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Aggression, Interactions, and Preference for Males in Female Siamese Fighting Fish (*Betta splendens*)

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Aggressive behavior has been widely studied in the male Siamese Fighting Fish (*Betta splendens*). Selective breeding for brilliant colors and long fins (features associated with more aggressive males) has resulted in highly aggressive behavior in the male morphotype (bright colors, long pectoral, dorsal and tail fins) commonly available in aquarium and pet stores. The wild-morphotype has uniform, dark color with shorter fins. While similar aggressive behaviors have been documented in females, comparatively little work has been done compared to the males. In this study, 8 females were paired in all possible female-female combinations to assess the degree of aggression exhibited by each individual. Aggressive fish were consistently aggressive and subordinate fish consistently subordinate, allowing for ranking of females in terms of their aggressive behavior. Female behavior was then tested in the presence of males, with observations between males and females and females and females when there were 2 females and 1 male present. The presence of males did change the behavioral patterns of some of the more aggressive females. Finally, preference for one of the two male phenotypes was examined. All of the females, regardless of their dominance ranking, chose the wild-type phenotype over the long-finned males, although the least aggressive fish often chose the less aggressive males or the control. These findings have many implications for the relationship between aggression and mate choice, and for choice between a supposedly more "attractive" male (those with exaggerated epigamic features) over a wild-type male with smaller fins and darker color.

Key Terms: *Betta splendens, aggression, mate choice, behavior*

Siamese fighting fish. (*Betta splendens* Regan, 1910), are popular aquarium and hobbyist fish. These fish are native to Thailand, and are found in the wild in flooded rice paddies and small ponds (Jaroensutasinee and Jaroensutasinee, 2001a). Males establish and defend territories, in the center of which they construct bubble nests to hold fertilized eggs. Females move in and out of territories, select a mate and lay their eggs which fall to the bottom. The male will then fertilize the eggs and carry them up to his bubble nest, where he will care for them until they hatch (Jaroensutasinee and Jaroensutasinee, 2001a). In the naturally occurring populations, wild-type males and females live together, although there are territorial disputes (Goldstein, 1975).

Wild males have long been used for sport fighting, with winners of contests more desirable as breeding males. The wild-type males that were the largest in size, had the longest fins, the most appealing colors, and most aggression, were bred to create a new phenotype, hyper-aggressive males with many brilliant colors and long, flowing fins (Myers, 1947). Due to these colorful and flashy features, they are commonly kept as pets and are commercially available in pet and fish supply stores.

Male Bettas have been the focus of behavioral studies of aggression because they are easy to maintain in the laboratory, and they exhibit

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easily identifiable behaviors (for example Allen and Nicoletto 1997; Fortelius 1957; Halperin *et al*. 1997; Halperin *et al*. 1998; Jaroensutasinee and Jaroensutasinee 2001b; McGregor *et al*. 2001; Matos *et al*. 2003; Robertson 1979 and others). These behaviors are discussed extensively in Simpson (1968) in which he identifies the orientations, movements and postures that are exhibited during aggressive displays as well as those considered to be non-aggressive behaviors. The more aggressive behaviors include broadside displays in which the dorsal, caudal and anal fins are extended and frontal displays in which the gill covers and branchiostegal membranes are flared as well as pectoral fin extension (Simpson 1968; Glesener 2001). Both broadside and frontal displays are designed to make the fish look bigger and more menacing. Other aggressive behaviors include tail beating (Simpson 1968; Robertson and Sale 1974; McGregor et al. 2001), chasing, charging, and biting (Simpson 1968; Halperin *et al*. 1997). Simpson (1968) also discusses pectoral fin beating, pelvic fin flickering and tail flashing. Non-aggressive behaviors, such as thrashing (rapid swimming movement away from stimulus or in a perpendicular motion to it), and deliberate evasion are also discussed, as well as behaviors such as exploring the aquarium which are not considered interactive. Halperin *et al.* (1997) believe that thrashing may be a response shown toward females rather than males (also called circling by Robertson and Sale 1974) or may be a product of small, confining aquaria.

Dominance (defined as success in contests by Qvarnström and Forsgren 1998), is clearly the norm for male Siamese fighting fish. In order to protect their nests and territories in the wild, they must dominate other males. Haller and Wittenberger (1988) studied the relationship between social status and energy-producing ability in male *Betta splendens* by establishing winners and losers in paired contests under controlled conditions. They were able to identify hierarchies, with certain fish continuing to dominate other fish. They also found a strong correlation between energy metabolism and dominant social behavior (Haller and Wittenberger 1988). Establishment of dominance hierarchies has been observed in other fish such as green swordtails (Franck *et al.* 1998).

Differences and similarities in behavior between males and females were noted by Simpson (1968). Both male and female *Bettas* can and will bite at each other for long periods of time until one fish stops displaying and begins to avoid the other. The winner of the battle flared its gills and bit twice as often as the loser, who mostly beat its tail in defense (Simpson, 1968). Simpson (1968) also studied how one fish affects the other's displays second by second. The encounters between paired fish ranged from seconds to almost half an hour in some instances (Simpson, 1968). This experiment also found that males act more aggressive and ready to display after they have been socially isolated from other males. Simpson (1968) did find differences between male-male and female-female confrontations. More aggressive males bit twice as often as their less aggressive opponent, while more aggressive females flared their gills twice as much as lesser aggressive females. One other interesting result was that the female winners in the encounters stopped displaying to the loser after a period of time. When they were both taken out and put next to mirrors, the winners displayed to it while the losers did not. This information suggests that the dominant female was up for another challenge while the less dominant fish was nervous after the original encounter and not ready to show aggression (Simpson, 1968).

Studies of male-male contests in the presence of females have also been done. Jaroensutaisinee and Jaroensutaisinee (2001b) studied sexual size dimorphism and male contest in wild *Bettas*. They found that larger males tended to win in male contests and gain greater access to females, and their size and aggression was attractive to females. When two or more males were placed around females their aggressiveness increased, compared to when they were by themselves. They fought each other until a winner was determined or the lesser dominant male began evading the dominant male. Females did not seem to have a preference between larger or smaller males, only for the winners of contests they observed (Jaroensutaisinee and Jaroensutaisinee, 2001b).

Doutrelant and McGregor (2000) also found that the males acted more aggressively towards each other in the presence of females. They concluded that this is because it is the males who protect the offspring while they grow and develop, so the female would want to pick the "fittest" male. They also found that male aggression increased with the presence of additional females.

