mean 3. Corresponding figures for contact pairs were 13, 1, and 5.

Dancing for position is a behavior trait involving both fish and was observed in every period in most of the pairings. The fish approach each other and begin to swim in a tight circle usually maintaining a very close distance between them. Individual and mutual challenging may both occur. Dancing for position was observed 100 times and was noted in 22 of the 34 pairings. Based only on those

pairings in which this activity took place, the maximum number per contact pair was 18, the minimum 1, and the mean 5 (Table 3).

As shown in Table 3, challenging was the most common activity during the period prior to the establishment of dominance without fighting. Dancing for position was second. Exploring, chasing, retreating, and biting followed in order. Actually, biting was noted in more pairings and more pair-mates were involved than was the case for chasing and retreating.

2. Activities prior to fighting. In those pairings where fighting occurred the activities that preceded it resembled those noted in the observations where dominance was established without fighting. Also the range of variation in duration of the initial period was similar. The maximum was 16 minutes, the minimum 1.5 minutes, and the mean 6.3 minutes (Table 4). In 19 of the 25 pairings the duration was 8 minutes or less. On the basis of the frequency classes employed in Table 4 the mode was 6-8 minutes.

TABLE 4

Durations of Periods Prior to Fighting
(25 Pairings)

Time (Min.)	No. of Pairings
0-2	2
2-4	6
4-6	4
6-8	7
8-10	2
10-12	1
12-14	1
14-16	1
16-18	1

In 19 of the 25 pairings one or both pair-mates reacted to the other as soon as the second fish was placed in the aquarium. In the other 6 the maximum time before the first reaction was 2 minutes, the minimum 0.33 minutes, and the mean 0.8 minutes. On the basis of the frequency classes employed in Table 5 the mode was 0.0-0.25 minutes.

In 24 of the 25 pairings the first reaction between the pair-mates took the form of challenging, while the other initial reaction was dancing for position.

TABLE 5

Time Elapsed Before First Social Reaction Prior to Fighting (25 Pairings)

Time (Min.)	No. of Pairings
0.0 -0.25	19
0.25-0.50	3
0.50-0.75	1
0.75-1.00	1
1.00-1.25	0
1.25-1.50	0
1.50-1.75	0
1.75-2.00	1

Seven of the initial challenges were mutual, and 17 were individual.

The total number of individual challenges for all 25 pairings was 1034. Both pair-mates exhibited individual challenging in all pairings, and the maximum number per individual was 82, the minimum 2, and the mean 21. For contact pairs these figures were 118, 6, and 41 respectively (Table 6).

Mutual challenges were observed in all of the pairings and totalled 263 (Table 6). The maximum number per contact pair was 23, the minimum 4, and the mean 11. Like individual challenges, mutual challenges were more numerous prior to fighting than in the corresponding period where no fighting occurred.

TABLE 6

Frequencies of Various Activities during the Periods Prior to Fighting (25 Pairings)

	Indiv. Chal.	Mut. Chal.	All Chal.	Biting*	Explor.*	Dance for Position
Totals for all Pairings	1034	263	1560	14	8	207
No. Pair-mates Involved	50	50	50	12	7	48
No. Pairings Involved	25	25	25	7	5	24
Max./Indiv.	82	23	94			24
Min./Indiv.	2	4	7			0
$\bar{V}$/Indiv.	21	11	31			8
Max./Pairing	118	23	142			24
Min./Pairing	6	4	14			0
$\bar{V}$/Pairing	41	11	62			8

*Maximum, minimum, and mean figures apply only to those pairings where activity occurred.

If mutual and individual challenges are combined and treated simply as general challenges the maximum per individual was 94, the minimum 7, and the mean 31. Corresponding figures for contact pairs were 142, 14, and 62. The total for all challenges for the 25 pairings was 1560.

Biting occurred in 7 of the 25 pairings and involved 12 pair-mates. Only 14 bites were recorded (Table 6). Considering only those individuals that bit, the maximum per fish was 3, the minimum 1, and the mean 1. It was also noted that biting occurred more frequently during this

period than in the corresponding period of the non-fighters. The mean per pairing was 2.

Exploring was considerably less prevalent in the period prior to fighting than was the case when dominance was established without fighting. In the former it was observed in only 5 of the 25 pairings. Only 7 pair-mates were involved and the total number of instances was 8 (Table 6). Considering only those individuals that actually explored, the maximum per individual was 2, the minimum 1, and the mean 1. The mean per pairing was 2.

