

# Dominance relationships in female *Herotilapia multispinosa* (Pisces: Cichlidae)

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Agonistic interactions between all possible pairings of 10 adult female rainbow cichlids (*Herotilapia multispinosa*) were observed in three round-robin tournaments. Specific behaviors and color patterns were found to characterize winning and losing fish. The outcomes of agonistic encounters were used to construct a hypothetical dominance hierarchy. This hierarchy was consistent over the three tournaments in that (1) the order of animals in the hierarchy remained relatively unchanged and (2) the relationship between the members of a particular dyad tended to remain stable. The latter was especially true for fish of widely different dominance rank.

The concept of dominance can be defined as a relationship between individuals in which one has precedence over others in agonistic encounters and in access to resources. In fish, dominance has typically been inferred from agonistic encounters in which the behaviors used to measure dominance are specified by the experimenter in advance. Using this method, a large number of studies have explored the effects of different variables—most notably, size, prior residence, and prior experience—on the outcomes of agonistic encounters in a variety of fish species (e.g., see Frey & Miller, 1972; Gorlick, 1976; McDonald, Heimstra, & Damkot, 1968). Fewer studies have concentrated on cichlid fish. De Boer and Heuts (1973), Figler, Dyer, Streckfus, and Nardini (1975), and Figler, Klein, and Peeke (1975) have examined the effects of experience and prior residence on dominance relationships in the jewel cichlid (*Hemichromis bimaculatus*).

One disadvantage of prior specification of behaviors to be used in inferring dominance is that the behaviors chosen may be inappropriate or inefficient, especially in lesser known species. It would seem preferable to allow the species being investigated to specify the behaviors to be observed. Although this may sound implausible, examples of such approaches can be found. One of these is a study by Barlow and Ballin (1976) investigating dominance in the polychromatic Midas cichlid (*Cichlasoma citrinellum*). These investigators formed groups of juvenile fish that varied systematically in color (gold or normal) and size (large, medium, or small), characteristics that are known to influence dominance status in this species (Barlow, Bauer, & McKaye, 1975; Barlow & Wallach, 1976). Observations of each fish were recorded, and a statistical profile of the group was made over 4 days of interaction. This procedure was

repeated for 12 different groups of fish, allowing the identification of those behaviors that best differentiated dominant from subordinate individuals. Another example of such an inductive approach to the measurement of dominance is reported by Frey and Miller (1972) in a study of the blue gourami. Recording a large number of behaviors, these investigators observed fish in dyadic agonistic encounters. They then divided the fish into two classes, those that won and those that lost, and tested statistically for differences in the frequency of each behavior for the two classes of individuals. Frey and Miller did not report specifically how they chose a winner and a loser for each encounter, but we have found with *H. multispinosa* that there is excellent observer agreement on the outcomes of fights. Observer agreement can be used to classify fish as winners or losers, and the frequencies of behaviors shown by animals when they fall into these two categories can be compared. The result should indicate those behaviors that are shown differentially by dominant and subordinate fish. In the study reported here, this method was used to determine, first, which behaviors and color patterns differed for winning and losing fish, and, second, whether the dominance relationships inferred from such behaviors were stable.

Female *H. multispinosa* were chosen as subjects because of their availability and because Baylis (1974) has provided an excellent, detailed description of behavior and coloration in this species. We were also able to use these descriptions to construct an observational checklist. Females rather than males were used because experiments by Weber and Weber (1975) have indicated that female dominance is important in mate selection in another Central American cichlid, *Cichlasoma nigrofasciatum*.

## METHOD

*H. multispinosa* is a New World cichlid found on the Atlantic slope of Central America (Miller, 1966). Although the species has

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not been studied extensively, its behavior, color patterns, and natural history have been described by Baylis (1974). *H. multispinosa* shows behavior patterns typical of a biparental substrate spawner (Baerends & Baerends-van Roon, 1950; Baylis, 1974; Brown & Marshall, 1978; Smith-Grayton & Keenleyside, 1978).