While aggressive behavior in males has been studied extensively, there have been few studies on females, and none examining female behavior in the presence of males. Female Bettas have been thought to be less aggressive and able to live in communities, and are commonly found together in aquaria (although observations by the authors of shredded fins and bite marks in females kept in community tanks suggest otherwise). Braddock and Braddock (1955) studied aggressive behavior in female *Betta splendens* dyads under laboratory conditions, and

Table I. Total number of observed behaviors for each female

Aggressive Positional	F1	F3	F6	F8	F9	F10	F11	F12
Broadside: Head to Head	3	39	1	34	6	9	13	24
Broadside: Head to Tail	0	7	0	18	11	9	6	5
Perpendicular	0	39	1	50	14	8	29	51
Head to Head	0	10	0	18	12	3	11	14
Aggressive Display								
Gill Flare	6	135	1	146	57	31	72	109
Fin Spread	5	79	30	66	40	40	55	66
Color Flash	8	0	1	41	0	18	12	25
Aggressive Action								
Chasing	2	59	0	76	16	9	24	65
Nipping and Biting	0	13	0	9	0	7	12	35
Non-aggressive								
Color Loss	12	2	7	8	5	12	9	3
Evading without Chase	23	9	24	2	15	9	14	11
Evading with Chase	20	10	53	3	19	20	32	17
TOTAL	79	402	118	471	195	175	289	425

discovered that females do exhibit the same behavior as males when paired with another female. They found that there was a period before actual fighting began in which one or both fish would challenge and display to the other. Fights occurred after an initial aggressive act such as biting, but aggressive behavior needed to be mutual for the fight to continue. After the surrender of one of the females, the winner would continue to display aggressive behavior for a short time, but the loser would retreat. As noted in Braddock and Braddock (1955), Noble (1939) suggested that females will form dominance hierarchies, but presented no evidence or details to support this.

There were three related goals to this study. The first was to determine whether female Bettas could be ranked in order of their aggressive behavior. The second goal was to examine whether this established ranking remained stable in the presence of males of both wild and long-finned phenotypes. The third goal was to examine female preference for males, to determine whether dominant females consistently preferred one male phenotype to the other.

Materials and Methods

Subjects

Fish were purchased from local aquarium stores, and included 8 female *B. splendens*, 2 wild-type male *B. splendens,* 4 long-finned male *B. splendens* and a golden male swordtail as a control. The age of the fish were not known, but they were kept in their individual tanks for a few weeks to make sure they were healthy. Bettas were kept in 23cmL x 13cmW x 15cmH plastic containers with lids containing approximately 1 liter of water, one fish per tank. Cardboard dividers were placed between all tanks so that the fish remained in visual isolation until they were used in a trial. They were fed freeze-dried TetraMin bloodworms every day and water in the small individual tanks was changed every 2-3 days. The test tank was a filtered aquarium containing approximately 35 liters of water and a gravel substrate. Temperature and pH were monitored daily to maintain homogenous conditions between the holding tanks and the test tank. Although fish are not included for review under Manhattanville's Animal Care and Use Committee, all fish were treated humanely and care was taken to

make sure their treatment followed appropriate animal care and use guidelines, in addition to following protocols outlined in previous studies.

Female Aggression Trials

Before each trial, pH and water temperature of the test tank and the tanks of the fish to be used were recorded in order to keep water conditions as consistent as possible for the fish and to reduce stress. The date, time, and general distinguishing characteristics of the fish to be used were also recorded. Every female was paired with every other female in 15-minute trials. They were allowed to swim freely together without being separated, and were monitored carefully to make sure they did not make actual contact with each other. Females are kept in communal tanks in aquarium supply stores, and although they can be aggressive to each other, they generally do not fight to kill like the males do. The fish were allowed to acclimate to the experimental tank before the trial began. The behavior of each female was observed and recorded as frequency data. Additional behaviors and overall comments regarding each pairing were noted. Care was taken to ensure that each fish was tested only once on a given day. Twelve behaviors were observed. These were subdivided into aggressive positional behavior, aggressive display behavior and non-aggressive behavior (Table 1). Two trials were completed, so each fish met every other fish twice. As previous researchers have noted that aggressive behavior in males increased as they faced more fish, the females were kept in physical isolation from the other fish in between trials. Fish were never studied more than once on a given day.

Female Behavior in the Presence of Males

In the second part of the experiment, females were again paired, but a male was added to the tank. The testing format was the same as for the female/female trials. The results were compiled in two ways: with the male present in the tank, female-to-female behaviors were recorded as well as female-to-male behaviors. All 28 female pairs were put with each male (wild-type, long-finned male, and control) twice. Every male was individually involved in 56 trials with the female pairs. All three of these 56 trial sets were combined for a total of 168 trials.

Female Choice

To determine the female preference for males, the two most aggressive and two least aggressive females, the wild-type males, long-finned males and control fish were used. The test tank was divided into three sections using standard mesh tank dividers. This permitted separation without complete visual and sensory isolation. For each trial, a female fish was placed in the center section. A long-finned male or control male was placed on one end of the tank, while a wild-type male or control male was positioned at the opposite end. The experimental trials were designed to allow each female to be exposed to all possible combinations of wild and long-finned males, as well as the control fish. The trials were 15 min. in length, and were timed from the moment the last fish was placed into the tank. A stopwatch was used to record the time the female spent interacting with either male. An interaction was defined as any obvious display behavior on the part of the female toward a particular male or any close proximity to the male, and this was interpreted as a preference toward a particular male. The total amount of time for each fish was calculated and analyzed. Following the completion of all possible combinations, the experiment was repeated. As in the two previous experiments, fish were kept in isolation between trials.

Results

Individual Behaviors

Behaviors were divided into aggressive positional, aggressive display, aggressive action behaviors and non-aggressive behavior. Aggressive positional behaviors include broadside head-to-head, broadside head-to-tail, and perpendicular confrontations. The broadside head-to-head interaction involved one fish approaching the other and staying beside it facing the same way. In most cases the second fish would swim away leaving the first fish the "winner" of the confrontation. The broadside head to tail interaction has the same result, but the aggressor is facing the opposite direction. The perpendicular confrontation involves the aggressor approaching another fish while swimming very close to its side. This usually results in the second fish swimming away. The head-to-head interaction is similar to the perpendicular display because the aggressor swims directly towards the other fish's head, causing the less aggressive fish to turn or swim away.

Aggressive display behaviors include gill flare, fin spread and color flash. Gill flare is the erection of the operculum and flaring of branchiostegal membranes. The gill flare is usually combined with another behavior like the two broadside displays, perpendicular, head-to-head or

Table II. Number of occurrences of each behavior with Chi-square results comparing Trial 1 to Trial 2 for each fish

	F1		F3			F6			F8			F9			F10			F11			F12		
	Tr.1	Tr.2	Tr.1	Tr.2		Tr.1	Tr.2		Tr.1	Tr.2		Tr.1	Tr.2		Tr.1	Tr.2		Tr.1	Tr.2		Tr.1	Tr.2	
BHH	3	0	22	17		1	0		19	15		2	4		9	0		7	6		12	12	
BHT	0	0	4	3		0	0		8	1		8	3		7	2		2	4		1	4	
PPD	0	0	25	14		0	1		30	20		9	5		6	2		19	10		27	24	
HH	0	0	6	4		0	0		8	1	*	6	6		1	2		4	7		10	4	
CH	1	1	45	14	***	0	0		53	23	***	12	4	*	9	0		21	3	***	41	24	*
GF	5	1	92	43	***	1	0		99	47	***	39	18	**	24	7	**	50	22	**	61	48	
NB	0	0	7	6		0	0		1	8	*	0	0		7	0		12	0		21	14	
CF	2	6	0	0		1	0		19	22		0	0		10	8		9	3		11	14	
FS	3	2	46	33		19	11		34	32		19	21		22	18		27	28		33	33	
CL	6	6	0	2		1	6		6	2		3	2		6	6		1	8	*	2	1	
EWOC	11	12	5	4		15	9		2	0		11	4		1	8	*	7	7		5	6	
EWC	12	8	7	3		43	10	***	1	2		15	4	*	10	10		29	3	***	11	6	
Total	43	36	259	143		81	37		280	173		124	71		112	63		188	101		235	190	