Dancing for position was observed in 24 of the 25 pairings and a total 207 examples was recorded. The maximum number of instances per contact pair was 24, the minimum 0, and the mean 8 (Table 6). This activity also occurred more often than in the corresponding period where no fighting followed.

Table 6 indicates that challenging was the most frequent activity during the period prior to fighting. Dancing for position had the second greatest frequency and was followed by biting and exploring in that order.

Chasing and retreating did not occur during the observations of the periods prior to actual fighting.

3. Activities during the period of fighting.

This period began with the first exchange of bites by the pair-mates. In the 25 pairings in which fighting took place, individual challenges immediately preceded the fights in 15, mutual challenges in 7, and dancing for position in 3.

This period varied in duration (Table 7). The maximum was 25.66 minutes, the minimum 0.05 minutes, and the mean 8.6 minutes. In the 22 pairings where duration was recorded, 10 such periods lasted 2 minutes or less. On the basis of the frequency classes employed in Table 7 the mode was 0-1 minute. In 3 pairings fighting had not ended at the termination of the observation periods, and the actual durations were not recorded. For consistency with the other observations a limit of 30 minutes was given to these 3 instances when making computations concerning the various activities.

TABLE 7

Durations of Fights
(22 Pairings)

Time (Min.)	No. of Fights
0-1	8
1-2	2
2-3	1
3-4	2
4-5	1
5-6	0
6-7	0
7-8	1
8-9	1
9-10	0
10-11	0
11-12	0
12-13	0
13-14	1
14-15	1
15-16	3

Certain activities characteristic of the preceding period were also noted during fighting. These were individual and mutual challenging, biting by one pair-mate, and dancing for position. Exploring was not observed. In contrast, multiple exchanges of bites and locking of jaws occurred only during fighting. All activities during the fighting period seemed to be accelerated, and both fish generally moved very rapidly at all times.

Individual challenging occurred in 23 of the 25 pairings, and a total of 858 such challenges were recorded. The maximum number per individual was 121, the minimum 0, and the mean 17. For contact pairs these figures were 230, 0, and 34 respectively (Table 8).

Mutual challenges totalled 333 and were observed in 20 pairings. The maximum per contact pair was 65, the minimum 0, and the mean 13 (Table 8).

When individual and mutual challenges were combined by counting the mutual challenges as individual challenges for each of the pair-mates, it was evident that some sort of challenging took place in 24 of the 25 pairings. There was a total of 1524 challenges for all pairings. Forty-five individuals were involved. The maximum number of all challenges per individual was 186, the minimum 0, and the mean 30. Corresponding figures for contact pairs were 360, 0, and 61 (Table 8). In one pairing neither pair-mate showed any type of challenging, and in 3, one fish did not challenge.

Multiple exchanges of bites were characteristic only of the period of actual fighting. These were most frequently directed at the mouth, but also involved other parts of the body. Since this activity was very rapid, it was impossible to count the number of single bites that took place, and only the number of exchanges was recorded. The frequency of these multiple exchanges varied greatly. Many times several occurred without being interrupted by any other type of activity. More often, however, a multiple exchange took place and was interrupted by some other activity such as challenging or dancing for position before it occurred again. Frequently multiple exchanges of bites were terminated by locking of jaws. The maximum number of multiple exchanges of bites per contact pair was 52, the minimum 0, and the mean 13. A total of 317 multiple exchanges were recorded for the 22 pairings in which they occurred (Table 8).

Dancing for position was a common activity during fighting. This was accompanied by other activities such as challenging and biting. Dancing for position varied in duration. Certain instances lasted only a few seconds while others continued for several minutes. It was observed 244 times in the 19 pairings in which it occurred at all. Considering only those pairings, the maximum per contact pair was 45, the minimum 1, and the mean 13 (Table 8).

TABLE 8

Frequencies of Various Activities
During the Periods of Fighting
(25 Pairings)

	Challenges			Bites		Other Activity	
	Indiv.	Mut.	Tot.	Indiv.	Mult. Exch.	Dance for Pos.*	Lock Jaws*
Total for all Pairings	858	333	1524	777	317	244	179
No. Pair-Mates Involved	42	40	45	48	44	38	36
No. Pairings Involved	23	20	24	25	22	19	18
Max/Indiv.	121	65	186	73	52	45	32
Min./Indiv.	0	0	0	0	0	1	1
$\bar{V}$/Indiv.	17	13	30	16	13	13	10
Max./Pairing	230	65	360	137	52	45	32
Min./Pairing	0	0	0	1	0	1	1
$\bar{V}$/Pairing	34	13	61	31	13	13	10

*Maximum, minimum, and mean figures apply only to those pairings where activity occurred.

