ASSESSMENT OF
SWIMMING PERFORMANCE, BODY SIZE AND AGGRESSION IN A DWARF CICHLID, *Nannacara anomala*

by

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Abstract

In this study, I investigated the ritualized fights of male *Nannacara anomala* to show that each distinct phase (lateral display, tail beating, and mouth wrestling) of the fight is used to assess a different aspect of resource holding potential (aggressiveness, body size and swimming performance). When animals go into an agonistic encounter, they often have little or no previous knowledge of their opponent's fighting ability (or resource holding potential). Assessment is the process by which strangers gain information about each other through repetition of informative behaviors. Generally fights are ritualized so that specific behaviors are associated with distinct phases within the fight. Aggressiveness of fish was established by measuring response time to an aggressive conspecific. Weight was used as a measure of body size. Swimming performance (stamina and maximum swimming speed) was determined by swimming each fish in a variable speed flow tank.

If all fights are taken into consideration, weight is the only factor for which winners were significantly different from losers ($p = 0.009$). However, if the fights are classified by the phase in which they ended, fights ending in tail beating have larger winners ($p = 0.003$) and fights ending in mouth wrestling have faster winners ($p = 0.008$). Opponents are using early stages of fights to assess body size and escalated stages to assess performance characteristics.

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Introduction

Male competition for mates occurs in many social systems (Alexander, 1961; Parker et al., 1974; Jakobsson, 1979). Contest outcomes can have a significant effect on the reproductive success of the competitors (reviewed by Huntingford and Turner, 1987). Since the aggressive encounters can be quite complex, predicting winners can be a difficult task. Traditionally, the size difference between competitors has been the best indicator of who will win the fight (Barlow et al., 1986; Beeching, 1992; Simmons, 1988). Unfortunately, size differences are only accurate for predicting abrupt contests that end without much physical contact. But aggressive encounters are not always brief. So the question remains: Are there good predictors of fighting ability for escalated fights? I designed this study to investigate what happens when animals in an aggressive conflict continue beyond the short bouts that are characteristic of size-determined outcomes. I used as a model system the graded aggressive displays of the dwarf cichlid *Nannacara anomala*. I used this system to show that *N. anomola* males are assessing varying characteristics throughout extended contests and that specific stages of a fight are associated with assessing unique characteristics.

In order to better understand behaviors associated with aggression, it is first necessary to investigate the fundamentals of fighting. Game theory was first applied to evolutionary biology in the early 1960's (Lewontin, 1961). This original view of game theory considered a species to be playing a game against nature to prevent extinction. More commonly, however, game theory considers individual members of a population to be playing games against each other. There are several applications of game theory that are used to model various animal conflicts (reviewed by Maynard Smith, 1982). Each of these models tends to build on previous ones both in complexity and in relevance to real-life situations.

The simplest of game theory models is the Hawk-Dove game proposed by Maynard Smith and Price (1973). In this model, individuals can adopt either of two fighting strategies, hawk or dove. 'Hawks' will always attack rapidly and inflict injury on their opponent. 'Doves' on the other hand, will display, but retreat immediately if their opponent attacks. Adopting a hawk strategy is only beneficial if the risk of injury in a fight with another hawk is low relative to the fitness gain to the winner. Since doves always retreat, there is no risk of injury. Therefore, if the risk of injury in a hawk vs. hawk fight is high relative to the payoff, it is more beneficial to choose a dove strategy.

The purpose for playing the hawk-dove game is to determine the evolutionarily stable strategy (ESS) for given circumstances (Maynard Smith and Price, 1973). An ESS is a strategy that cannot be invaded by a mutant strategy if all members of the population adopt it. The ESS is stable in that individuals playing another strategy will do worse than those playing the ESS. For aggressive behavior, this could mean that individuals not using the ESS have a lower chance of winning a fight or have a higher chance of getting hurt.

In the case of the basic hawk-dove model, the ESS is dependent on the hawk's ability to inflict injury on its opponent. If there is no risk of injury in a hawk fight then the hawk strategy is the ESS. A mutant dove could not invade this population since a hawk always wins against a dove. If, however, there were some cost associated with being in a hawk fight, the ESS would be some combination of hawks and doves. The exact ESS (Huntingford and Turner, 1987) is dependent on:

1. the available strategies;
2. the cost and benefits they entail;
3. their frequencies.

Through analysis of the hawk-dove model, a stable point (i.e. the frequency of hawks and doves in the population) can be found for various circumstances.

Since it was proposed in the early 1970's, many additional strategies have been considered in the classic hawk-dove model. In Maynard Smith and Price's (1973) original formulation of the model, they introduced a 'bully', and a 'retaliator'. A bully always attacks initially, but retreats if the opponent attacks. A retaliator attacks only if it is attacked first. Caryl (1981) proposed a 'prudent hawk' strategy where the player initially attacks like a hawk, but eventually withdraws from the competition after a suitable time period. Although each of these models is still a gross oversimplification of reality, they do provide a framework for the investigation of more complicated models.

In 1974, Maynard Smith introduced a model known as the 'war of attrition'. In this model it is assumed that the contest is between two equally matched doves. Since doves will only display, the winner of the bout will be the one that is willing to display for the longest. Maynard Smith proposed that there is no pure ESS for this case since individuals that are willing to display for longer will always win contests.

This, however, is not the case since displaying for a period of time is in fact costly. This cost can be due to a loss of time spent on other behaviors or simply due to energy expenditure. Therefore, the ESS for a war of attrition will be a tradeoff between the amount of time spent displaying and the cost involved in that display.

Asymmetries and Assessment

The models derived in war of attrition theory to date have involved contestants that are similar to each other in fighting ability. Krebs and Davies (1981) were among the first to suggest that an actual war of attrition may not exist since most bouts are actually decided on by some sort of asymmetry between individuals. This asymmetry could be due to relative fighting ability, the prior possession of a resource, or the relative benefit obtained from the resource (Parker, 1974). The relative benefit obtained has an effect on the organism's motivation, which in turn can have an effect on its fighting success (Enquist and Leimar, 1987).

The first of these asymmetries, a difference in fighting ability, is generally referred to as organisms' resource holding potential, RHP (Parker, 1974). Certain individuals are simply better at attaining on holding onto resources than other. RHP is simply a measure of this ability. It can be made up of both intrinsic and extrinsic factors. Intrinsic factors are those that are defined by the physiology of the organism. Some factors would include body size, endurance, speed and aggression. Extrinsic aspects of RHP are those that are dependent on past experiences. Hack (1997) showed that two extrinsic factors, burrow residency and bout initiation, affect the outcome of cricket fights. Recent fighting success can also affect an organism's RHP through psychophysiological mechanisms (Chase et al., 1994).

The main problem with both the hawk-dove model and the war of attrition model is that they are not based on realistic behavioral mechanisms (Enquist et. al., 1990). In an actual fight, opponents rarely enter the fight with specific intentions to perform a particular strategy. The reason for this is that contestants generally enter the fight with very limited knowledge of their opponent's fighting ability, RHP. More realistically, as a fight proceeds, opponents gain information about their relative fighting abilities and use this information to decide what strategies to use (Parker, 1974).