BHH=Broadside head-to-head, BHT=Broadside head-to-tail, PPD=Perpendicular, HH=Head-to-head, CH=Chasing, GF=Gill flare, NB=Nipping and biting, CF=Color flare, FS=Fin spread, CL=Color loss, EWOC=Evading without chase, EWC=Evading with chase, * Significance at the .05 level, ** Significance at the .01 level, *** Significance at the .001 level

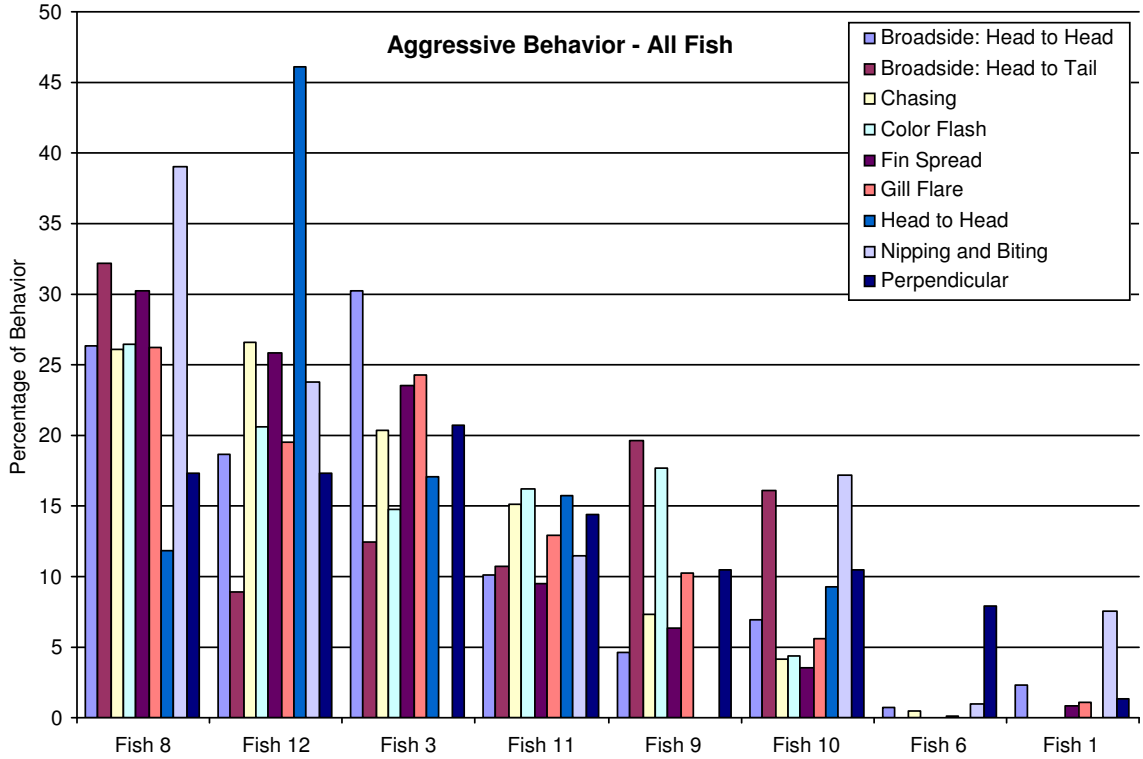

Figure 1. Each fish exhibited a different repertoire of aggressive behavior, and were ordered in terms of aggression, with F8 and F12 as the most aggressive females, and F6 and F1 as the least aggressive.

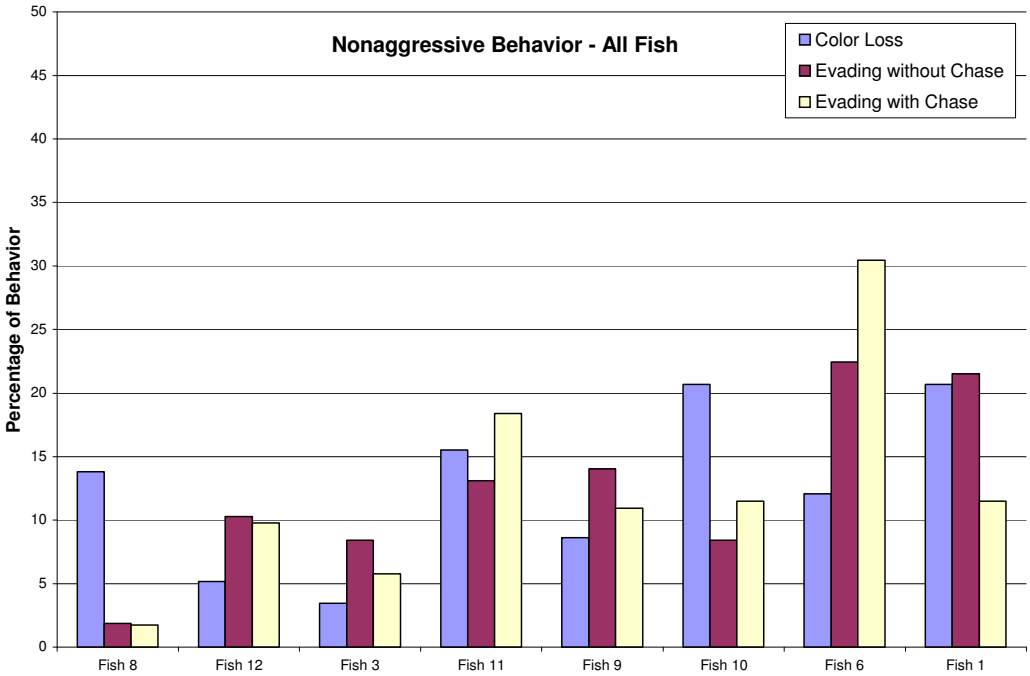

Figure 2. Each fish exhibited varying types of nonaggressive behavior. Fish are ordered from left to right as most aggressive to least aggressive. F6 and F1 exhibited the most nonaggressive behaviors.

