Female and male Texas cichlids (*Herichthys cyanoguttatum*) do not fight by the same rules

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Selection usually acts differently on males and females during intrasexual competition for resources and/or mates. Nevertheless, agonistic behavior has been examined both theoretically and empirically mostly in males. Our research questions whether males and females follow the same rules of engagement in intrasexual contests as predicted by the sequential assessment model (SAM). The SAM predicts negative correlations between contest intensity and duration and the magnitude of asymmetry in resource holding power (RHP) between the contestants, such that the most escalated contests are those between similarly endowed individuals. We staged male and female intrasexual contests with varying degrees of body size asymmetry under a round robin design using the monogamous Texas cichlid fish (*Herichthys cyanoguttatum*) as a study case. We used Mantel’s matrix analysis to compare how the behavioral content, duration, structure, and outcome of male and female contests were affected by the relative body size of the contestants. In the case of males, relative size in each contest predicted outcome, duration, and frequency of conventional and escalated behaviors according to prevailing theory. Female contest structure and outcome, however, were not predicted by the relative size of contestants. We discuss our results in terms of other asymmetries that might be important in structuring female contests, and we propose potential approaches to study female–female aggression. Key words: behavioral sex dimorphism, body size asymmetry, fight theory, *Herichthys cyanoguttatum*, intrasexual contests, Mantel test, sequential assessment, Texas cichlids. [Behav Ecol 15:102–108 (2004)]

The accuracy of each contestant’s assessment is expected to be positively related to the asymmetry in RHP between them. When the asymmetry in RHP is great, simple low-risk visual assessments are likely to yield accurate information to both contestants and result in rapid resolution of the contest. However, mutual assessment of RHP is more prone to errors in contests with little asymmetry, and thus, contestants may require behaviors that involve physical contact in order to accurately judge their opponent’s RHP. Such contests are expected to proceed through a sequence of increasingly risky behaviors until there is a resolution. Thus, the SAM predicts negative correlations between RHP asymmetry and contest duration and contest intensity. Contests between individuals of greatly different RHP are expected to be short in duration and involve no escalated behavior; whereas contests between individuals with similar RHP are expected to last longer and to involve more escalated behaviors. In either case, the individual with lower RHP is expected to retreat and leave the contested resource to the individual with higher RHP.

Although contest models such as the SAM are not gender specific (but see Hammerstein and Riechert, 1988), it has been far more common to test their predictions in males. The gender bias is understandable because the most conspicuous animal contests in nature are typically those between males of polygynous species. However, females are often forced to compete for resources (e.g., territories and/or mates) and therefore often engage in intrasexual agonistic encounters. For example, females have been frequently observed in nature competing for the highest-quality males in a population (Cunningham and Birkhead, 1998), either as a result of skewed operational sex ratios that cause suitable males to be a limited resource (see Vincent et al., 1994) or because limited reproductive resources are dominated by a small percentage of available males (see Johnson, 1988; Slagsvold and Løgfjeld, 1994; Walter and Trillmich, 1994). In addition to mate competition, females commonly compete for territories and other critical resources (see Heinrich and Bartholomew, 1979; Horne and Itzkowitz, 1995; Johnsson et al., 2001).

Although intrasexual female contests are not rare in nature, there is no apriori reason to expect that female contests follow the same patterns discovered in male contests. In fact, given the basic differences in the way that males and females secure mates and maximize reproductive success (Trivers, 1972), comparisons of their intrasexual fighting seem well warranted, although very few have been conducted (Dale and Slagsvold, 1995; Holder et al., 1991; Pie, 1998). In comparison with studies of males, female–female agonistic competition has received very little attention (Berglund et al., 1993; Johnsson et al., 2001).

Aggression has frequently been studied in fishes, perhaps most notably in the cichlids (Pisces: Cichlidae). There are a handful of studies of cichlids that have noted an overall similarity in male and female intrasexual contests. For
example, several studies (Barlow et al., 1986; Koops and Grant, 1993) have found that the duration of male and female contests was not significantly different and therefore combined male and female data for their analyses. However, comparisons of the structure of male and female contests were not presented in these studies. Male Texas cichlids (Herichthys cyanoguttatus) emphasize lateral displays, whereas females emphasize chasing and biting when defending offspring against intruders (Itzkowitz, 1985; Itzkowitz and Nyby, 1982). Similarly, female firemouth cichlids (Cichlasoma meeki) chased intruders more often than did males, but jaw-locked less (Neil, 1984). Holder et al. (1991) showed that male Midas cichlids (Cichlasoma citrinellum) had higher aggression scores and were more variable in their aggression than were females.