Sequential Assessment Game

In order to understand what factors are being assessed in fights, it is first necessary to gain a good understanding of the method by which the information is acquired. Several attempts have been made to model information acquisition (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981; Enquist and Leimar, 1983). This sequential assessment game allows combatants to acquire information as the fight proceeds. Currently the most sophisticated such model in existence is that of Enquist and Leimar (1983). Since its development, the model has been tested in various species including fish (Enquist and Leimar, 1987; Enquist et al., 1990; Franck and Ribowski, 1989), insects (Hack, 1997), and amphibians (Robakiewicz, 1992).

Several aspects of real fights have lead to the development of the sequential assessment model (Enquist et al., 1990). First is the realization that fights generally take place between strangers that have no previous knowledge of their opponent's fighting ability. This means that any information about the other's fighting ability must be obtained during the fight itself. Second, behavioral elements are repeated throughout the course of a fight. This suggests that some assessment is going on. Third, fight lengths increase as the difference between contestants decreases (Austad, 1983), implying that information is being acquired; more information is needed when the asymmetry between contestants is small.

In the sequential assessment model, contestants proceed as follows: contestants enter the bout with no previous knowledge of their opponent's relative RHP; contestants are randomly drawn from a population that is normally distributed about some average RHP. Past fighting experience will give contestants an idea of their RHP relative to the general population.

During each step of the fight, information is gathered in a manner similar to statistical sampling. Prior to the first step of the fight, the contestants' only estimate of their relative fighting ability is from previous experience. If they have no previous fighting experience, they can only assume that their relative fighting abilities are equal. Since the contestants only have a limited amount of information, there is some amount of random error involved with this estimate. After the first step of the fight, the contestants assess their relative RHP. Each of these assessments has random error associated with it. In order to minimize this error, behavioral elements are repeated. This is similar to increasing the sample size in statistical sampling.

Although actual strategies used are dependent on the species of animal being studied, in general fights will proceed through a series of strategies. The first set of strategies in a fight is usually very low cost. In most cases, this is usually some sort of visual assessment (Hurd, 1997; Keeley and Grant, 1993; Carpenter, 1995). As the fight proceeds, each of these steps becomes more and more costly (Lopez and Martin, 2001). Often times, only the final step of a bout will involve contact where there is actual possibility of injury.

Part of the reason that the costs for various steps in a fight escalate as the fight proceeds is that it is to an animal's benefit to find out as much about its opponent as it can without injuring itself (Parker, 1974). However, it is difficult to directly test an opponent's fighting ability without physical contact. Therefore the first steps in a fight attempt to test fighting ability through indirect means. These generally include displays to show an individual's size. But size can be faked, so unless size differences are extreme, they are not reliable indicators of fighting ability.

Once size is established, the next steps in a fight generally involve slightly more direct displays of strength, speed, or agility that may or may not involve actual physical contact. The key of these intermediate steps is that the actual risk of injury is still low. Examples of some intermediate strategies include antennae lashing in house crickets (Hack, 1997), tail beating in cichlid fish (Enquist et al., 1990) in which one fish beats with its tail and water is pushed against the other fish, or roaring in red dear (Clutton-Brock and Albon, 1979).

Finally, the highest levels in a fight tell the animals the most about relative fighting ability. They do so, however, with the greatest risk of personal injury. In male house crickets (Hack, 1997) these escalated steps can involve kicks, head charges, or actual wrestling where there is a possibility of permanent injury. Revero et al. (2000) also performed a study that monitored the heartbeat of individual crabs to show that energetic costs of fighting increased with fight length.

Not all animal fights lead to the highest levels of physical contact. In fact, many bouts are decided in the first few steps of noncontact display. The fight continues until one of the contestants decides that its RHP is significantly lower than its opponent's. If it is assumed that a fight is just a way of gaining information about relative fighting abilities, there are only two main decisions for the contestants to make; continue fighting or quit. Therefore, only the loser decides when the fight is over. It is possible, however, that at some point in the fight, one contestant may decide that it has a distinct advantage over its opponent. While the winner does not end the fight, it may force its opponent into retreat by accelerating the fight (Clutton-Brock and Parker, 1995).

The fact that assessment occurs in a fight is relatively undisputed. How animals assess the information and what information is actually being assessed are still relevant questions. The sequential assessment model proposed by Enquist and Leimar (1983) describes how the animals acquire information. An example output of this model is shown in Figure 1. This figure shows a fight lasting 24 steps. A step would be equivalent to one repetition of a behavioral element in a fight. Each line (A and B in the model) represents one animal's perception of its own relative fighting ability. The third line in the graph (the switching line) represents the point at which the animal should quit due to its lower fighting ability. When the fight starts, there is a large difference between the switching line and zero since only large differences in fighting ability can be distinguished at this point in the fight. This switching line asymptotes to zero.

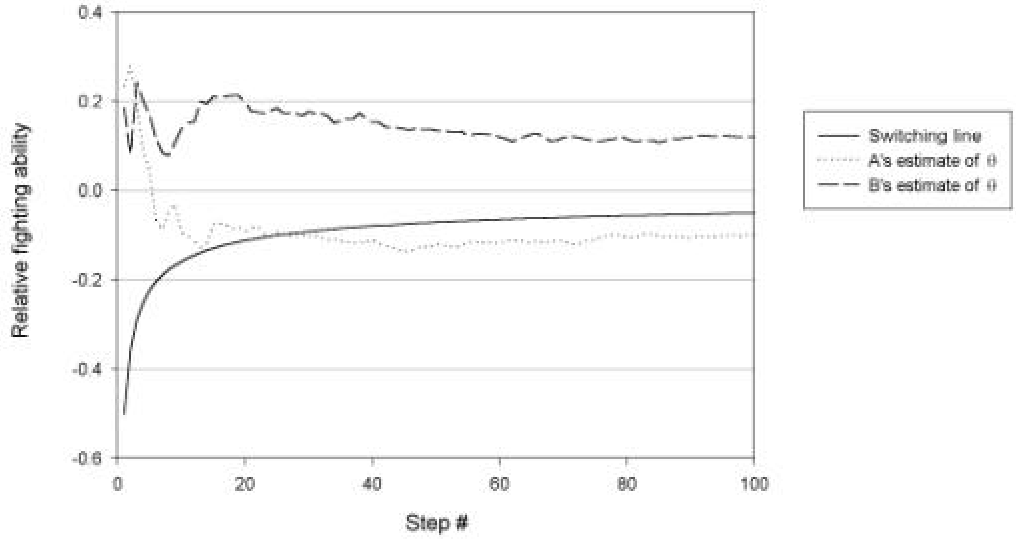

Figure 1. Sample Output for the Sequential Assessment Game. An example of a contest between two conspecifics, A and B, lasting 24 steps. The fight ends when A's estimate of θ drops below the switching line.

Analysis of this model provides a few important conclusions (Enquist and Leimar, 1983). The first is that the number of steps in a fight is negatively correlated with the difference between the contestants' fighting abilities. The model also predicts that fights are organized into one or more phases. Each phase should be associated with different behaviors that are used to convey unique information about each opponent's fighting ability. Escalated phases tend to be more dangerous than early phases. Since closely matched individuals are more likely to end up in escalated phases, it is more costly to meet an opponent of equal strength than one that is stronger. The model also suggests that rates of behavior are constant in each of the phases and that the division into phases is independent of the contestants relative fighting abilities. This relative fighting ability should, however, be positively correlated with the number of phases.