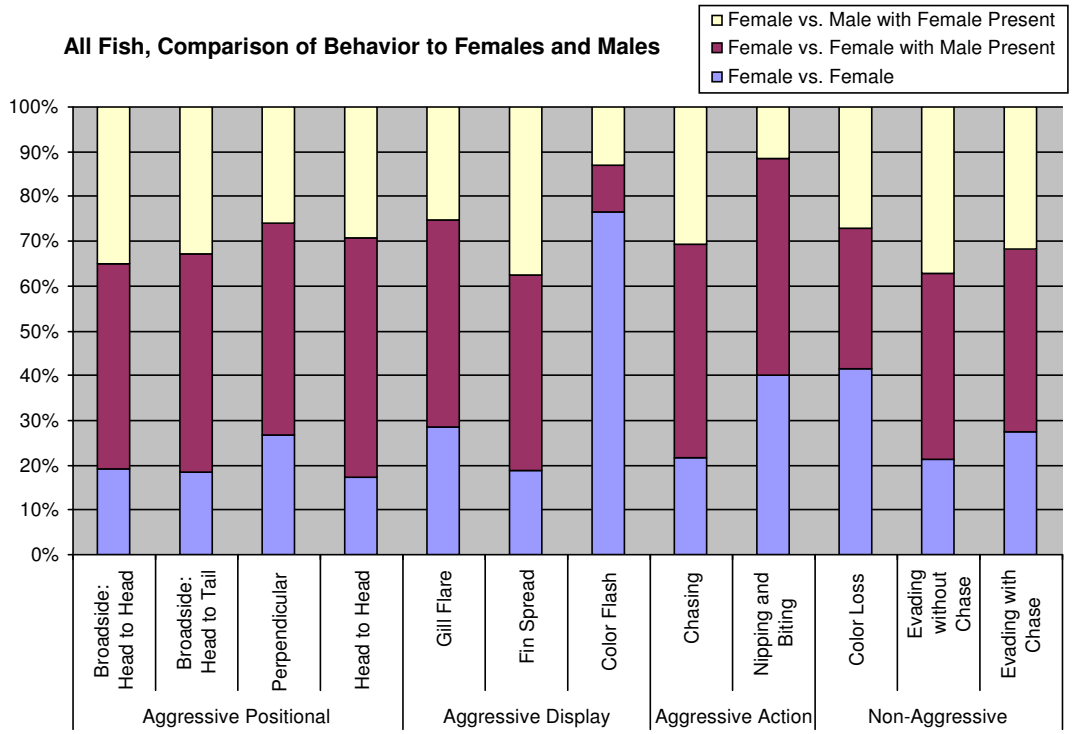

Figure 3. When all behaviors from all females are combined, there is consistent behavior to both males and females, although more behavior was directed at females when a male was present.

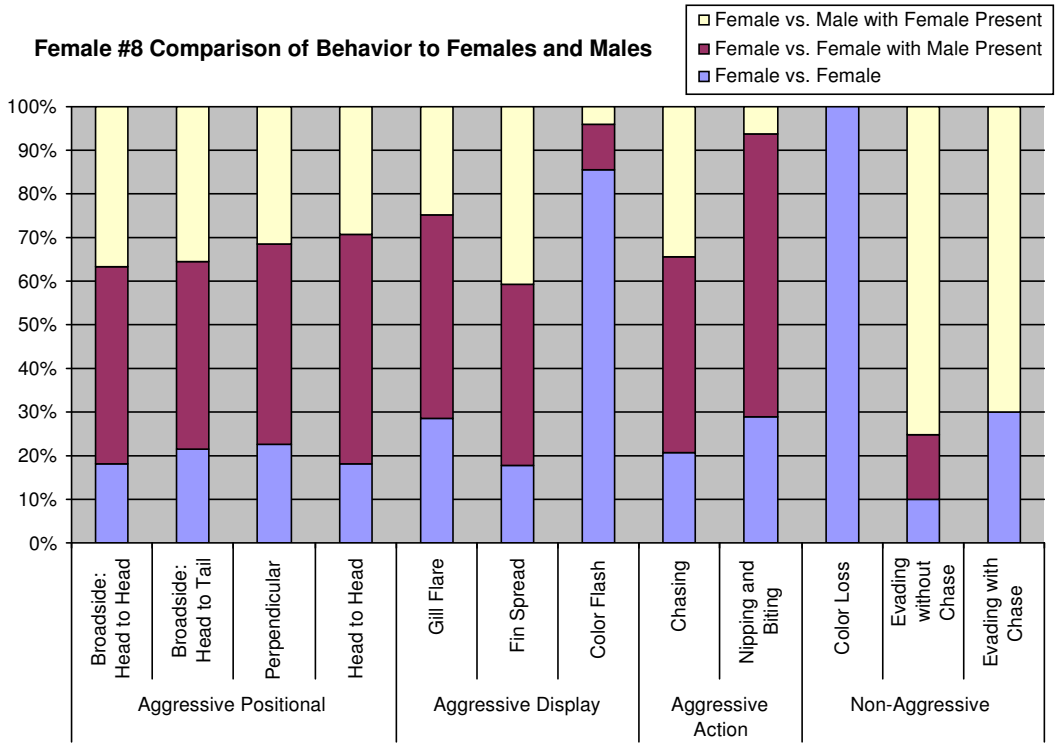

Figure 4. Female #8 was consistent in her aggressive behavior, except for color flash and color loss. More nonaggressive behavior was directed at males when a female was present.

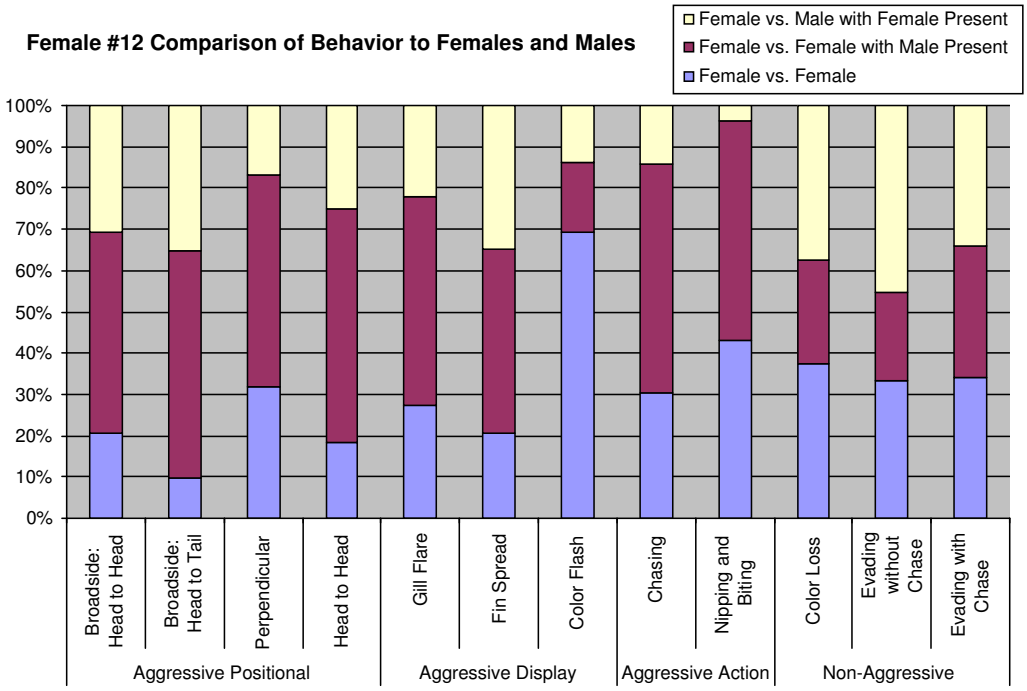

Figure 5. Female #12 was consistent in her aggressive behavior, but more aggressive behavior was directed at females when a male was present.