The 10 female *H. multispinosa* used in this experiment were obtained locally. Prior to the experiment, they had been housed together in a 170-liter aquarium. Water temperature was maintained at 21° to 24°C. A 12/12 light-dark cycle, with lights on from 0900 to 2100, was in effect throughout the experiment. Fish were fed daily on Tetramin flakes. *H. multispinosa* is a sexually monomorphic species, and it is not always easy to differentiate males and females. Our females were identified as such by previous observation of spawning or by the shape of the ovipositor, for it is broad and blunt and can be differentiated from the male organ, which is slender and sharply pointed.

Encounters between pairs of individuals (dyads) were observed in three round-robin tournaments. Each encounter was termed a "bout." A tournament consisted of 45 bouts in which each of the 10 fish met every other fish one time. In the entire experiment, three tournaments were conducted, making a total of 135 bouts. Over the three tournaments, each fish met every other fish a total of three times, once in each tournament.

Each bout occurred in one of five identical 38-liter aquariums in which each dyad had been housed, separated by an opaque plastic partition, for approximately 47 h. Bouts occurred during the middle of the light phase of the light-dark cycle. Dyads were determined randomly, with the restriction that no fish could have consecutive encounters in the same aquarium. A bout began with the first interaction between the fish after the partition had been removed and continued until the two observers agreed that a dominance relationship had been established. If no interaction had occurred within 20 min, the encounter was terminated and was scored as a draw. One observer tape-recorded a verbal account of each bout, which was later transcribed to a written record. A second observer made a written record, which was used for a reliability check. To avoid being influenced by the first observer's verbal reporting, the second observer wore headphones through which music was played.

Both observers used checklists based on Baylis' (1974) observations of behaviors and color patterns in *H. multispinosa*. Behaviors recorded included pushing or ramming (we could not reliably differentiate the two), chasing, pitching-up, tailbeating, and jawlocking. Detailed descriptions of these behaviors can be found in Baylis' (1974) paper. In addition, we recorded fleeing, defined as rapid swimming away from the other fish, and drifting, defined as slow, undirected movement through the water with the head above or below the horizontal. Color patterns recorded included the ground color (light or dark), the eye color (light or dark), the occurrence of the central spot (Spot #5 in Baylis' terminology), the lateral stripe, and dorsal barring. *H. multispinosa* can change eye color and patterns of spots and stripes very rapidly. The bright yellow ground color seen in fish in reproductive condition takes longer to develop. (Baylis reports several days.) We recorded color patterns at the beginning of each bout, periodically throughout the bout, and again at the end of each bout.

Winners and losers of each bout were determined by observer agreement. After each encounter was concluded, the fish were weighed, and new dyads were selected and placed in different aquariums in which they were again isolated until the next bout, which occurred about 47 h later. Fish were distinguished by size, shape, and individual markings. In those bouts involving similar-looking fish, fin-punching of each member of the dyad was done prior to the isolation period.

## RESULTS

### Evaluation of Behavior and Color Patterns

Interobserver reliability on behavior measures was evaluated using Pearson product-moment correlation

coefficients. Two measures, pushing and tailbeating, occurred with sufficient frequency to be evaluated across all three tournaments. Correlations for these measures were: pushing [ $r(92) = .95$ ,  $p < .005$ ]; tailbeating [ $r(92) = .97$ ,  $p < .005$ ]. Chasing, fleeing, drifting, and pitching-up occurred frequently enough to be evaluated only in the first tournament. Correlations were: chasing [ $r(17) = .94$ ,  $p < .005$ ]; fleeing [ $r(17) = .82$ ,  $p < .005$ ]; drifting [ $r(17) = .96$ ,  $p < .005$ ]; and pitching-up [ $r(17) = .71$ ,  $p < .005$ ]. Probabilities are based on one-tailed tests. Jawlocking did not occur in enough bouts to permit statistical evaluation of interobserver reliability. Although all of the preceding correlations were statistically significant, we considered the interobserver reliability for pitching-up to be too low to permit further analysis of this behavior.