Several studies have shown that this is an accurate representation of the way in which animals acquire information. Parker and Thompson (1980) tested an earlier formulation of the model in dung flies. In 1988, Hammerstein and Reichert analyzed the model in an experiment with the spider, *Agelenopsis aperta.* Then in 1990, Enquist et al. tested predictions of the model in the cichlid fish, *Nannacara anomala*. The overall conclusion of these experiments is that assessment strategy is rather well predicted by the sequential assessment model.

Since fighting ability can only be assessed accurately through actual physical contact, there is much debate over what factors animals are assessing. Since the early stages of a fight generally involve purely visual displays, it is apparent that relative size is an important assessment factor. Several studies have shown that relative individual size is correlated with the probability of victory (Enquist et. al., 1990; reviewed by Huntingford and Turner 1987). Others have also shown the influence of body coloring (Bakker and Sevenster, 1983), endurance (Marden and Waage, 1990) and aggression (Barlow et. al., 1986).

Some have suggested that the factors that animals are assessing change as a fight proceeds (Enquist and Leimar, 1990; Robakiewicz, 1992). This suggests that different behaviors are used to demonstrate different abilities. For instance, it is possible that lateral displays at the beginning of a fight are all that are needed to assess size differences (Enquist et al., 1986). Once size is assessed, animals may then move on to behaviors that demonstrate other qualities such as speed, or aggression. While this seems reasonable, very little research has been done to directly test the theory.

In this study, I examined fighting behavior in a dwarf cichlid, *Nannacara anomola*. The aggressive behaviors of *N. anomala* have been studied quite extensively (Jacobsson et al., 1979; Enquist and Jakobsson, 1986; Enquist et al., 1990; Brick, 1998). In social situations, male *N. anomola* set up a dominance system with one alpha male and several beta males. A male's position is dependent on its success in ritualistic fights with other males. The fights themselves take place with or without the presence of females and follow a very set pattern. All fights start with low risk behaviors such as lateral display, but have the potential to escalate to higher risk behaviors (Jakobsson, 1979). I show that in extended contests males use levels of escalation to assess different aspects of RHP, including physical, behavioral, and performance parameters.

Materials and Methods

The aim was to assess the relative importance of weight, aggressiveness, and swimming performance in determining the outcome of an aggressive interaction. I first collected physical and performance data for each fish. To establish aggressiveness, I exposed fish to an aggressive conspecific and recorded their latency to perform a lateral display. Swimming performance (stamina and maximum swim speed) was established by swimming each fish in a variable speed flow tank. Once potential RHP components were established, fish were paired up based on the data. Each pair was given an opportunity to fight and establish a relative dominance.

I obtained juvenile *Nannacara anomala* Regan (Perciformes: Cichlidae) from a local wholesaler in November, 2000. Individuals beginning to show male characteristics were moved into 40 L holding tanks in December, 2000. Three fish were placed in each holding aquarium with an opaque barrier separating individuals from each other both physically and visually. Each section of the holding tanks contained approximately 2cm of gravel and one 4cm diameter clay pot. Throughout the experiment, temperatures were maintained at 27 ± 1°C. Fish were fed twice daily on a diet of commercial fish flakes. Fish (a total of 44) used in the experiment were sexually mature and weighed 0.75-2.25g. All experiments took place in February, March, and April, 2001.

Measurement of Characteristics

Weight

Fish weights were monitored on a weekly basis. To weight fish, a small beaker of water was placed on a balance. I then tared the balance and placed the fish in the beaker. Prior to being placed in the beaker, the fish was blotted with a dry paper towel. If a fish lost significant weight (> 0.05g) from one week to the next, I monitored its weight for one more week and removed the fish from the experiment if weight loss continued.

Aggression

To assess aggression, I exposed each fish to a competitor and measured the amount of time it took the fish to display to the competitor. For each fish, I obtained a significantly smaller (50 – 85 % by weight) male competitor from a group tank of *N. anomala*. Competitors were placed in a transparent plastic jar with a removable opaque covering. Jars with competitors were placed directly into the corner of each holding tank. As soon as the jar was placed in the tank, the fish were given three minutes to acclimate to the new addition and the opaque covering was removed so the fish could see the competitor. I began timing as soon as the covering was removed and stopped the timer when the experimental fish approached the jar and performed a lateral display. If fish refused to display for 10 minutes, I stopped the trial and recorded a latency to display of 10 minutes.

The above procedure was repeated three times for each fish. To minimize observer affects, all aggression experiments were videotaped. Tapes were analyzed at a later date.

Performance

To assess swimming performance, I designed and built a variable speed swim tank (Fig. 2). The swim tank was a 120-L recirculating system with water pumped through by a vertically mounted propeller blade. A ¾ h.p. motor was connected to the propeller shaft by a belt and pulley. The speed of the propeller could be adjusted by changing the size of the pulley on the motor or the propeller shaft. Water being moved through the system was either pumped through the main testing chamber or through a bypass. Large ball valves mounted on each of the passages allowed for adjustment of flow through each. Closing the valve on the test chamber and opening the valve to the bypass completely stopped the movement of water in the testing chamber. Conversely, when the bypass valve was closed and the other valve was opened, all of the water moved through the testing chamber. Through adjustment of both pulleys and valves, water flow in the test chamber could be adjusted from 0 – 50 cm/s. A Marsh-McBirney model 2000 flow meter measured water speeds in the test chamber.

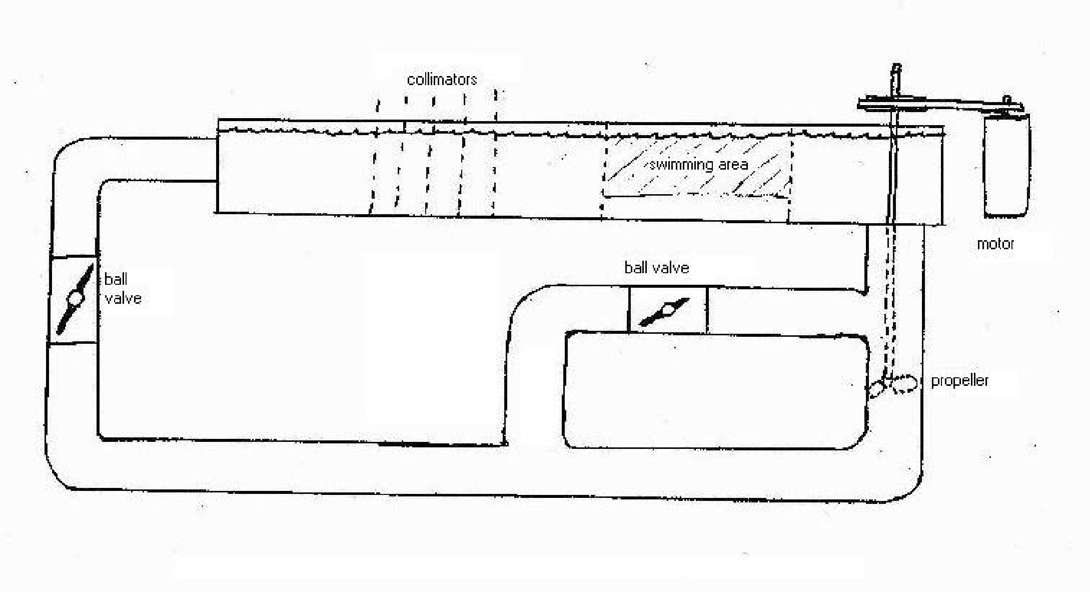

Figure 2. Illustration of Flow Tank. The flow tank illustrated above was used for measuring performance characteristics of each fish.