In the present study, we staged intrasexual male and intrasexual female contests using monogamous, bipartential Texas cichlids, H. cyanoguttatus, to examine whether the relative body size of the opponents affects the durations and the outcomes of the contests of both sexes similarly. Male and female Texas cichlids are aggressive and seem to draw from the same behavioral repertoire (e.g., lateral display, chasing, biting, mouth wrestling; Itzkowitz, 1985; Itzkowitz and Nyby, 1982). Our primary aim was to explore agonistic behavioral dimorphisms in relation to the SAM. We chose to compare our contest results to predictions of the SAM because previous studies on male cichlids have shown that their contests closely follow such predictions (see Keeley and Grant, 1993; Koops and Grant, 1993).

METHODS

Experiments were conducted under laboratory conditions at Lehigh University, Pennsylvania, USA. Sexually mature Texas cichlids, H. cyanoguttatus, were captured from wild populations in San Antonio, Texas, USA. After transport to the lab, they were held in 525-l unisexual stock tanks and fed sinking trout chow three times daily. Sex was determined externally by the shape of the female ovipositor, which is broad and blunt and can be differentiated from the male organ, which is slender and sharply pointed. The temperature was held from 26°C–28°C and a 12 h/12 h light/dark cycle was maintained. Ten fish of each sex were haphazardly netted from stock tanks. They were visually and physically isolated from one another for 72 h before the contests in filtered 42-l holding tanks, and otherwise were maintained exactly as fish in stock tanks. The standard lengths, widths, and heights were measured for each isolated fish. We used the formula for the volume of an ellipse to calculate their estimated volume (volume = standard length × height × width × π/6). Estimated volume was used rather than a linear measurement (e.g., standard length) because the volume estimate accounts for significantly more body weight variance (Macías-Ordóñez R and Draud M, unpublished). The size ranges of males and females were 65–230 cm³ and 68–154 cm³, respectively.

Intrasexual round-robin contests

Intrasexual agonistic behavior was elicited by staging contests between all possible pairings of same-sexed individuals. A round-robin tournament was conducted for each sex, in which every fish met every other same-sexed fish once. Contests were conducted in one of two identical filtered 315-l aquariums, each containing a sand substrate and a clay flowerpot placed on its side in the center. Flowerpots are readily accepted by cichlids as spawning sites and refuges (Itzkowitz, 1985); thus, we used them to promote fighting. The order of the contests was determined haphazardly with the restriction that no fish could take part in consecutive contests. Two observers (M.D. and R.M.O.) transported two fish to an experimental arena by capturing them from their holding tanks with a large mesh net and releasing both simultaneously into the arena. The observers then sat behind a blind, kept written accounts of each contest, carefully monitored fish for injury, and determined at what point one of the fish was victorious. During the contests, the identity of individual fish was easily known to the observers who used differences in a combination of characteristics, including size, shape, and fin anomalies. Identities were also confirmed later from the videotapes. Victory was decided when one fish consistently and continuously chased its opponent, while the opponent retreated or hovered motionless near the surface. In addition, sole ownership of the flowerpot was also used to support the decision of which fish won the bout.

Contests began with the first interaction between the fish and were allowed to continue for up to 15 min. Previous work in our laboratory suggested that the majority of contests would be resolved within this time period. If either opponent seemed in danger of being injured, the bout was terminated before 15 min. If at the end of 15 min there was no interaction, the contest was terminated and scored as a draw. If at the end of 15 min the fish were still fighting and a winner could not be determined, the contest was terminated and scored as a tie. One particularly violent fight was scored a tie and terminated after 9 min. After each contest, fish were returned to their respective holding tanks, where they remained until their next bout. All staged contests were videotaped for later viewing by a third “blind” observer (J.V.) to perform careful and detailed accounts of tallied and timed data, several years after videotaping.

Videotape analysis

Timed events included tail beating and mouth wrestling. Tail beating was recorded when both fish were observed positioned side by side and facing in opposite directions while both made exaggerated movements of the caudal fin. The two fish moved in a circle during tail beating. Mouth wrestling was recorded when both fish were observed facing each other, with their lips locked (premaxilla and dentary), simultaneously pushing each other back and forth. Tailled behaviors included lateral displays, frontal displays, and chases. A lateral display was recorded when a fish presented its lateral surface to its opponent and extends all unpaired fins. A frontal display was recorded when a fish faced its opponent while extending all unpaired fins. We were often unable to judge whether a display was frontal or lateral, and because there seemed to be many intergrades of these fin displays, we combined all such behavior for analysis. A chase was recorded when a fish was observed swimming rapidly and directly toward the other fish, causing it to swim away.