In order to determine the specific behaviors that best differentiated winners from losers, we compared the frequency of occurrence of each behavior for the two classes of fish. Two behaviors, pushing and tailbeating, occurred with sufficient frequency to provide scores for winners and losers in each bout. To analyze the frequencies of these behaviors for winners and losers, we calculated, first, the average number of pushes delivered by each fish to its opponent when it won and when it lost. These two scores were then compared for the 10 fish using the Wilcoxon matched pairs signed ranks test. Because this test required complete data, it was necessary to supply missing scores for those fish that did not win or did not lose any bouts in a particular tournament. In the first tournament, one fish lost no bouts, while in the second and third tournaments, one fish lost no bouts and one fish won none. The missing data points were supplied by assigning the overall mean score for that tournament. For example, in Tournament 2, Fish 7 lost no bouts and Fish 10 won none. Both animals were assigned a pushing score of 1.46 pushes (the overall average for that tournament). Separate Wilcoxon tests were conducted for each of the three tournaments. A similar analysis was performed using the tailbeat measure.

Table 1 shows the average pushing score for each fish when it won and when it lost for each of the three tournaments. Wilcoxon tests revealed significant differences in pushing between fish when they won and when they lost for all three tournaments (Tournament 1:  $T = 6.0$ ,  $p < .05$ ; Tournament 2:  $T = .0$ ,  $p < .01$ ; Tournament 3:  $T = 7.0$ ,  $p < .05$ ). The frequency of tailbeating did not differ significantly for winning and losing conditions.

The other recorded behaviors did not occur frequently enough to provide scores for winners and losers in each bout. Therefore, they were totaled for the 45 bouts in each tournament. The total number of times each of these behaviors occurred in winners and in losers is shown in Table 2. Since the same fish fell into winning and losing categories, the cells cannot be considered as independent. Consequently, phi coefficients were used to evaluate significance.

**Table 1**  
Average Number of Pushes for Each Fish When It Won and When It Lost for the Three Tournaments

Fish	Tournament 1		Tournament 2		Tournament 3	
	Won	Lost	Won	Lost	Won	Lost
1	7.00	.67	4.00	.00	7.00	.29
2	3.00	.80	2.33	.17	2.67	.25
3	4.00	.60	2.00	.00	.00	.00
4	6.25	5.84*	3.29	.00	1.78	2.19*
5	3.00	.33	4.40	.00	6.75	.40
6	11.33	.50	1.20	.67	.67	1.00
7	7.40	16.00	3.00	1.46*	4.25	4.00
8	11.75	1.67	2.00	.00	5.67	.00
9	22.00	1.00	2.50	.71	4.00	.00
10	12.75	1.00	1.46*	.11	2.19*	.71
Mean	8.84	2.84	2.62	.31	3.50	.88

\*Data points estimated.

**Table 2**  
Frequency of Chasing, Fleeing, and Drifting by Winning (W) and Losing (L) Fish in the Three Tournaments

Behavior	Tournament 1			Tournament 2			Tournament 3		
	W	L	Phi	W	L	Phi	W	L	Phi
Chasing	17	1	.48†	4	0	.23*	0	0	0
Fleeing	2	26	.63†	0	9	.35†	0	0	0
Drifting	1	17	.48†	0	8	.33†	0	0	0

\* $p < .01$ . † $p < .05$ .

**Table 3**  
Frequency of Color Characteristics in Winning (W) and Losing (L) Fish in the Three Tournaments

Color Character	Tournament 1			Tournament 2			Tournament 3		
	W	L	Phi	W	L	Phi	W	L	Phi
Eye Color									
Dark	0	28	.75†	0	27	.70†	0	28	.76†
Light	39	11		41	14		38	10	
Central Spot				10	38	.69†	7	33	.69†
Dorsal Bars	15	27	.30†	4	22	.47†	4	9	.18
Lateral Stripe	28	22	.16	27	35	.23*	18	22	.11

Note—No central spot data were available for Tournament 1. \* $p < .05$ . † $p < .01$ .