The test chamber was a 2m long (15cm x 17cm in cross-section) Plexiglas section with water flowing in at one end and out at the other. Two cm of gravel covered the bottom of the test chamber. The first 1.2m of the flow chamber were used to collimate the flow with several plastic grates. Downstream of the collimators was a 45cm long enclosure in which a fish could be placed. The enclosure was bounded on the up stream and downstream ends by aluminum screening. Also, a U-shaped piece of Plexiglas ran along the length of the enclosure to prevent fish from swimming along the bottom corners of the test chamber where water velocities tended to be slower.

To assess stamina, I swam fish at a set speed for up to 30 minutes or until the fish became exhausted, whichever came first. The speed for each fish was based on the animal's general swimming ability and its standard length (measured from the front of the fish to the caudal peduncle). Before a fish was tested, the water velocity was first calibrated to a speed corresponding to 6 body lengths per second (bl/s) for the given fish. Once the flow velocity was calibrated, the system was stopped, and a fish was placed in the swimming enclosure. The fish was given a five-minute acclimation period in still water. After five minutes, the fish was allowed to orient itself upstream and then I started the flow of water. Anytime the fish came in contact with the downstream end of the enclosure, it was tapped on the caudal fin with a small plastic rod.

When I would first start the flow of water, some fish began swimming immediately while others refused to swim away from the back wall. When fish refused to swim, they were given a five-minute break and tested again. If they still refused to swim, the procedure was repeated the next day at six bl/s. If fish still refused to swim on the second day, they were given a 24-hour rest and the procedure was repeated at 5 bl/s. If they still refused to swim, the procedure was repeated the next day at 4 bl/s. At 4 bl/s, all fish were able to start swimming without being pushed downstream end of the enclosure.

Once a speed at which each fish could swim was determined, the fish was allowed to swim for up to 30 minutes. Whenever a fish rested on the back wall, it was tapped on the caudal fin which caused the fish to stop resting and swim up current. The fish was considered exhausted if it got tapped three times in a row without swimming off the back wall. Trials were stopped after 30 minutes. Fish capable of swimming for 30 minutes often continued for several hours (personal observation from preliminary trials). Once a reasonable swimming speed was found for each fish, the procedure was repeated on two more consecutive days to give a total of three stamina measurements for each fish.

Maximum swim speeds were also calculated for each fish. For these experiments, a flow meter was placed downstream of the swimming enclosure so tank speeds could be monitored throughout the experiment. Water speeds within the enclosure correlated with those downstream of the enclosure in the following logarithmic relationship:

$$s_E = 15.661 * \ln(S_M) - 27.375$$

where S_E is the actual speed (cm/s) in the enclosure and S_M is the measured speed (cm/s) downstream from the enclosure. Before placing a fish in the enclosure, the water velocity was adjusted to 3 bl/s. Once calibrated, the flow tank was stopped and the fish was placed in the enclosure. After a five-minute acclimation period, I waited until the fish positioned itself in the upstream direction and then started the tank. The fish was allowed to swim at the initial speed for 10 seconds. The speed was increased by approximately 2 cm/sec at 10 seconds and every 5 seconds thereafter. This continued until the fish got pinned on the downstream end of the enclosure. Fish were prevented from resting on the back by being tapped on the tail following the method outlined above for the stamina experiment. When the fish failed to respond to three tail taps, the speed of the water was noted and the tank was stopped.

Paired Aggressive Encounters

I set up paired bouts based on weight, aggression, and swimming ability (swimming stamina and maximum swim speed). Opponents differed in at least one of the four measured characteristics. No fight took place between fish that were housed in the same holding tank. Each fish was isolated for at least one week before any given fight. This isolation period was necessary to minimize effects of previous fighting experience.

I moved opponents into separate sides of a 40 L experimental tank on the day prior to the fight. A removable opaque divider separated the fish in the tank. Each side of the tank contained one 4cm clay pot (placed close to the center divider), one foam filter, one small tank heater and approximately 2cm of gravel. By providing identical territories in each side of the tank, the fish were given equal resources to fight over. The clay pots were placed in the tanks to provide a hiding place for the fish, and to give it a focal site for its territory.

Fish remained in separate sides of the experimental tank overnight. This gave fish time to settle into their new territory. On the following day, I removed the divider and permitted fish to interact. I staged aggressive bouts between 1000 and 1500h. Experimental tanks were housed behind an opaque curtain and all encounters were videotaped.

Videotaped aggressive encounters were analyzed for timing and structure. Each fight began when one fish approached the other and performed a lateral display. This began the display phase of the fight. Males in a fight show stereotypically aggressive or submissive behaviors. Aggressive display involves spreading the fins, operculae and gular regions, and characteristic changes in color. Submissive fish relax their fins and stop making aggressive advances. If one fish became submissive during any stage of the fight, the fight was considered complete, and I designated the aggressive fish as the winner.

Fights that do not end in the display phase progress to tail beating. In this phase, one fish positions itself so its caudal fin is facing its opponent. The tail beater then uses its tail to push water against the other fish. Once this phase started, fish would often switch roles, alternating between being the tail beater and the recipient. Bites or bumps would sometimes occur in this stage when one fish would use its mouth to bite or push the other fish. If one fish did not submit during this phase, the fight would progress to mouth wrestling. In this phase, the fish would lock jaws and push and pull each other around until one fish gave up.

Data Analysis

Data were analyzed using Statistica 5.5 (StatSoft, Inc., 2000). Data were transformed as necessary to fit assumptions of classical techniques (specific transformations are indicated in the Results section). Nonparametric analyses were used when data did not fit the classical assumptions.

Results

Weight

Weight was monitored throughout the study as a way to assess health of the fish (Appendix A). Weights used in the analysis, however, are those measured on the day of experimentation. During experimentation, fish weights ranged from 0.86 – 2.36g. I considered opponents with a weight difference of more than 1% on the day of a fight to have significantly different weights.

Aggression

I recorded latency to display to a conspecific on three different days for each of the 45 fish (Appendix B). Fish were never observed to respond aggressively to the test apparatus alone; the presence of a conspecific was necessary to elicit aggressive behavior. Analysis of variance showed no significant differences among the replicates (F = 2.20, p = 0.12). The quickest time to display was 3 seconds while the slowest time to display exceeded the 10-minute time limit imposed on the experiment (7 out of the 45 fish went 10 minutes without displaying in at least one of the three replicates). I based each individual's aggression scores on his two fastest replicates. An average time to display was calculated from these two replicates. Averages were ln-transformed to normalize the data. I used the transformed scores to compare aggressiveness between two different fish. Aggression scores ranged from 2.07 to 6.01 (SE = 0.15, Fig. 3) with a low score representing a highly aggressive individual. Fish that differed in aggression by more than 1.96 standard errors were considered to have significantly different aggressions.