Statistical tests

To rule out gross differences in amount of aggressive behavior between sexes as a confounding factor testing the SAM predictions, overall male and female values were compared by using a Kruskall-Wallis nonparametric ANOVA on each recorded variable. The effects of the relative size of contending pairs on contest variables (outcome, total duration, display and chase frequency, tail beating, and mouth wrestling duration) were analyzed by using the Mantel test (Sokal and Rohlf, 1995). This randomization test calculates the association between two independent “dissimilarity matrices” describing the same set of entities (i.e., interacting individuals), and then
estimates whether the association is stronger than one expected by chance. This test is designed to compare attributes that result from multiple combinations (i.e., interactions, fights) of a limited number of entities (i.e., individuals) and, therefore, does not assume that each combination (i.e., fight) is independent of the others. Thus, the test is well suited to examine data generated by using round-robin designs.

Analysis for males and females was identical and performed separately. We constructed a dissimilarity matrix for the size difference of the fish in each contest. The 10 individuals were arranged along rows and columns from smallest to largest, and only the lower half of the matrix was filled (a half-matrix). The cell corresponding to each pair contained the difference of the estimated volume of larger contender minus the estimated volume of the smaller contender (therefore, all values > 0).

Likewise, dissimilarity half-matrices were built for each dependent variable with the same arrangement as the independent variables. Previous exploration of the Mantel test using perfectly inversely correlated dissimilarity half-matrices showed that the sensitivity of this test to inverse correlations was matrix-size dependent, and the asymptotical cross matrix correlation coefficient (CMC) for a 10 × 10 matrix, as those in this experiment, was only 0.33. Given that some of the previous predictions of the SAM model and war of attrition model (WOAM) to be tested involved inverse relations (e.g., size difference should be negatively correlated to contest duration, Table 1), all dependent variables were coded so that alternate hypothesis were always positive correlations. In other words, if the prediction was true, a positive correlation would always be obtained.

For instance, contest outcome was coded as the value obtained by the larger fish: a value of 1 was assigned to all fights in which the larger contender won the fight, a value of 0 for those cases in which the larger contender lost the fight, and a value of 0.5 for ties or draws (Table 2). If, as predicted by the SAM, larger contenders usually defeat smaller contenders, larger values in the relative size dissimilarity matrix would be associated to one’s in the contest outcome dissimilarity matrix, and smaller values to 0.5’s and zero’s, so a positive correlation should be expected.

For contest duration, the cell corresponding to each contestant combination contained the duration of their contest in 3-min intervals. We would have preferred to have the increased statistical power afforded by recording this variable in seconds (i.e., a continuous variable). However, we opted to use discrete time intervals because we were often unable to know the exact “end” of the fight, because the winning and losing roles often slowly emerged over several minutes. Because SAM predicts a negative correlation between the relative size of the contestants and contest duration, an “inverse” contest duration dissimilarity matrix was built. This was performed by subtracting each contest duration from 15 (the longest time a contest was allowed to continue without a winner or potential injury). Thus, for our alternate hypothesis, we expected a positive correlation between relative size and the inverse contest duration. For the same reason, we developed inverse duration dissimilarity matrices for tail beating duration and mouth wrestling duration. These latter two variables were recorded and coded in seconds.

Given the nature of predictions involving displays (see Table 1) and in order to avoid negative correlations as alternate hypotheses, the corresponding dissimilarity matrix was filled with the proportion of the total number of displays performed in the contest by the smaller contender. That is, as the size difference between the two contestants becomes larger, the SAM predicts that the smaller fish will do proportionally more displaying. For the same reasons, the chases dissimilarity matrix was filled with the proportion of the total number of chases in the contest performed by the larger contender. Here again, our alternate hypothesis is designed to expect a positive correlation between the relative size of the contestants and the proportion of chases performed by the larger contestant.

The Mantel test was run by using Mantel.XLA-VBA add-in macro, written by R.A. Briers. Each test was preformed by using 1000 randomizations.

RESULTS

Male and female amounts of aggressive behavior

Overall, males and females did draw equally from the same behavioral repertoire. No significant differences were found between the amount of total male and female aggressive behavior involved in each fight as measured by all but one of the recorded variables, total displays (Kruskal-Wallis H1,N = 34), the largest fish in all cases (Table 2). The outcomes of female contests, however, were not correlated with size difference between the opponents (Mantel Z CMC = 0.22, p = .54). The occurrence of ties (n = 10) was unrelated to size difference between the female opponents. In addition, eight out of 45 female contests were won by the smaller fish, and 27 contests were won by the larger (Table 2).