Individual biting was also characteristic of this period but with much greater frequency than in the preceding period (Table 8). The maximum number per individual was 73, the minimum 0, and the mean 16. For contact pairs these figures were 137, 1, and 31 respectively. The total number of bites for the 25 pairings was 777. Forty-eight pair-mates were involved, but in two pairings one of the pair-mates did not bite.

Locking of jaws occurred only during the period of fighting. Frequently a multiple exchange of bites preceded this activity. Locking of jaws involved mutual tugging and pulling while the pair-mates turned over and over as they slowly sank to the bottom of the aquarium. The bodies of the fish were rigid and the fins spread as in challenging. No accurate record of the duration of this activity was made, but some instances lasted only a few seconds while others lasted as long as 60 seconds. Considering only those pairings in which locking of jaws was observed, the maximum per contact pair was 32, the minimum 1, and the mean 10. It occurred in 18 of the 25 pairings with a total of 179 instances (Table 8).

The fighting period involved the greatest amount of activity in the sequence, and the actual physical contact between pair-mates was greatest then. In comparison to the period prior to fighting, individual challenging and mutual challenging occurred with less frequency. Individual biting was much more frequent during the fighting period, while the occurrence of two new activities, multiple exchanges of bites and locking of jaws, gives further indication of the vigorous activity characteristic of this period.

In each pairing the intensity of color saturation of both fish was greater during this period than in the other periods of the same pairing. The intensity frequently varied

with respect to a particular fish, but during locking of jaws, both pair-mates were as dark in intensity of color saturation as at any other time in the observation period.

4. Activities following the establishment of dominance without fighting. In the absence of fighting, dominance was considered established when one pair-mate retreated without subsequent aggressive behavior.

In 26 of the 34 observations individual challenging immediately preceded the first retreat, while in one, mutual challenging was the preceding activity. Biting preceded the first retreat in 2 pairings and dancing for position in 5. In every case retreating immediately followed some type of aggressive behavior by one or both fish.

At the moment of the first retreat all of the subordinate fish quickly became less saturated with regard to the color of both body and fins. The color saturation of the dominant individuals became less much more slowly, if at all.

During this period dominant individuals differed in many respects from their subordinates (Table 9). The former challenged 1267 times in 34 pairings while the latter challenged only 409 times in 26. The means were 37 and 16, respectively. In nearly all cases, individual challenges exhibited by the subordinates were defensive in nature, and occurred only when they were approached and cornered by the dominant individuals. The dominants bit the subordinates during 24 pairings and registered a total of 113 observed bites compared to 0 for the subordinates. The dominant individuals did not retreat at all but chased the subordinates 1115

times, while the latter retreated 1208 times and did not chase. Exploring was recorded 225 times in 31 pairings for the dominant fish and only 81 times in 21 pairings for the subordinates. The means were, respectively, 7 and 4. Thus the dominant fish had a much greater freedom of movement within the aquarium. Mutual challenging occurred 41 times in 9 pairings, and dancing for position occurred 40 times in 7. Mutual reactions were not as frequent as individual reactions during this period.

TABLE 9
Activities Following the Establishment of Dominance Without Fighting
(34 Pairings)

	Indiv. Chal.	Mut. Chal.	Bites	Retreat	Chasing	Explor.	Dance for Pos.
Dominants	1267	41	113	0	1115	225	40
Subordinates	409	41	0	1208	0	81	40

5. Activities following surrender subsequent to fighting. The periods of active fighting were followed by periods thought to correspond to the periods following the establish ment of dominance where no fighting occurred. They began with the first definite retreat by one of the pair-mates. After this the individual that retreated exhibited little or no aggressive behavior.

In 12 of the 22 pairings, individual challenging immediately preceded the first retreat. Mutual challenging preceded it in 2, as did individual biting, while locking of jaws occurred in 4 pairings. Dancing for position and multiple exchanges of bites each preceded the initial retreat in one pairing.

The changes in the intensity of color saturation by both the winners and losers were very similar to those shown in the corresponding periods where no fighting took place. In every instance the winners were of a darker color saturation than the losers.