Chasing was exhibited more frequently by winners than by losers in Tournaments 1 and 2. Losers exhibited fleeing and drifting more frequently than did winners in Tournaments 1 and 2. No fleeing, drifting, or chasing occurred in Tournament 3. Jawlocking, since it is a mutual behavior, cannot differentiate winners from losers and was not analyzed.

The occurrence of different color patterns at the end of each bout was also evaluated using phi coefficients. The frequency of occurrence of each color pattern in winners and losers is shown in Table 3. Winners always displayed light eye color, while dark eye color occurred only in losers. Dorsal barring occurred more frequently in losers than in winners in Tournaments 1 and 2. The central spot occurred

more frequently in losers than in winners in Tournaments 2 and 3. With the exception of Tournament 2, the occurrence of the lateral stripe did not differentiate winners from losers.

**Evaluation of Hierarchy Consistency**

In order to evaluate the consistency of the hierarchy over the three tournaments, points were assigned to each fish based on the outcome of each bout as follows: Two points were given for a win, 1 point for a tie, and 0 points for a loss. This procedure allowed the construction of a hypothetical dominance hierarchy with ratio scale characteristics. Pearson product-moment correlation coefficients showed that the hierarchies of Tournaments 1 and 2 correlated significantly [ $r(8) = .76, p < .01$ ]; Tournaments 1 and 3 also correlated significantly [ $r(8) = .92, p < .01$ ], as did Tournaments 2 and 3 [ $r(8) = .90, p < .01$ ]. Changes in the position of fish in the hierarchy are presented in Figure 1.

It is also possible to evaluate the reliability of a hierarchy by looking at the extent to which the relationship between any two fish is stable. This was done by comparing the outcomes for each dyad across the three tournaments. Comparing the outcomes of bouts between Tournaments 1 and 2, there were 38 pairs of bouts in which clear outcomes occurred in both tournaments. Of these, 28 outcomes were the same and 10 were reversed. Comparing Tournaments 2 and 3, there were 36 pairs of bouts with clear outcomes. Of these, 33 outcomes were the same and 3 were reversed. If only random factors determine the outcome of any agonistic interaction, we would expect approximately half of the outcomes in each tournament to be reversed in the next tournament. Considering the reversal or nonreversal of dyadic relationships to represent a binomial population with  $p = q = 1/2$ , we found significantly fewer reversals than would have been expected. For Tournaments 1 and 2,  $z = 2.93, p < .01$ ; for Tournaments 2 and 3,  $z = 4.70, p < .01$ .

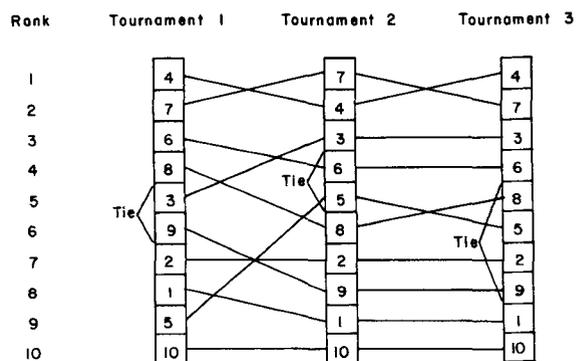


Figure 1. Changes in the dominance hierarchy over the three tournaments (numbers in each block are the individual identification numbers of the fish).

We can also examine the positions in the hierarchy of those dyads showing reversals in their relationships. Examining the 45 possible dyads across the three tournaments, there were 24 dyads that had a consistent relationship throughout and 21 dyads that showed at least one reversal or at least one draw. By finding the difference in dominance scores for the members of each dyad, we can determine if there is a relationship between the positions of individuals in the hierarchy and the tendency for reversals in their relationship to occur. This was accomplished by averaging the dominance scores from the three tournaments for each fish to determine a mean dominance score. A difference in dominance scores was then obtained by subtraction for each dyad. A *t* test comparing stable dyads with those with reversals or draws showed that the stable dyads had a larger average difference in dominance score [mean difference for stable dyads = 7.2 points; mean difference for unstable dyads = 3.7 points;  $t(43) = 3.33$ ,  $p < .01$ ], indicating that reversals were more likely to occur between individuals that were similar in dominance score. Such reversals occurred at the extremes of the hierarchy as well as in the middle. It should be noted that the value of *t* in this test may be somewhat inflated, because these data, due to the nature of dominance rank, do not strictly meet the assumption of independence.