Contest outcome

The size difference between the two males was significantly correlated to the outcome (Mantel Z CMC = 0.53, p = .01). Ties (n = 11) were more likely to occur between males of similar size, whereas a winner emerged at larger size differences (n = 34), the largest fish in all cases (Table 2). The outcomes of female contests, however, were not correlated with size difference between the opponents (Mantel Z CMC = 0.22, p = .54). The occurrence of ties (n = 10) was unrelated to size difference between the female opponents. In addition, eight out of 45 female contests were won by the smaller fish, and 27 contests were won by the larger (Table 2).

Contest duration

Male and female contests differed with regards to the relationship between contestant size difference and contest duration. Although the duration of male contests was weakly inversely

| Table 1 Predicted correlations by the sequential assessment model (SAM) between size difference and the dependent variables, and the observed associations in males and females |
|-----------------------------------------------|-------------------------------|-------------------------------|
| Relative size of contestants vs. dependent variables | Relationship predicted by SAM | Observed relationships |
| Contest outcome: payoff to larger fish | + | + | 0 |
| Proportion of displays by smaller fish | + | + | 0 |
| Proportion of chases by larger fish | + | + | 0 |
| Contest duration | − | − | 0 |
| Escalated behavior | − | − | 0 |

+ indicates a positive correlation; −, a negative correlation; and 0, no correlation.
DISCUSSION

The SAM predicts that the relative size of the opponents will determine the outcome, such that larger size differences will be associated with quick and decisive determination of a winner, which is always the larger. These predictions should apply to either sex. We found that male contests fit the predictions but female contests did not. Male contests were largely determined by relative body size (Table 2). Every decided male contest ended with the larger fish victorious, and the occurrence of tied contests was significantly correlated with size difference in males, occurring mainly when there was minimal size difference. Female contests were distinctly different. Eight female contests (18%) ended with the smaller fish victorious, and this was true even in cases in which the size difference was considerable (range = 0.1–54%; median = 24%), and although there were 10 tied female contests, their occurrence was unrelated to size asymmetry (Table 2).

The SAM also predicts that contests between opponents with similar RHP will require more refined assessment and more risky escalated aggressive behavior to settle. Consequently, the duration of such contests should be longer than contests in which the opponent’s RHP is clearly different (e.g., large body size difference). Accordingly, in male fights the number of the most risky behaviors, mouth wrestling and tail beating, was negatively correlated with body size asymmetry (Figure 1, top panel), as was the duration of the fighting. In the case of females, however, SAM predictions were not met because neither contest duration nor the quantity of escalated behavior were related to size asymmetry (Figure 1, bottom panel).

In addition, males, but not females, followed SAM predictions regarding the fighting strategy of each contestant in terms of conventional behavior. When the size disparity between male opponents was greater, the fish assumed dominant and subordinate roles more thoroughly, with the smaller fish performing a greater proportion of displays.
(i.e., subordinate behavior) and the larger fish performing a greater proportion of chases (i.e., dominant behavior). However, the degree of size asymmetry was not related to the proportion of chasing or displaying done by the larger or smaller female contestant (for a summary of the SAM predictions and results, see Table 1).

Taken together, these results clearly show that male, but not female, intrasexual contests followed the predictions of the SAM. We ruled out the possibility that such sexual difference was owing to lower fighting activity in one sex by showing that both sexes engage in similar amounts of aggressive behavior. Thus, we conclude that females may use different rules or perhaps different trait asymmetries than do males to settle their conflicts.

**RHP or resource payoff value**

Interestingly, most of the few studies that have tested the effect of body size on female contests have also found that body size is not as important a determinant of contest outcome as it is for males (Dale and Slagsvold, 1995; Kouvula et al., 1993; Robinson, 1985; although see Pie, 1998, for an exception). This is intriguing because all of the organisms for which this finding has been reported are largely monomorphic (i.e., males do not possess weapons), and thus, it seems likely that larger body size should confer the same advantage to both sexes.

One potential explanation is that female contests may be decided more often by the value of the contested resource than by asymmetries of RHP. This theory predicts that animals fight with an intensity that is positively correlated with the value of the resource (Bishop et al., 1978; Enquist and Leimar, 1987). Thus, we would expect contests involving asymmetric animals in terms of resource payoff value (RPV), to be decided by such asymmetry, even in cases of clear RHP asymmetry. The animal that values the resource more is expected to invest more energy and/or take larger risks in the contest and therefore is expected to win. Many studies have shown that asymmetries of RPV are just as important as asymmetries of RHP in predicting the outcome of male contests (Dugatkin and Biederman 1991; Dugatkin and Ohlsen, 1990; Lindström 1992; Yokel, 1989).