chasing. Sometimes, the less aggressive fish counters the aggressor's gill flare with a gill flare of its own. This does not last very long and eventually the less aggressive fish will flee from the aggressor. Like the gill flare, fin spread (stiffening and expanding of the fins) is done in conjunction with other behaviors. Color flash is a pigment change of a fish that gives the appearance of being brighter than its original color. Like gill flare and fin spread, this is usually done in conjunction with other behaviors. Aggressive action behaviors include chasing, nipping and biting. Chasing involves one fish following or chasing another fish while the other fish tries to flee. Nipping and biting is usually done by the aggressor during perpendicular display and chasing. During perpendicular display, the side of the less aggressive fish is nipped or bitten and during chasing the tail fins are nipped or bitten.

Non-aggressive behaviors include color loss, and evading with or without chase. Color loss is the reduction of the pigment in the fish causing it to look gray or striped in appearance. This is usually seen in the less aggressive fish after an aggressive act by another fish. Evading without chase involves the less aggressive fish fleeing from the aggressor. In this behavior the aggressor does not pursue the fleeing fish. In evading with chase the aggressor does pursue the less aggressive fish around the tank.

Aggression Results

The experiment began with 12 females, but 4 died during the second trial, so F2, F4, F5, and F7 are not included in the final results. In 56 trials, the eight females displayed 2,493 behaviors. Of the 2,493 behaviors 1,815 were aggressive and 678 were non-aggressive (Table 1).

There were differences in the number of aggressive versus non-aggressive behaviors for each fish. F8 was the most active fish and had the most aggressive behaviors and the least non-aggressive behaviors. F12 and F3 were also very active and aggressive. F1 and F6 were the least aggressive fish. F11 had roughly the same amount of aggressive and non-aggressive behaviors. In general, F8 exhibited the most aggressive positional and display behaviors, but F12 and F3 were also very aggressive. F1 and F6 were the least aggressive. There is a very clear order of most aggressive (F8) to least aggressive (F1) as F8, F12, F3, F11, F9, F10, F6 and F1 (Fig. 1). Non-aggressive behaviors are shown in Figure 2.

Since the trials were combined, it is important to understand any differences between Trial 1 and 2, specifically regarding any socialization effects on fish when they are exposed to other fish on a repeated basis. The small sample sizes for most behaviors indicate that the statistical results are not robust, but in general, the behaviors that were the most numerous in Trial 1 were also the most numerous in Trial 2 with a few exceptions. Two of the aggressive behaviors, chasing and gill flare were the most different, with less occurrences in Trial 2, although overall, these were consistently displayed behaviors in both trials (Table 2).

Female-Female Interaction with Male Present

Overall Behavior. In 168 trials with a male present in the tank, 3,961 total behaviors were observed between females (3,453 aggressive and 508 non-aggressive). Behavior between males and females included 2,711 total behaviors (2,285 aggressive and 426 non-aggressive). Results changed when a male was introduced into the tank. Pearson Chi-Square and Mann-Whitney U tests were performed on the data to compare behavior with and without males and behavior to females versus males. All fish except for F2 and F10 had significantly different behaviors when a male was present ($N=78$, $df=77$, Pearson Chi-Square Value= 3525.69, $p \leq 0.00$). (Table 3).

The behavior of all fish combined indicated that there were more interactions between females when a male was present than when the male was absent. Females interacted less with males when another female was present (Fig. 3). These results suggest that females are more interested in interacting with females, regardless of a male's presence in the tank.

When the behaviors of individual fish were compared between females alone, and then to females and males when there was another individual present, there are interesting differences. The 2 most aggressive fish, F8 and F12, and the 2 least aggressive fish, F6 and F1, are compared here. With the exception of color flash and color loss, F8 exhibited more aggressive behaviors to other females when a male was present, although they were similarly aggressive without the male. More nonaggressive behaviors were shown to the male when the female was present (Fig. 4). A very similar pattern was exhibited by F12, however this female was even more aggressive to other females when a male was present, and showed less aggressive behaviors toward the male when the female was present (Fig. 5).

The 2 least aggressive fish, F6 and F1 showed very different behavioral patterns than the aggressive females. Like the more aggressive females, F6 did exhibit more aggressive behaviors to other females when the male was present. However, she did not nip or bite other females or males, neither

Table III. Comparison of all behavior between females when a male is absent (F-F) and present (with M).

	F-F Trials (N)	F-F with M Trials (N)	Total (N)	Mann-Whitney U	Sign.
FISH 1	79	130	209	3640	***
FISH 3	402	552	954	105050.5	
FISH 6	118	227	345	10799	**
FISH 8	469	857	1326	188048.5	*
FISH 9	195	556	751	47105.5	**
FISH 10	175	344	519	28793.5	
FISH 11	289	545	834	71567.5	*
FISH 12	425	750	1175	140592	***