The winners challenged the losers in 20 pairings with a total of 419 individual challenges. The loser challenged only 68 times in 11 pairings. The means were 21 and 6, respectively. Most of the losers challenges seemed to be defensive in nature. The winners bit the losers 46 times in 12 pairings and were not bitten in return. The winners did not retreat but chased the losers 516 times. The losers retreated from the winners 448 times and did not chase. The winners explored 86 times in 16 pairings compared to 22 times in 7 pairings for the losers, indicating a freer movement on the part of the winners. The means were 5 and 3, respectively. The mutual activities, mutual challenging and dancing for position, were even more noticeably absent in these periods than in the corresponding periods without fighting (Table 10). There were 6 mutual challenges observed in 3 pairings, and only 2 instances of dancing for position, both in the same pairing.

TABLE 10
Activities Following Surrender
Subsequent to Fighting
(22 Pairings)

	Indiv. Chal.	Mut. Chal.	Bites	Retreats	Chasing	Explor.	Lance for Pos.
Winners	419	6	46	0	516	86	2
Losers	68	6	0	448	0	22	2

6. Intensities of color saturation. No truly objective system was used to classify the differences in color saturation. The fish were merely identified as dark, medium, or light. An individual identified as "dark" exhibited vivid blue and orange alternating dorso-ventral stripes along the body. The dorsal and ventral fins were bright blue, while the caudal fin was bright orange. "Medium" indicated that the fish clearly showed the blue and orange stripes along the body, but not as vividly. Also the fins were less saturated. A "light" fish showed only faint blue and orange stripes along the body, and the tail fin was pale orange. The dorsal and ventral fins were almost colorless.

The intensities of color saturation varied greatly among the individuals, and the classification was not used to describe the exact intensities of all the fish observed at all times. It did enable the observer to make a comparison of the relative color saturations of each of the pair-mates during the various phases of each observation period. Thus, both were consistently dark or medium during the period prior to the establishment of dominance or fighting as well as during the period of actual fighting. Immediately after dominance was established either by fighting or not the winner was always darker than the loser. This does not mean that the dominant fish was always dark and the subordinate always light. Instances occurred in which the winner of one pairing was actually lighter than the loser of another.

In most pairings the winners and dominant fish retained a darker color saturation than the losers and subordinates until the observation periods were terminated. In some cases both pair-mates exhibited the same intensity after dominance had been established for a period of time.

7. Comparison with female Betta splendens.

Braddock and Braddock (1955) gave an extensive account of the aggressive behavior patterns of the Siamese fighting fish, Betta splendens. The data gathered in the study of the Paradise fish indicate a marked similarity between the two species.

While many of the activities were essentially the same for Bettas and Paradise fish, there was one outstanding exception. Dancing for position was noted throughout the entire observation period in this study while its rough equivalent, jockeying for position, was observed only during the period of actual fighting among the Bettas.

Prior to actual fighting there was a period where the fish reacted both to each other and to their surroundings. In both studies the durations of these periods prior to fighting were similar. Based on 35 pairings the mean time for the Bettas was 6.6 minutes compared to 6.3 minutes for 25 pairings of the Paradise fish.

The mean time that elapsed before the first social reaction of the Bettas was 33.4 seconds based on 35 pairings and 48 seconds for the Paradise fish based on 25 pairings. Individual challenging was the predominant first reaction in both studies. Among the Bettas this occurred in 22 of the 35 pairings; the other 13 were initiated by mutual challenges. In 24 of the 25 Paradise fish pairings, social reactions began with challenging. Seventeen of these challenges were individual and 7 were mutual.

A comparison of the relative frequencies of aggressive activities throughout the periods prior to fighting indicates that individual challenging was the most common reaction in both studies. This activity occurred in nearly all of the Betta pairings and was universal among those of the Paradise fish.

Mutual challenges occurred in all pairings in both studies and was the second most frequent activity.

Instances of chasing and retreating were recorded in the Betta observations and were absent in this study during the period prior to fighting. Biting was much more frequent in the Betta study. Exploring was noted in both but instances were not frequent.

In both species some pair-mates fought while others did not. The period of actual fighting among the Bettas was of longer duration and seemed to involve greater activity than the corresponding period among the Paradise fish. The mean time for the Betta pairings was 51.5 minutes for 35 pairings compared to 8.6 minutes for 25 Paradise fish observation periods.

Similar activities were observed in both species, and although they were observed less often in the Paradise fish study, this was probably because the mean time for the period of fighting was approximately 6 times less than in the Betta observations.