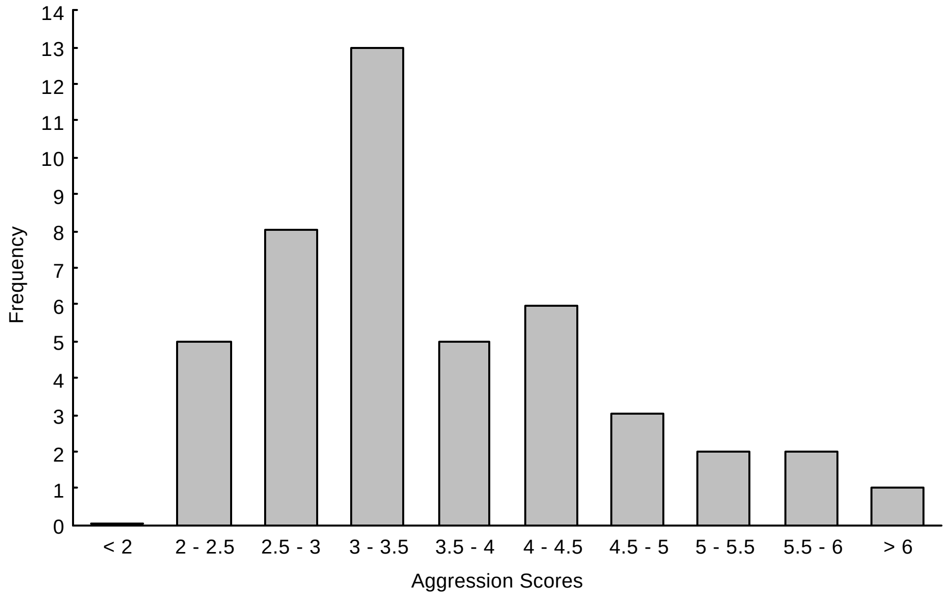

Figure 3. Distribution of Aggression Scores: The fastest 2 out of 3 latency to display times are averaged and ln-transformed to give aggression scores for each of 45 fish.

Stamina

I recorded time to exhaustion for each fish on three consecutive days at a speed based on the size and swimming ability of the given fish (Appendix C). Fifteen of the fish were tested at speeds corresponding to 4 body lengths per second (bl/s), 20 were tested at 5 bl/s and 10 were tested at 6 bl/s. Stamina times ranged from 18 seconds to over 30 minutes. ANOVA showed no significant differences among the replicates for any of the three groups (F = 1.78, p = 0.19 for those tested at four body lengths per second; F = 0.32, p = 0.73 for those tested at five body lengths per second; F = 0.98, p = 0.40 for those tested at six body lengths per second). For each fish, I used the longest replicate as the stamina measurement for further experiments (Fig. 4). Fish with stamina differences of more than one quartile (±1710s for those tested at four body lengths per second; ±355.5s for those tested at five body lengths per second; ±158s for those tested at six body lengths per second) were considered to have significantly different staminas.

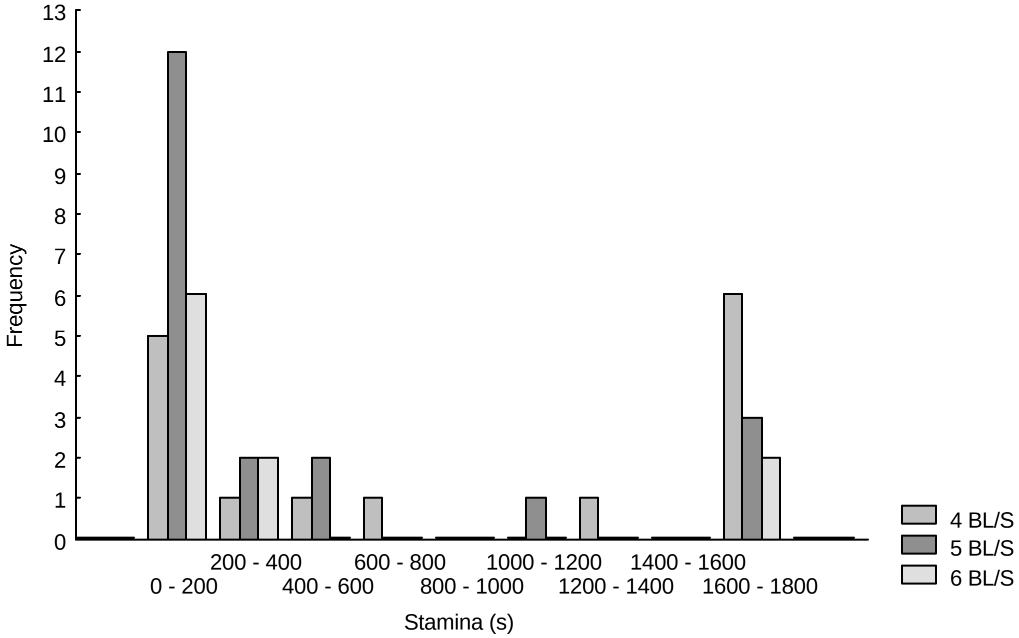

Figure 4. Distribution of Staminas: Staminas for 45 fish are based on the longest of three runs in a flow tank. Fish were run at 4 body lengths/second (BL/S), 5 BL/S, or 6 BL/S depending on their swimming ability and standard length.

Maximum Swim Speed

I established maximum swimming speeds for each fish on three consecutive days (Appendix D). ANOVA showed no significant within individual differences in maximum swimming speed on the three days (F= 2.79, p = 0.07). Maximum speeds were averaged over the three days to give a single maximum speed for each fish. These final average values ranged from 16.03 to 31.53cm/s (SE = 0.63, Fig.5). Fish differing in speed by more than 1.96 standard errors were considered to have significantly different maximum swim speeds.

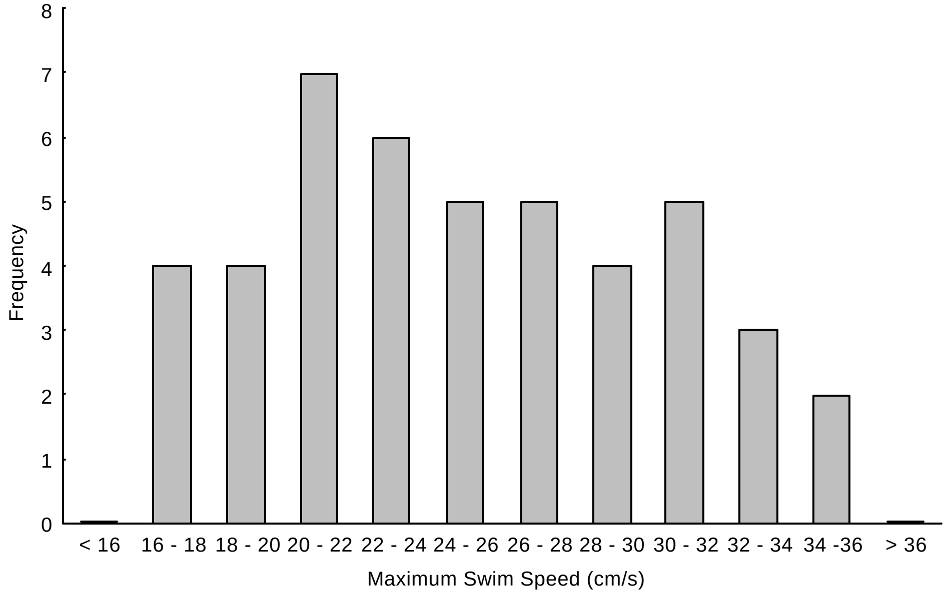

Figure 5. Distribution of Maximum Swim Speeds: Maximum swim speeds are based on the average of three swimming trials.