Note: * p≤.05; ** p≤.01; *** p≤.001

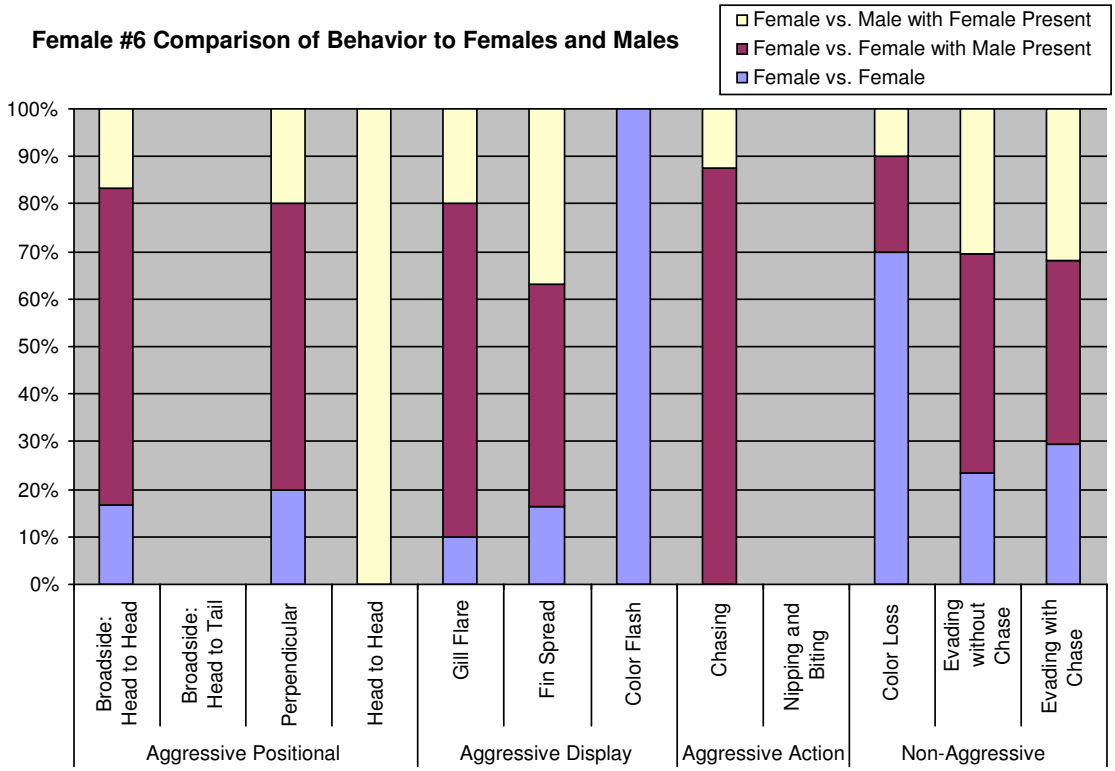

Figure 6. Female #16 was one of the least aggressive females, but was still more aggressive toward females when a male was present, with the exception of head to head, which was solely exhibited to males.

did she approach other fish broadside head to tail. She also exhibited all her head to head behavior toward males only (Fig. 6.). The least aggressive female, F1, showed very few behaviors to other fish at all. The majority of her behavior was directed at another female only when there were no other fish present. In addition, she was equally nonaggressive to males and females with and without other fish (Fig. 7).

Aggressive Positional Behavior. The frequency of the individual behaviors between females also changed when a male was present in the tank. There were higher frequencies of perpendicular

confrontations with females when a male was introduced, and fewer occurrences of head to head and broadside head to head. F1 did not display any of these behaviors when a male was present. The behavior between females and males was also different. There were higher frequencies of both broadside behaviors as well as head to head confrontations (Table 4).

Aggressive Display and Aggressive Action Behavior. There were almost no color flashes when a male was present, and a higher frequency of fin spread versus gill flare between females when a male was present. Behavior toward the male included more fin spreads and fewer gill flares and color flashes. Females spent more time nipping and biting each other when there was no male present, but more time chasing each other when there was a male in the tank. As in the aggressive positional behavior, F1 stopped displaying all behaviors when a male was present. There was almost no nipping and biting toward the males, but more chasing than with the females only (Table 4).

Non-Aggressive Behavior. There was a higher frequency of color loss when a male was present and more evading without chase. There was a higher frequency of the females evading males without chase, and lower occurrences of evading with chase and color loss (Table 4).

Female Preference for Males

The 2 most aggressive females (F8 and F12) and the 2 least aggressive females (F1, F6), were used in this experiment. While the females spent a large portion of the combined 30 minutes with little interaction with the males, in general, all the females spent more time interacting with wild-type males than the long-finned males or the control male. Fish 1 and Fish 6 both spent slightly more time interacting with the control male in two pairings (M1 and the Control, and WM1 and the Control). In the pairing between WM2 and M2, F8 spent over 40% of the time interacting with WM2. Whenever paired with a control, the females all spent more time interacting with the Betta male, except in the pairing noted previously. Fish 8 also spent more time interacting with M1 when paired with WM1 (Table 5).

Discussion

Females clearly exhibit all the aggressive behaviors commonly associated with males, and use these in their interactions with other fish. While aggressive behaviors have been previously defined by various researchers, differences between postural, display and action aggressive behaviors were identified during the course of this study, and the frequency of these behaviors varied widely across female fish. This was statistically significant, indicating that all fish were different in their behaviors compared to each other.

Examination of the individual behaviors exhibited by each fish reveals interesting patterns. While F8 was the most aggressive overall, and had the highest percentage of aggressive positional and aggressive display behaviors, F12, the second in aggressive order, exhibited the most nipping and biting, and much chasing of other fish, although the chasing percentage was still lower than F8. Fish 10 and F11 each showed varied arrays of aggressive behavior, although F11 generally approached fish head-on more. This position allows the fish access to the body of the other fish, enabling more biting behavior to occur. F3, which ranked higher than either F10 or F11 in overall aggressive behavior, did not display as much aggressive positional behavior as action or display. Fish 1 and F6 showed almost no aggressive behavior at all, and spent the most of their time evading other fish, either with or without chase. Interesting, F8 very rarely evaded other fish. These differences indicate that some fish can be aggressive in their appearance when confronting other fish, but will not necessarily chase and bite.

Female Aggression with a Male Present

When compared to the behavior observed between females when there was no male present, there are interesting differences. F8, the most aggressive female, showed a reduction in all behavior toward other females when a male was present, and more behaviors observed toward a male than to females. In addition, F8 displayed no aggressive behavior toward other females when the male was present, and only non-aggressive behavior. In contrast, F12, the second most aggressive female, showed increased aggressive behavior toward other females when the male was present, and less aggression toward the male. The least aggressive fish, F1 and F6, showed more aggressive behavior toward other females when a male was present, but almost no behavior toward the male. These 2 fish also exhibited the most non-aggressive behavior to both females and males.

Female Mate Choice

Although a significant portion of their time was spent wandering about the tank, all females spent more time interacting with the wild-type males than

Table IV. Comparison of frequencies of behavior toward females and males with and without other fish present.

		F/F	F/FwM	F/MwF	F/F	F/FwM	F/MwF	F/F	F/FwM	F/MwF
Behavior		F1	F1	F1	F3	F3	F3	F6	F6	F6
Agg. Positional	Broadside: Head to Head	3	0	0	39	44	40	1	4	1
	Broadside: Head to Tail	0	0	0	7	26	14	0	0	0
	Perpendicular	0	0	0	39	45	28	1	3	1
	Head to Head	0	0	0	10	25	19	0	0	1
Agg. Display	Gill Flare	6	0	0	135	123	84	1	7	2
	Fin Spread	5	1	2	79	152	141	30	87	68
	Color Flash	8	0	0	0	0	0	1	0	0
Agg. Action	Chasing	2	0	0	59	89	76	0	7	1
	Nipping and Biting	0	0	0	13	12	10	0	0	0
Nonaggressive	Color Loss	12	26	21	2	0	2	7	2	1
	Evading without Chase	23	59	33	9	18	21	24	47	31
	Evading with Chase	20	44	20	10	18	48	53	70	58

		F/F	F/FwM	F/MwF	F/F	F/FwM	F/MwF	F/F	F/FwM	F/MwF
		F8	F8	F8	F9	F9	F9	F10	F10	F10
Behavior	Broadside: Head to Head	34	85	69	6	46	36	9	24	18
Agg. Positional	Broadside: Head to Tail	18	36	30	11	23	14	9	16	10
	Perpendicular	50	102	70	14	44	27	8	20	8
	Head to Head	18	52	29	12	46	12	3	14	8
	Gill Flare	146	236	127	57	162	90	31	56	33
Agg. Display	Fin Spread	66	152	151	40	128	97	40	97	83
	Color Flash	41	5	2	0	0	5	18	1	4
	Chasing	76	166	127	16	67	28	9	26	33
Agg. Action	Nipping and Biting	9	20	2	0	2	4	7	2	0
	Color Loss	8	0	0	5	2	3	12	7	5
Nonaggressive	Evading without Chase	2	3	15	15	13	22	9	35	25
	Evading with Chase	3	0	7	19	23	17	20	46	10