Correlations of the hierarchy with the body weight of fish were statistically significant but not particularly strong. Body weight correlated positively with dominance score in Tournament 1 [ $r(8) = .54$ ,  $p < .05$ ], Tournament 2 [ $r(8) = .65$ ,  $p < .025$ ], and Tournament 3 [ $r(8) = .54$ ,  $p < .05$ ]. (Probabilities are based on one-tailed tests.) Correlations with body length were similar in magnitude and direction.

## DISCUSSION

The first issue addressed in this study was whether specific behaviors and color patterns could be found that would differentiate winning from losing fish. A number of behaviors, including pushing, chasing, fleeing and drifting, did occur with significantly different frequencies in winners and losers. In agreement with Barlow and Ballin (1976), contesting (indicated here by tailbeating) did not reliably differentiate winners and losers. Of those behaviors differentiating winners and losers, pushing was the only one that occurred frequently enough to be generally useful in dominance assessment. Chasing, drifting, and fleeing occurred fairly frequently in the first tournament, although not in all bouts. In Tournament 2, the frequency of these behaviors dropped substantially, and in Tournament 3, they did not occur at all. In contrast, pushing—although dropping across the

three tournaments, especially between Tournaments 1 and 2—was still occurring at a mean rate of 3.5 pushes per bout by winning fish in the third tournament. Thus, pushing appeared to be the only behavior that continued to be consistently shown by dominant fish even after a dominance relationship had been established. The decrease in agonistic behavior as dominance relationships are established has been reported many times (Van Kreveld, 1970; Wilson, 1975) and causes problems in assessing dominance relationships in established groups. In *H. multispinosa*, it appears that pushing continues to occur with sufficient frequency to provide a useful measure of dominance in established groups, at least if relationships are inferred from dyadic encounters. It remains to be seen whether this finding will hold when fish are observed in a group.

A number of aspects of the color pattern differed in winning and losing fish. However, only one characteristic, dark eye color, never occurred in winning fish. In addition, the frequency of occurrence of dark eye color did not decrease over the three tournaments. To the extent that it does characterize losers (about 70% of losers showed dark eye color), it could be useful in identifying subordinate fish in established groups. On the other hand, while several characteristics, including the central spot and dorsal barring, occurred more frequently in losers than in winners, these characteristics did occur in winners. The results for light eye color were similar; although light eye color occurred more frequently in winners than in losers, it did occur in losers. An extreme color pattern with dark eye color and strong dorsal and ventral barring occurred only in losers that were being attacked by the dominant fish. Drifting tended to occur in the same situation.

The second question addressed by this study concerned the stability of the hierarchy over the three tournaments. If relationships were unstable, it would be difficult to see how they could consistently relate to other measures of dominance such as differential access to resources. However, both methods of assessing the stability of the hierarchy, correlations between the hierarchies generated in the three tournaments and assessment of the consistency of relationships in each dyad over the three tournaments, showed that relationships were quite stable, especially after the first tournament. Although it is not clear that these relationships represent a true dominance hierarchy such as that observed in primates, the stability in relationships does show that correlation with resource access and reproductive success would, at least, be possible. This finding suggests that cichlid fish could provide a good model for the study of relationships between dominance, resource access, and reproductive success.

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revision accepted December 15, 1980.)

## ERRATUM

Roitblat, H. L. Coding and coding processes in pigeon short-term memory. *Animal Learning & Behavior*, 1980, 8, 341-351—The chi-square values reported in Table 1 were computed incorrectly. The actual values are all highly significant. Therefore, the first sentence of the last full paragraph on page 346, column 1, should read: "For all five of the birds serving in Experiment 2, the distribution of first-choice errors was significantly different from that expected on the basis of the inattention model."