The types of bites were analyzed to a greater degree in the Betta work than was done in this study. However, single and multiple exchanges of bites were frequent in both.

Locking of jaws occurred only during the fighting periods in both studies but was not characteristic of very short fights (less than 15 minutes) among the Bettas. Since only 5 pairings of Paradise fish lasted over 15 minutes, it is significant that for them this activity was relatively common.

Like jaw-locking, jockeying for position was observed only during the fighting period among the Bettas, but its rough counter-part, dancing for position, was recorded in all periods of this study.

Injuries were extensive among the Bettas due to their savage biting while very few were noted among the Paradise fish.

Definite dominance-subordination relationships were established in both studies with or without fighting. In In both, the dominant individuals were more aggressive and had a much greater freedom of movement within the aquarium. The subordinates tended to retreat or to make way for the dominant fish.

No indication of a revolt on the part of a subordinate fish was noted in either study.

Relative size of the pair-mates was a fairly reliable basis upon which to predict the winner of a fight, but there were exceptions in both studies. Based on 22 Paradise fish pairings the larger fish won 13 times and the smaller 3. In 6 pairings the pair-mates were of equal size.

In this study, as in the Betta observations, a rough comparison was made between the relative frequencies of the various types of challenging both during the periods prior to fighting and the periods of actual fighting. This was done by dividing the total number of instances of each activity by the total duration in minutes of the appropriate period.

The sum of the durations of all periods prior to fighting was 159 minutes, while the corresponding figure for the fights was 216 minutes. The average number of individual challenges per minute for the periods prior to fighting for all 25 Paradise fish pairings was 6.5. The equivalent figure for the fights was 4.0.

This situation was reversed in the Betta study, the corresponding numbers being 0.9 and 1.4 for 21 pairings.

Among the Paradise fish mutual challenges averaged 1.7 and 1.5 per minute respectively for the periods prior to fighting and of actual fighting while for Bettas these figures were 0.9 and 0.4.

It is doubtful that dancing for position among Paradise fish is the same type of activity as the jockeying for position of the Bettas in that it represents a tendency to replace mutual challenging as fatigue increases during the course of a fight. This was suggested for jockeying in the Betta study. However, if it is assumed that such a relationship does exist, one may add the totals of dancing for

position to those of mutual challenging and obtain an average per minute during the period prior to fighting of 3.0. For the period of actual fighting the figure is 2.6. In the Betta study the corresponding figure involves the fighting period only since jockeying did not occur at any other time, and the average was 1.9. On this basis the Bettas showed a marked increase of the frequency of mutual challenging during fights while the Paradise fish did not.

These data indicate no increase in the frequency of mutual challenging during the fights of Paradise fish. Jockeying for position among the Bettas and dancing for position among the Paradise fish are probably not comparable, and this may be one of the causes of the difference.

The Bettas had a complex system of color changes as compared to Paradise fish, and a comparison of the changes in relation to various activities would be extremely difficult. The most noticeable color changes in both species occurred at the end of a fight when a dominance-subordination relationship was established.

IV. DISCUSSION

As was stated previously, the primary purpose of this work was to discover the various activities involved in the establishment of dominance-subordination relationships among Paradise fish, Macropodus opercularis. Also, a comparison was made between the activities of this fish and those of Bettas (Braddock and Braddock, 1955), with the hope of finding consistent differences that could be used as criteria in future studies involving these two species.

The periods prior to fighting resembled the periods prior to the establishment of dominance without fighting. The maximum and minimum durations were similar (Tables 1, 4) as were the mean durations which were 6.3 and 5.2 minutes respectively.

The times that elapsed before the first social reactions were similar for both periods (Tables 2, 5). The mean for the periods prior to fighting was 0.8 minutes while 0.9 minutes was the mean for the periods prior to the establishment of dominance without fighting. There was no significant difference here. Therefore, it was impossible to predict the probability of a fight on this basis.

In both periods the most common initial reaction was challenging. In both, individual challenging predominated over mutual challenging (periods prior to the establishment of dominance without fighting 33 to 1, and the periods prior to fighting 17 to 7).

Therefore, the occurrence of individual challenging as the initial social reaction was not a criterion of the probability of subsequent fighting or its absence. However, those pairings in which fighting later occurred did show a significantly greater proportion of mutual challenges as the first social reaction between pair-mates, and it is evident that fights were much more likely to occur in those pairings where the first reaction was an initial challenge.