		F/F	F/FwM	F/MwF	F/F	F/FwM	F/MwF
Behavior		F11	F11	F11	F12	F12	F12
Agg. Positional	Broadside: Head to Head	13	50	36	24	57	36
	Broadside: Head to Tail	6	20	14	5	28	18
	Perpendicular	29	44	26	51	82	27
	Head to Head	11	29	26	14	43	19
Agg. Display	Gill Flare	72	124	69	109	204	88
	Fin Spread	55	119	106	66	144	112
	Color Flash	12	2	2	25	6	5
Agg. Action	Chasing	24	75	60	65	118	30
	Nipping and Biting	12	12	3	35	43	3
Nonaggressive	Color Loss	9	5	3	3	2	3
	Evading without Chase	14	24	24	11	7	15
	Evading with Chase	32	41	25	17	16	17

Note: F/F=Female to Female behavior; F/FwM=Female to Female behavior with a Male present; F/MwF=Female to Male behavior with a Female Present

Table V. Comparison of the percentage of time spent with each male in each combination, "winner" of each pairing is in bold.

Female	Long-finned Male 1	Wild-type Male 1	No Interaction
Fish 8	**25.11**	6.17	68.72
Fish 12	7.94	**10.22**	81.83
Fish 6	1.72	**3.44**	94.83
Fish 1	0.44	**4.33**	95.22
	Long-finned Male 1	Wild-type Male 2	No Interaction
Fish 8	11.44	**20.33**	68.22
Fish 12	5.06	**9.44**	85.50
Fish 6	0.89	**6.11**	93.00
Fish 1	0.89	**2.83**	96.28
	Long-finned Male 1	Control	No interaction
Fish 8	**23.61**	1.94	74.44
Fish 12	**8.17**	5.28	86.56
Fish 6	2.67	**3.44**	93.89
Fish 1	**3.67**	3.00	93.33
	Long-finned Male 2	Wild-type Male 1	No interaction
Fish 8	13.28	**18.50**	68.22
Fish 12	6.61	**14.06**	79.33
Fish 6	3.11	**7.78**	89.11
Fish 1	4.28	**10.06**	85.67
	Long-finned Male 2	Wild-type Male 2	No interaction
Fish 8	5.67	**42.50**	51.83
Fish 12	9.06	**16.11**	74.83
Fish 6	3.39	**5.61**	91.00
Fish 1	1.11	**8.61**	90.28
	Long-finned Male 2	Control	No interaction
Fish 8	**15.28**	1.72	83.00
Fish 12	**5.89**	3.00	91.11
Fish 6	**4.17**	1.44	94.39
Fish 1	**4.89**	2.44	92.67
	Control	Wild-type Male 1	No interaction
Fish 8	7.56	**17.78**	74.67
Fish 12	5.50	**13.67**	80.83
Fish 6	3.00	**13.28**	83.72
Fish 1	**5.22**	0.61	94.17
	Control	Wild-type Male 2	No interaction
Fish 8	2.83	**28.61**	68.56
Fish 12	3.67	**15.11**	81.22
Fish 6	2.72	**5.78**	91.50
Fish 1	1.89	**3.78**	94.33

with the long-finned males or the controls. However, females did prefer the long-finned male whenever they were paired with the control. One difference was the more time that F8 spent with one of the long-finned males, M1. In two previous studies conducted at Manhattanville College, aggressive females preferred red colored males to any other color (La Rosa, unpublished data; McKenzie, unpublished data). M1 was red, and this might be explanation for the higher response from F8. There were also a few instances where the control was preferred over the *Betta* male. This only occurred in 2 pairings of the less dominant females, and was only by a very small margin. A probable reason for this occurrence is the possibility of the control fish as a "safer" choice to the non-aggressive females. In these instances, the male *Betta* would display as the female approached, thus scaring her away. The swordtail control did not

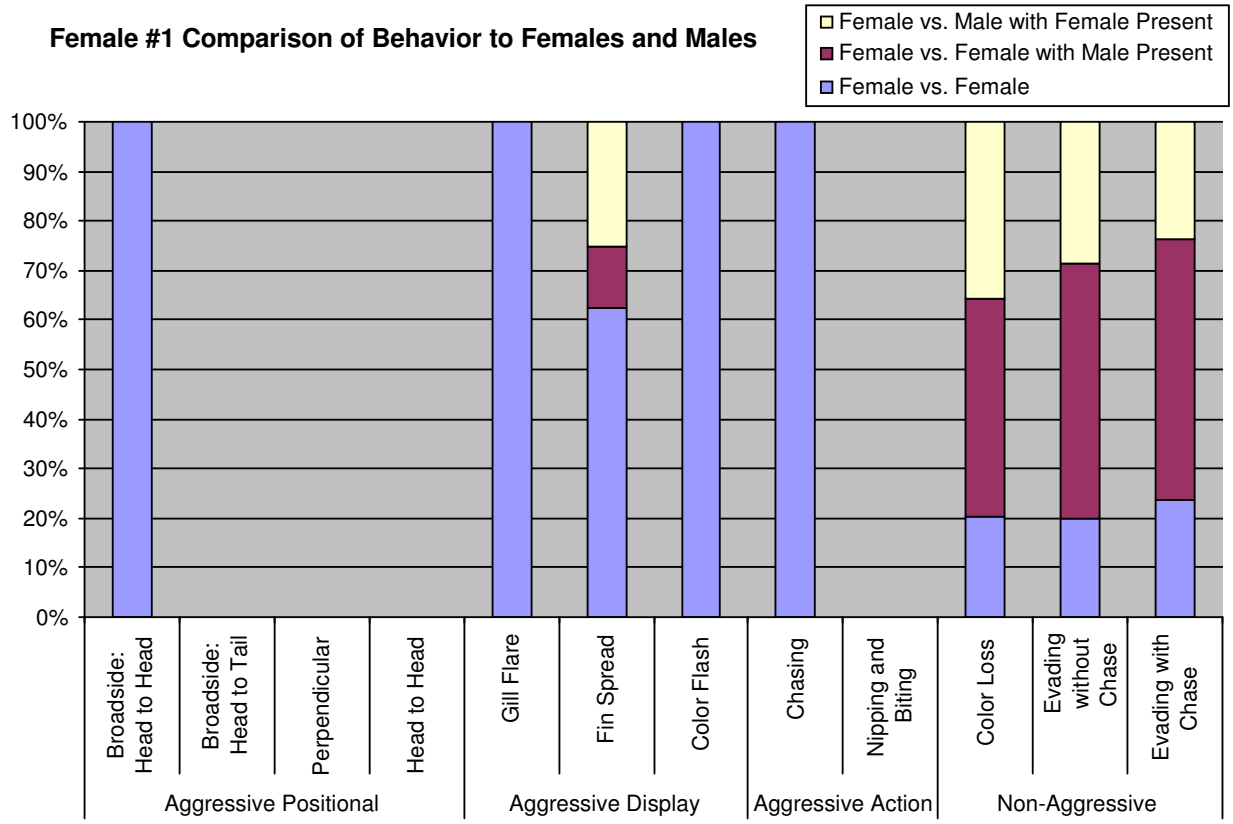

Figure 7. Female #1 was the least aggressive female. She showed very little behavior at all to any fish, but was most aggressive to other females when there was no other fish present. Her nonaggressive behavior was similar overall to males and females with or without other fish.

display, which might have made the female feel less intimidated.