The few studies that have examined female contests suggest a different scenario than for male contests. Female contests seem to be far more sensitive to asymmetries of RPV than to asymmetries of RHP. Robinson (1985) found that the intensity of contests between female yellow-rumped caciques (Aves: Cacicus cela) was determined by the value of the contested resource. For example, females fought with more intensity over established nest sites than over sites in which nest building had not yet begun (i.e., nest sites of lower RPV). On the other hand, male yellow-rumped cacique contests were decided by asymmetries of weight, with heavier males dominating lighter ones. Dale and Slagsvold (1995) found that intrasexual female territorial contests were not determined by asymmetries in RHP (i.e., body size or age) in pied flycatchers (Aves: Ficedula hypoleuca) but rather were influenced strongly by asymmetries in territory residence times of the opponents. They argued that territory residence times were directly correlated with the value of the mating opportunity (i.e., RPV) because the knowledge of other mating options may become outdated with increasing time.

Were female Texas cichlid contests in the present study more affected by asymmetries in RPV than by asymmetries in RHP? Even though all females were competing for the identical spawning resource (i.e., flower pot), it is possible that each female valued it differently. Like all teleost fishes, female cichlids go through an ovarian cycle that takes a certain amount of time. As the oocytes become more mature (i.e., nearing vitellogenesis, final maturation and ovulation), the female has less time to find a mate and a spawning resource. Although the females in our contests were kept in unisexual stock tanks under identical conditions for several weeks before the contests, they still could have been at different points in their ovarian cycles. If they were at different points, we would expect that those females closest to spawning would value the spawning resource more highly and thus be expected to fight more intensely for it. Under these circumstances, it is possible for small females that are closer to spawning to fight more intensely for the spawning resource and to be victorious over larger females that were not as far along in their ovarian cycle.

In support of this notion, Holder et al. (1991) found that the aggressive levels of individual female cichlids were highly variable over time and were highest late in the ovarian cycle, when they were closer to spawning. The same correlation between female aggressive intensity and reproductive cycle has been repeatedly reported in mammals (Ayer and Whitesett, 1980; Hirth, 1977; McDonough, 1994; Murie and Harris, 1988) and birds (Breiehagen and Slagsvold, 1988; Gowaty and Wagner, 1988).

This leads to a more general conclusion regarding the way that males and females value contested resources. We expect that when males are fighting over resources that directly lead to mating success (e.g., nest sites), those resources have essentially the same value to all males, and thus, their contests are determined primarily by asymmetries in RHP. On the other hand, resources that females convert to the production of offspring are usually highly variable over time and are determined by how close the female is to spawning.
of eggs (e.g., nest sites and the forage resources associated with them) will be valued differently by females depending on their reproductive condition at the time of the contest.

**Do female Texas cichlids engage in wars of attrition?**

Assuming that our female Texas cichlid contests were structured by asymmetries in RPV, we can further speculate on the possible alternative fight strategy. For example, although asymmetries of RHP are often easy to assess (e.g., differences in body size can be readily visually and physically assessed), it is possible that females cannot assess asymmetries in RHP and/or RPV. If females cannot determine how highly their opponents value the resource, then the general predictions of a mutual assessment model like the SAM would likely not be followed. In this case, females may set their fight strategy based solely upon their own RPV.

WOAM applies to contests in which mutual assessment is impossible and in which opponents choose their fighting strategy based solely upon their own RHP and/or RPV (Bishop and Cannings, 1978; Parker and Thompson, 1980). WOAM contests are not expected to progress through tiers of increasingly risky aggression, but rather are settled with more or less uniform aggressive behavior. This could be consistent with our results of female contests because female behavior was unrelated to opponent traits that could be readily assessed (i.e., relative size). In addition, the duration of WOAM contests is not expected to correlate to the relative difference in RHP or RPV between the contestants, because the length of the contest is determined by the persistence time of the less well-endowed contestant. Here again, our results were consistent with the WOAM, because the duration of female contests was unrelated to RHP asymmetries.

The way females fight has been overlooked. In light of our results, future studies on fight theory should consider sex-specific differences in fighting strategies. Our results and those of similar studies suggest a dichotomy in the way the sexes respond to asymmetries of RHP or RPV, and future studies should be sensitive to this.

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