Similar activities were observed throughout both periods (Tables 3, 6). Individual challenging had high frequency during the periods prior to fighting. It averaged 6.5 per minute as compared to 4.3 individual challenges per minute in the periods prior to the establishment of dominance without fighting. Also, mutual challenging had greater frequency in the periods prior to fighting, 1.7 as compared with 0.6 for the periods prior to the establishment of dominance without fighting.

Both types of challenging were more common in those pairings in which fights followed. Individual challenging occurred one and one-half times as often and mutual challenging more than twice as often. This clearly indicates a relationship between the frequency of challenging in general and the probability of a subsequent fight and suggests that this activity when repeated frequently enough may be a mechanism that builds aggressiveness in the pair-mates to the point where actual fights are possible.

Dancing for position occurred almost twice as often in the periods prior to fighting as in those prior to the establishment of dominance without fighting. The frequencies per minute were 1.3 and 0.6 respectively.

Taken with the relative frequencies of both types of challenging, dancing for position may be regarded as an indicator of fight probability. The nature of this activity is such as to suggest a relationship with challenging and it may also contribute to a building up of general aggressiveness.

Exploring was observed in the periods prior to the establishment of dominance without fighting with a frequency of 0.3 per minute. It occurred so seldom in the periods prior to fighting that a determination of its frequency was not recorded here (Table 6). Although this activity was infrequent as compared with challenging and dancing for position it involved more time per instance. Therefore, its presence in the periods prior to the establishment of dominance without fighting in contrast to its general absence in the periods prior to fighting has significance. Exploring probably is the result of a lack of aggressiveness between pair-mates.

Biting was observed so infrequently in either period that an attempt to compare frequencies would have no significance.

In summary, certain activities associated with aggressiveness (challenging and dancing for position) were displayed with significantly greater frequencies in the periods prior to fighting. Exploring, which may be associated with a lack of aggressiveness was more characteristic of the periods prior to the establishment of dominance without fighting. Biting and locking of jaws appear to be aggressive activities that occur only after a general buildup of aggressiveness has occurred. Therefore, challenging and dancing for position may be regarded as builders and maintainers of aggressiveness in this species while biting and jaw-locking are its foremost expressions.

The periods prior to fighting were terminated with the first rapid exchanges of bites by the pair-mates. This action was the criterion chosen for the beginning of a fight. In every instance the fights were immediately preceded by some form of aggressive action on the part of one or both pair-mates.

The highest frequencies of aggressive activities occurred during the periods of active fighting. These periods had a mean duration of 5.6 minutes. The mean for the periods prior to fighting was 6.3 minutes.

Two activities occurred only during fights: multiple exchanges of bites and locking of jaws. Furthermore, individual biting, which was common here occurred only sporadically at other times. Its frequency during fights was 3.6 per minute. These three were largely responsible

for the great increase in total aggressive activity and physical contact between the pair-mates during this period. Exploring was not observed during fighting.

Most of the activities recorded for the periods prior to fighting were also observed during fighting (Tables 6, 8).

Individual challenging decreased in frequency in these periods. Prior to the period of fighting its frequency per minute was 6.5. The corresponding frequency for the fights was 4.0.

There were no significant differences in the frequencies of mutual challenging and dancing for position when the two periods were compared.

In summary, when the periods prior to fighting are compared with periods of actual fighting it is apparent that certain activities occurred only during fights. These were multiple biting and jaw-locking. One activity, exploring, was recorded only during the periods prior to fighting. All of the other activities, individual challenging, mutual challenging, individual biting, and dancing for position, occurred during both periods. However, individual biting was typical only of the fights, while there was a significant decrease in the frequency of individual challenging during the fighting periods.

In general these data reinforce the conclusions drawn from the comparison of the periods prior to fighting with those prior to the establishment of dominance without fighting. Thus, the supposedly non-aggressive activity, exploring, decreased at a time when initial aggressiveness

would be expected to be at a high level, while the indicators of aggressiveness, mutual challenging, dancing for position, and biting of all types either remained the same or increased in frequency. The decline in individual challenging probably indicates its replacement by aggressive activities of a higher level, namely jaw-locking and biting.

If, for purposes of comparison, the average per minute of all aggressive activities are totaled for the periods prior to fighting and for the periods of actual fighting, the results are 9.6 and 12.5 respectively. This indicates, in a general way, the presence of an actual increase during fights.