Comparing the results from both wild-type males shows an interesting pattern. The most aggressive females, F8 and F12 preferred WM2, whereas, the least aggressive females, F1 and F6 preferred WM1. Possible explanations for this lie in the level of aggression of the male fish. WM2 was more active and aggressive than WM1, and the less aggressive females tended to avoid him. In this particular study, a red long-finned male and a white long-finned male were used, and although one of the wild-type males had a reddish hue, it would be interesting to include a very dark blue long-finned male in future research.

The results of this study are significant for several reasons. Certain females are more aggressive than others, and are consistently aggressive in multiple pairings. It is possible to rank a group of females in terms of their aggression. When males are present, the dynamics of aggressive posturing and display do change in both the aggressive and non-aggressive females. In addition, the more aggressive females spent more time in close proximity to, and displaying to, the wild-type phenotype of the species, rather than the hyper-aggressive phenotype with the epigamic features designed to attract mates. The more aggressive females did seem to prefer the more aggressive of the wild-type males, with the less aggressive females preferring the less aggressive males and the control, but the overwhelming preference for this phenotype over the brightly colored, flash-finned males is quite interesting. Selection for these exaggerated morphological features has been an artificial process, supposedly to breed more aggressive fish that will win in contests, and yet it does seem to have an effect on female choice.

As mentioned previously, Jaroensutaisinee and Jaroensutaisinee (2001) found that when females observed contests between wild males, they tended to prefer the winners. In this study, females did not observe male-male contest as the males were separated from each other and from them. It would be

interesting to see how more aggressive females would react to contests between wild and long-finned males. It would also be interesting to see how the long-finned males would fare in the natural environment in competition with the wild-type phenotype. If the long-finned males are not chosen by the females, then it can be suggested that hyper-aggressiveness is not preferable for mates, even if these males have morphological features traditionally thought of as adaptations for sexual attraction. Thus, if females reject these males, then their "adaptations" may actually hinder their ability to attract the opposite sex.

The sample size used in this study is small, but the goals were to repeat all trials to examine whether fish were consistent in their behavior. While some degree of socialization may have occurred (i.e. the lower frequency of some behaviors in Trial 2), overall, the pattern of inherent aggression versus non-aggression in individual fish remained the same.

In conclusion, the results of this study indicate that complex aggressive behavior exists in both sexes of *Betta splendens*, and more research needs to be done to explore the interaction within and between sexes in order to better understand the relationship between adaptation, aggression, and sexual preference in this species.

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References

Allen, J. M., & Nicoletto, P. F. (1997). Response of *Betta splendens* to computer animations of males with fins of different lengths. *Copeia, 1*, 195-199.

Braddock, J. C., & Braddock, Z. I. (1955). Aggressive behavior among females of the Siamese fighting fish, *Betta splendens*. *Physiological Zoology, 28,* 152-172.

Doutrelant, C., & McGregor, P. K. (2000). Eavesdropping and mate choice in female fighting fish. *Behavior, 137*, 1655-1669.

Fortelius, S. (1957). Studies of Anabantid fishes. *Zoological Bidrag fran Uppsala, 32*, 95-597.

Franck, D., Klamroth, B., Taebel-Hellwig, A., & Schartl, M. (1998). Home ranges and satellite tactics of male green swordtails (*Xiphophorus helleri*) in nature. *Behavioral Processes, 43*, 115- 123.

Glesener, R. R. (2001). "Betta Behavior " Chapter 8 in Symbiosis: A Custom Laboratory Program for Biology, Pearson Custom Printing.

Goldstein, S. R. (1975). Observations on the establishment of a stable community of adult male and female Siamese fighting fish (*Betta splendens*). *Animal Behavior, 23*, 179-185.

Haller, J., & Wittenberger, C. (1988). Biochemical energetics of hierarchy formation in *Betta splendens*. *Physiology and Behavior, 43*, 447-450.

Halperin, J. R. P., Giri, T., & Dunham, D. W. (1997). Different aggressive behaviors are exaggerated by facing vs. broadside subliminal stimuli shown to socially isolated Siamese fighting fish, *Betta splendens*. *Behavioral Processes, 40,* 1-11.

Halperin, J. R. P., Giri, T., Elliott, J., & Dunham, D. W. (1998). Consequences of hyperaggressiveness in Siamese fighting fish: cheaters seldom prospered. *Animal Behavior, 55*, 87-96.

Jaroensutasinee, M., & Jaroensutasinee, K. (2001a). Bubble nest habitat characteristics of wild Siamese fighting fish. *Journal of Fish Biology, 58*, 1311-1319.

Jaroensutasinee, M., & Jaroensutasinee, K. (2001b). Sexual size dimorphism and male contest in wild Siamese fighting fish. *Journal of Fish Biology, 59*, 1614-1621.

Matos, R. J., Peake, T. M., & McGregor, P. K. (2003). Timing of presentation of an audience: aggressive priming and audience effects in male displays of Siamese fighting fish (*Betta splendens*). *Behavioral Processes, 63*, 53-61.

McGregor, P. K., Peake, R. M., & Lampe, H. M. (2001). Fighting fish *Betta splendens* extract relative information from apparent interactions: what happens when what you see is not what you get. *Animal Behavior, 62*, 1059-1065.

Myers, G.S. (1947). The varieties of the Siamese fighting fish. *The Aquarium Journal, 18*(6), 19-21.

Noble, G. K. (1939). The experimental animal from the naturalist's point of view. *American Naturalist, 73*, 113-126.

Qvarnström, A., & Forsgren, E. (1998). Should females prefer dominant males? *Trends in Ecology and Evolution, 13*, 498-501.

Regan, C. T. (1910). The Asiatic fishes of the family Anabantidae. *Proceedings of the Zoological Society of London*, 767-787

Robertson C. M. 1979. Aspects of sexual discrimination by female Siamese fighting fish (*Betta splendens* Regan). *Behavior, 70*, 3-4.

Robertson, C. M., & Sale, P. F. (1974). Sexual discrimination in the Siamese fighting fish (*Betta splendens*, Regan). *Behavior, 54*, 1-25.

Simpson, M. J. A. (1968). The display of the Siamese fighting fish, *Betta splendens*. *Animal Behavior Monographs, 1*, 1-74.