Correlation of Characteristics

There were no significant correlations among any of the four physical or performance characteristics that I measured (Table 1). This observation provided confidence that the parameters I measured could be analyzed separately without concerns about cross-correlation of physical parameters on performance parameters.

Table 1. Correlation of Characteristics: No significant correlations were found among any of the four measured characteristics (weight, aggression, stamina and maximum swimming speed). Values for stamina are split up into three groups based on the speed at which the fish was swum in body lengths per second (bl/s). Reported statistics are Pearson R-values.

		N		**weight**	**aggression**	**stamina**			**max speed**
						4	**5**	**6**	
weight		45	R	1					
			p	0					
aggression		45	R	-0.225	1				
			p	0.137	0				
	4 bl/s	15	R	-0.35	-0.43	1			
			p	0.201	0.111	0			
stamina	5 bl/s	20	R	-0.258	-0.008	-	1		
			p	0.272	0.973	-	0		
	6 bl/s	10	R	-0.2	-0.128	-	-	1	
			p	0.58	0.725	-	-	0	
Max speed		45	R	0.1	-0.102	0.328	0.301	0.485	1
			p	0.515	0.504	0.233	0.197	0.894	0

Staged Aggressive Encounters

I performed a total of 69 staged aggressive encounters (Appendix E). Of these fights, 53 pairs had significantly different weights, 45 had different aggressions, 15 had different staminas, and 53 had different maximum swim speeds. No fish fought in more than 6 fights. Of the fish that were in multiple fights, 6 different fish won every fight they were in and 6 different fish lost without exception. Given that this is a relatively small percentage of all fights, it seems reasonable to assume that competitors were assessing each encounter separately, and not carrying forward information from previous encounters that might predispose them to be consistent winners or losers.

Fights varied in both length and the phase in which they ended. Fights lengths ranged from 3 to 2160s with a mean of 245.41s (SE = 47.79). Eleven fights ended in the lateral display phase, 29 ended in the tail beating stage, and 29 ended in the mouth-wrestling phase. There were no correlations among the times spent fighting in each stage and the differences in measured RHP parameters of the opponents (Table 2).

Table 2. Correlation of Time Spent Fighting with Differences Between Opponents: The amount of difference in fighting ability of the opponents had no influence on the time spent fighting. Reported statistics are Pearson R-values.

Time spent		Weight	Aggression	Stamina	Max Swim Speed
Displaying	N	69	69	29	69
	R	-0.124	0.0246	-0.1044	-0.0388
	p	0.31	0.841	0.59	0.752
Tail Beating	N	58	58	22	58
	R	-0.1766	-0.0877	0.3816	0.1231
	p	0.185	0.513	0.08	0.357
Mouth wrestling	N	29	29	9	29
	R	-0.1533	0.0393	-0.1839	-0.0889
	p	0.427	0.84	0.636	0.646
Total time in fight	N	69	69	29	69
	R	-0.2281	0.0189	-0.011	-0.0005
	p	0.059	0.877	0.955	0.997

Calculated aggression scores were a poor predictor of how the fish reacted in the actual fight. Fish with high aggression scores were not more likely to escalate to the next phase of fighting first. The fish with a significantly higher aggression score displayed first in 25 of 41 fights (Sign test, $p > 0.05$), and beat his tail first in 15 of 37 fights (Sign test, $p > 0.05$). There was, however, significance in the number of fights in which an aggressive fish bit more often than a less aggressive opponent. In 23 fights with fish of differing aggression in which bites occurred, higher aggression fish bit more often (19 times, Sign test, p = 0.001).

If all of the fights are taken into consideration, it appears as though body size is the only factor that fish are effectively assessing throughout the fight. Winners also had higher weights in 34 of 52 fights in which there was a significant weight difference (Sign test, p = 0.009, Table 3, Fig. 6).

Table 3. Categorized fight outcomes: Frequencies are given for the number of times a winner had a significantly higher RHP characteristic. Significant values are denoted by an asterisk (Sign test, $p < 0.05$). Opponents appear to be accurately assessing weight in the tail beating phase and maximum swim speed in the mouth wrestling phase. If all fights are taken in to consideration, it appears as though opponents are only assessing weight.

Fights ending in	Total	Fights when winner had higher[1]			
		weight	aggression	stamina	Max speed
Lateral Display	11	7/10	2/4	3/4	5/8
Tail Beating	29	19/24*	13/19	3/7	9/22
Mouth Wrestling	29	8/18	12/21	1/4	18/24*
All phases	69	34/52*	27/44	7/15	32/53

1. The first number denotes the number of times a winner had a significantly higher score. The second number denotes the total number of times opponents had significantly different scores for each parameter.

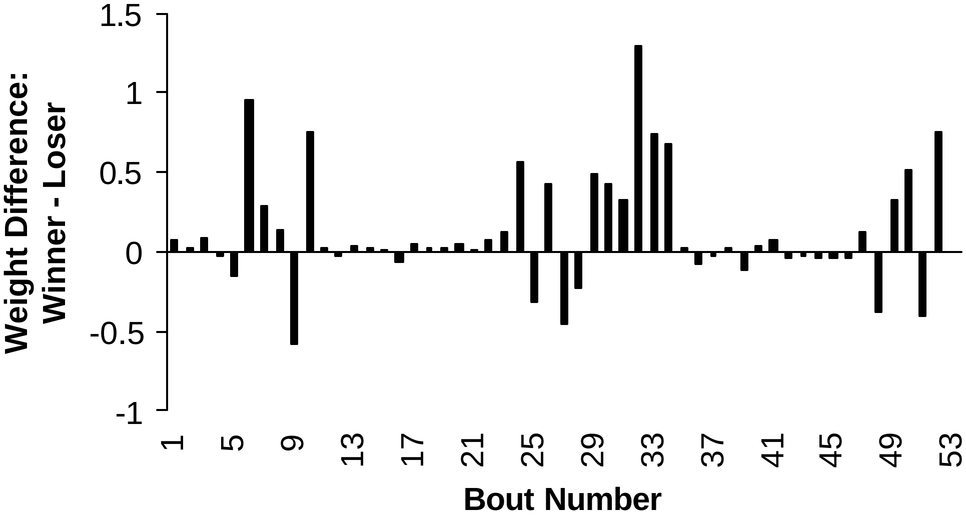

Figure 6. Weights of winners versus losers for all fights. These data account for 53 fights in which opponents had significantly different weights. Height of the bars is the difference in weight of winners and losers. Positive values indicate the winner was bigger than the loser, whereas negative values indicate the winner was smaller than the loser. Winners had higher weights in 35 of 53 fights (Sign test, p = 0.009).

To investigate the possibility that fish used different phases to assess different RHP components, I categorized fights by the phase in which they ended (Table 3). Eleven fights ended in lateral display, 29 ended in tail beating and 29 ended in mouth wrestling. Of the 29 fights that ended in the tail beating, 24 were between opponents with significantly different weights; nineteen of the winners were fish with higher weights (Sign test, p = 0.003, Fig. 7). Of the fights that ended in mouth wrestling, 24 were between opponents with different maximum swim speeds; eighteen of the winners were fish with higher maximum swim speeds (Sign test, p = 0.008, Fig. 8). It appears as though fish are assessing weight in the tail-beating phase and swimming ability in the mouth-wrestling phase.