Except for a few instances of chasing and retreating observed prior to the establishment of dominance without fighting in two pairings, these activities were recorded only after dominance was established either by fighting or not.

After dominance was established by either method the winners or dominants were observed to have complete freedom of movement within the aquarium. This is shown clearly by comparing the frequencies of exploring for the dominants and winners to those of the subordinates and losers (Tables 9, 10). The mean per pairing for the winners was 5.4 and for the losers 3.1.

Corresponding figures are 7.3 for the dominants and 3.9 for subordinates.

The effect of the dominance-subordination relationship

on the behavior of the pair-mates can be shown by comparing the frequencies of chasing and retreating. There were no observed instances of winners or dominant fish retreating but they chased frequently. Also, losers and subordinates were not observed to chase but retreated frequently.

Biting was also displayed only by the despot in both instances.

Challenging was a frequent activity on the part of both winners and dominants. The losers and subordinates were observed to challenge but less frequently and only when approached and cornered by the aggressors.

Mutual activities were almost absent in the periods subsequent to fighting. Six mutual challenges were observed in 3 pairings and 2 instances of dancing for position were recorded in one.

These figures were significantly higher for the periods following the establishment of dominance without fighting. Mutual challenging occurred in 9 pairings with an average of 4.6 per pairing. Dancing for position was recorded in 7 pairings with an average of 5.7 per pairing.

The very low frequencies of mutual activities during the period subsequent to fighting must have been the result of strong dominance-subordination relationships between the pair-mates.

Mutual activities which indicate a high level of aggressiveness in both pair-mates, showed a sharp decrease after dominance was established with or without

fighting. Individual aggressive behavior was largely confined to the dominants and winners, as was the non-aggressive exploring.

When the aggressive activities of individuals that have won fights are compared to those of fish that have established dominance without fighting, certain similarities and differences are apparent. The winners of fights averaged 21 individual challenges per pairing while the dominants averaged 37. The winners chased 23 times, while the dominants chased 33 times. These differences may have been due to simple fatigue on the part of the winners or may reflect a stronger dominance-subordination relationship established by actual fighting.

Biting, which is characteristic of the periods of actual fighting occurred with similar frequency in both instances. Also, there was no significant difference in the frequencies of exploring when the winners were compared with the dominants.

A similar comparison between losers and subordinates who achieved this status without fighting must be confined to data concerning individual challenging and retreating since biting did not occur among them and exploring was too infrequent to have significance.

It seems significant that the losers of actual fights challenged on the average of only 6 times per pairing while the subordinates challenged 16 times. Also the subordinates retreated 35 times compared with a mean

per pairing of 20 times for the losers. Thus the losers and subordinates appear to reflect the behavior of winners and dominants, and the same causes probably underlie the difference in each case.

Many of the same activities noted here were also noted in the Betta study (Braddock and Braddock, 1955). Both individual and mutual challenges were observed prior to and during fighting.

The Bettas differed from the Paradise fish in that individual challenges increased from 0.9 per minute to 1.4 per minute during fighting while among the Paradise fish a frequency of 6.5 per minute during the periods prior to fighting decreased to 4.0 during active fighting.

Unlike the condition among the Paradise fish where mutual challenges had a mean frequency of 1.7 during the periods prior to fighting and 1.5 during actual fights the Bettas showed a decrease in these activities from 0.9-0.4 over corresponding periods.

Individual bites were more frequent among the Bettas prior to fighting but were not as frequent during fighting. Based on 35 fights the Bettas showed 0.3 bites per minute prior to fighting and 1.8 per minute during fighting. Based on 25 fights corresponding frequencies for Paradise fish were .09 and 3.6 respectively.

Dancing for position was observed both prior and during fighting in this study, while in the Betta study the rough equivalent, jockeying for position, was recorded only during fighting. The frequency of this activity was

1.3 per minute prior to fighting and 1.1 per minute during fighting among the Paradise fish. For Bettas the frequency of jockeying was 1.5 per minute during fighting only.

In both studies locking of jaws was observed only during the fighting period. For the Bettas this activity occurred 0.5 times per minute while among the Paradise fish it occurred 0.6 times per minute.

In both studies exploring was observed prior to fighting but not during fighting. For Bettas this occurred 0.2 times per minute and only .05 times for Paradise fish.

By totalling the various activities per minute for the periods prior to fighting and during fighting for both species relative frequencies of general aggressive activity may be compared. For Paradise fish 9.6 activities per minute occurred prior to fighting; 12.5 activities per minute occurred during fighting. Corresponding frequencies for Bettas were 2.5 and 6.9.

Although the duration of fights was considerably longer among the Bettas a comparison between the frequencies of aggressive activities indicates that the fighting period in the Paradise fish involved more such activity.

It should be noted that frequency is not the entire story in such comparisons. Duration of each instance of any activity should also be considered. In this case, the Bettas may merely have sustained many or all of the recorded individual reactions longer.

The effect of dominance-subordination relationship on the pair-mates in both cases was very similar. The

winners showed complete freedom of movement within the aquarium and complete dominance over the losers. The losers, in contrast, had little freedom of movement and were subject to attack by the winners.

The frequencies of the various activities of both species and the types of aggressive activities displayed indicate that both are very belligerent. There is, however, a greater tendency for Paradise fish not to fight. Thirty-four of the 59 pairs in this study did not fight. No other explanation than the general nature of the species can be offered at this time.

Fighting among Bettas causes greater damage than occurs among Paradise fish.

It must be remembered when considering the frequencies of the various activities and when determining the relative belligerency of the two species, that male Paradise fish are being compared with female Bettas. If males of both species had been compared, undoubtedly the frequencies of the various aggressive activities among the Bettas would have been greater, since Noble (1939) stated that males are too belligerent to establish any type of dominance relationship. However, Noble, and Smith (1937), indicated that extreme male aggressiveness and rapid activity would make a detailed analysis difficult, if not impossible.

The agonistic behavior displayed by male Paradise fish may be related to territoriality. The dominant fish may establish a territory which is defended against intruders. If a nest is built and mating occurs, the male

guards the nest. This is an important factor with respect to survival of the young.

Another possible advantage inherent in aggressive behavior of this type may concern success in mating. Among Bettas mating does not occur unless both individuals exhibit certain of the patterns that occur during fighting (Braddock, J. C.--personal communication - 1956). These may be mutual releases for the various elements of the mating sequence.

Dominance can be established without fighting. This is an advantage in that fighting individuals are subject to attack by other animals while fighting, and the increase in color saturation during fighting may actually attract predators. Also, the injuries due to fighting might greatly weaken one or both fish thus making them more suspectible to predation.

There appear to be both advantages and disadvantages when the adaptive significance of aggressive behavior of this type is considered. It may be possible that the establishment of dominance is the adaptive value rather than the way in which it is established. If this should later prove to be the case, then, the less aggressive Paradise fish, which are able to achieve this result frequently without preliminary fighting are more advanced in this respect than the Bettas, and the latter should then be considered behaviorally the more primitive of the two species.

V. SUMMARY

1. Male Paradise fish established dominance-subordination relationships with or without preliminary fighting when paired in a small aquarium.

2. There was a period prior to fighting consisting of aggressive activities both individual and mutual, e.g. individual and mutual challenging, biting, and dancing for position, along with certain non-social activities, e.g. exploring and resting.

3. There was a corresponding period prior to the establishment of dominance without fighting in which occurred activities similar to those observed in the period prior to fighting, but the frequencies of aggressive activities were less and that of exploring was greater. This probably indicated a marked difference in belligerency between such pair-mates.

4. Fighting began as a response to an aggressive act, and a high threshold of mutual aggressiveness was probably necessary if it was to occur.

5. During the period of fighting all non-social activities ceased. Mutual aggressive activities and actual physical contact between pair-mates increased. This was indicated in part by two new activities, locking of jaws and multiple bites which were observed only during this period.

6. Fights ended with a definite retreat by one of the pair-mates. Initially the defeated fish lost much of its color saturation but in some cases regained it later.

7. After the establishment of a dominance-subordination relationship with or without fighting the winner and dominant fish freely bit and chased its subordinate. The frequencies of mutual aggressive activities were less than those of preceding periods.

8. No revolts on the part of the subordinates or losers were noted.

9. Color saturation reached its greatest intensity during fighting. This was also true for Betta splendens, (Braddock and Braddock, 1955).

10. Aggressive activities of the Paradise fish were similar to those noted in the Betta study. Available data indicate that in both studies, individual challenging was an important mechanism for establishing a threshold of aggressiveness between the pair-mates.

11. Dancing for position among Paradise fish and jockeying for position among Bettas may not be completely comparable. This might be a factor in determining the decrease in the frequency of mutual challenging during the period of fighting among Paradise fish, and the increase in this activity in the Bettas.

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