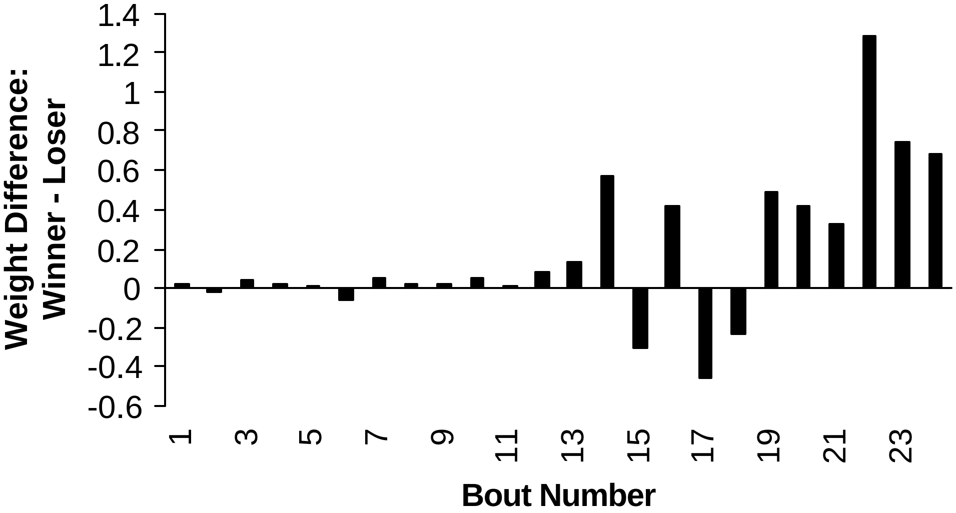

Figure 7. Weights of winners versus losers for fights ending in tail beating. These data account for 24 fights ending in tail beating in which opponents had significantly different weights. Height of the bars is the difference in weight of winners and losers. Positive values indicate the winner was bigger than the loser, whereas negative values indicate the winner was smaller than the loser. Winners had higher weights in 19 of 24 fights (Sign test, p = 0.003).

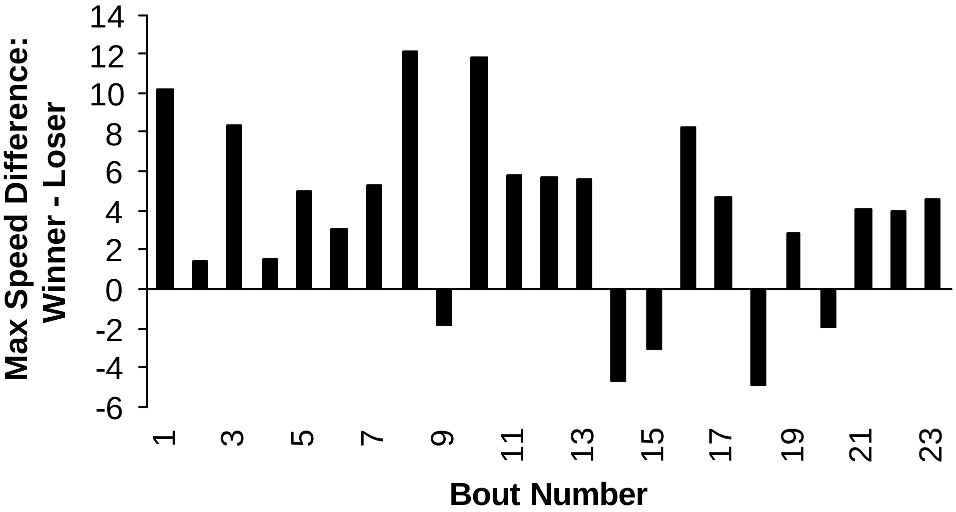

Figure 8. Max speeds of winners versus losers for fights ending in mouth wrestling. These data account for 23 fights ending in mouth wrestling in which opponents had significantly different maximum swim speeds. Height of the bars is the difference in speed of winners and losers. Positive values indicate the winner was faster than the loser, whereas negative values indicate the winner was slower than the loser. Winners had higher weights in 18 of 23 fights (Sign test, p = 0.008).

Discussion

I studied the graded aggressive responses of male *N. anomala* to show that fights are broken up into distinct phases that are each used to assess unique aspects of relative RHP. I predicted that decisions to give up would be based on information gained in the stage in which they were fighting. Winners had higher weights in fights that ended in tail beating (Table 3 and Fig. 7). Winners also had higher maximum swim speeds in fights that ended in mouth wrestling (Table 3, Fig.8), suggesting that specific behaviors are associated with unique aspects of RHP. This study is the first to show that *N. anomala* are assessing swimming ability in escalated stages of fights. One very important aspect of this study is the fact that if these fights are not categorized by the stage in which they ended, swimming performance does not appear to have any affect on the outcome of the fight. Since only 29 of the 69 fights escalated to the level of mouth wrestling, opponents were able to assess swimming performance only in the small percentage of fights that escalated to mouth wrestling.

Upon examination, the link between swimming performance and social dominance seems consistent with predictions. In the mouth-wrestling phase of a fight, contestants lock jaws and try to push against the strength of their opponent. The action is very similar to the way in which a fish moves upstream in fast moving water. While it is unlikely that fish are trying to assess swimming ability itself, it is reasonable that swimming ability is directly related to fighting ability. Physiologically, maximum swim speeds are determined both by the rate at which the muscles on each side on the tail can contract and relax and the actual size of those muscles (Brill, 1996). Those same muscles are very important in determination of which fish is the strongest mouth wrestler. In this way, swimming performance accurately mimics the physiological performance of mouth wrestling.

It is not surprising that winners are assessing relative size in fights. Enquist et al. (1990) used *N. anomala* to show that weight asymmetries not only helped predict which fish was going to win the fight, but also that the degree of asymmetry was correlated with the length of specific stages. Other researchers have also demonstrated animals' use of relative body size as an indication of RHP (Barlow et al. 1986 in Midas cichlids, *Cichlasoma citrinellum*; Dowds and Elwood 1985 in hermit crabs, *Pagurus longicarpus*; Robertson 1986 in the Australian frog, *Uperoleia rugosa*; Keeley and Grant 1993 in convict cichlids, *C. nigrofasciatum*; Hack 1997 in crickets, *Acheta domesticus*). Unlike these studies, the present study shows that most of this assessment takes place in a specific phase of the fight. While assessment of relative body size may continue at later phases, most differences were determined within the tail-beating phase.

Body size is certainly not the only indicator of RHP that animals are assessing in fights (Garland et al., 1990; Robakiewicz, 1992; Cardwell et al., 1996). Robson and Miles (2000) size-matched lizards and found that dominant individuals had higher staminas and higher sprint speeds. The fact that animals assess qualities other than body size should not be surprising since body size alone is a relatively poor indicator of reproductive success (reviewed by Ellis, 1995). Age (Wolf et al., 2000), hormone levels (Jenson et al., 2001), and performance (Jayne and Bennett, 1990) have all been shown to affect individual reproductive success in a variety of species.

It is also possible that performance may affect fitness indirectly since faster and/or stronger individuals may be better at avoiding predators.

Throughout the fights, there were three distinct phases: 1. lateral display, 2. tail beating, and 3. mouth wrestling. Although not all fights contained tail beating and mouth wrestling, the order of phases was always the same. Bites were not considered a discrete phase since they were generally directed towards the mouths of opponents and were therefore assumed to be failed attempts at mouth wrestling. Mouth wrestling could not proceed unless both contestants were ready to escalate. The order of behaviors in the fights seemed to follow the sequential assessment model (Enquist et al., 1990), which suggests that it is to an animal's benefit to gain as much information about an opponent as possible without expending energy or risking injury. If differences are not found, then the opponents should escalate to higher risk behaviors that more directly test fighting ability. Throughout the cichlid fights, the behaviors became more and more costly both energetically and through the risk of injury. There was very little cost associated with lateral display. However, since no physical contact occurred throughout this stage, it also revealed minimal information about fighting ability. Direct physical contact also rarely occurred during tail beating. For this reason, there was very little risk of injury associated with the phase. There were, however, small energetic costs associated with tail beating that made it a more costly phase than lateral display. Mouth wrestling, the most escalated stage of fights, was by far the most costly. Opponents were in contact with each other throughout the entire phase and were continually exerting themselves.

Of the fights that ended in lateral display there was no difference between winners and losers for any of the four measured RHP components (Table 3). Part of this may be due to small sample size since only 11 out of 69 fights ended in lateral display. However, after watching several fights, I believe the small sample size is an artifact of the way in which the fights progress. Most of the fights that ended in lateral display did so in the first minute of fighting. For these fights that ended relatively quickly, it appears as though the fish that quit simply was not willing to fight on the day of the bout. In these fights, the first fish to display was almost always the winner of the bout. By convention, I assumed the fight started as soon as one fish started displaying. In cases where the loser decided to quit without actually displaying, it is likely that no actual assessment of size occurred. There may, however, have been some assessment of relative motivation, which I did not measure. In these cases, it seems as though the loser of the fight was simply less motivated to fight.

Most of the fights for which size was accurately assessed went on to some amount of tail beating. This seems reasonable since tail beating reveals much more about an opponent's fighting ability than lateral display with only a small increase in cost (Payne and Pagel, 1996). Therefore, if opponents truly want to get a good estimate of body size, they have very little to lose by taking part in tail beating.

Fish did not appear to be assessing stamina in the study. Although fights that escalate to mouth wrestling were highly intense throughout this phase, fights were relatively short and therefore did not give contestants much of a chance to assess stamina. Also, due to the natural history of the fish, determining each fish's inherent stamina was a nontrivial task. *N. anomala* are native to slow moving streams and rivers of South and Central America. Since they are not accustomed to swimming in fast moving water for long periods of time, they are not very willing to do so in a swim tank environment. Some fish simply were not willing to swim at high speeds and slower speeds had to be used. It did not appear as though these fish were unable to swim at high speeds or were physically exhausted. Others consistently swam from one day to the next and could swim for hours if tested at lower speeds. Since some fish were more reluctant to swim at high speeds than, these reluctant fish had to be tested at lower speeds. This stratification of the data made comparison of various staminas difficult. Since swimming against fast currents for long periods is something these fish rarely do, it seems unlikely that this sort of stamina measurement is a good estimator of RHP.

Similar problems were avoided in the "maximum swim speed" measurements due to changes in protocol. Since all fish were willing to swim at slow speeds, for these experiments the swim tank was started at speeds equivalent to 3 body lengths per second. All fish were willing to swim at this speed and seemed to be willing to continue swimming as long as the water speed was increased slowly. Maximum swim speeds seemed to be a much more consistent measure from day to day than did stamina measurement. Maximum swim speed seemed to be a much more reliable predictor of swimming ability and a more reasonable indicator of fighting ability than did stamina.

I measured each fish's aggression as a latency to display to an aggressive conspecific. According to the measured aggression scores, winners were not more aggressive than losers. I found no significance whether fights were categorized by the stage in which they end or not. In measuring latency to display, I was hoping to quantify the inherent aggressive tendency of each fish. This latency to display measure may have not been the best choice for accomplishing this task. Since level of aggression is something that varies tremendously from one day to the next and with varying environmental conditions, it may have been better to measure aggression on the day of the fight. I chose not to do this because I felt as though taking a latency to display measurement just prior to a fight might affect the fish's motivation, and have influence on the outcome of the fight itself.

Another way to get around this problem of measuring aggression may be to measure it in the fight itself. Aggressive tendencies can be demonstrated through the latency to perform a behavior, the rate at which a behavior is repeated, or even the intensity of the behavior. In the cichlid fights, I found significance in the number of time winners and losers performed bites. In fights in which bites occurred, winners bit more often than losers. This suggests that fish may be assessing aggression at some point in the fights.

In summary, I have shown that *N. anomala* are using an escalating series of behaviors to systematically assess various components of RHP. Furthermore, I have shown that through these contests, opponents are primarily basing whether or not to continue fighting on information gained in the phase in which they are involved. One of the most important aspects of this research is the fact that opponents are indeed assessing various components of RHP. Opponents use early, low risk phases of fights to assess general size and escalated phases to assess more direct aspects of fighting ability such as strength and speed. Through this work I showed that although size is an important aspect of RHP, performance characteristics can also have a significant effect on the outcome.

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Appendix A – Fish Weights

Fish weights were monitored on a weekly basis throughout the study. Fish were also weighed on the day of experimentation for use in the analysis.

Fish ID	Weight(g)								
	4-Feb	**12-Feb**	**26-Feb**	**11-Mar**	**19-Mar**	**24-Mar**	**2-Apr**	**9-Apr**	**23-Apr**
1	0.86	0.93	0.95	0.97	0.98	0.94	0.96	0.96	0.95
2	0.89	1.00	1.17	1.24	1.24	1.25	1.28	1.26	1.36
3	1.04	1.11	1.06	1.08	1.04	1.02	1.04	1.05	1.02
4	0.72	0.88	0.93	1.07	1.09	1.17	1.22	1.29	1.40
6	1.11	1.16	1.12	1.12	1.09	1.08	1.09	1.07	1.06
8	0.89	0.97	0.97	1.03	0.92	1.00	0.99	0.97	0.95
9	0.76	0.86	0.90	0.95	0.94	0.92	0.94	0.92	0.93
11	1.06	1.30	1.32	1.48	1.48	1.51	1.55	1.61	1.63
12	1.46	1.78	1.86	2.09	2.09	2.23	2.27	2.36	2.33
13	1.13	1.33	1.44	1.62	1.55	1.59	1.58	1.55	1.56
14	0.90	0.94	1.01	1.07	1.10	1.07	1.07	1.13	1.15
15	0.75	0.78	0.82	0.84	0.81	0.85	0.83	0.82	0.81
16	0.71	0.78	0.82	0.90	0.83	0.86	0.89	0.91	0.92
20	1.03	1.13	1.19	1.17	1.19	1.16	1.18	1.18	1.22
21	1.43	1.22	1.34	1.52	1.55	1.55	1.61	1.65	1.73
22	1.43	1.56	1.74	1.95	1.96	1.97	2.01	1.97	1.92
23	1.51	1.66	1.71	1.88	1.81	1.79	1.78	1.80	1.79
24	0.94	0.96	1.00	1.03	0.99	1.02	1.05	1.11	1.04
25	1.05	1.23	1.35	1.57	1.62	1.66	1.72	1.67	1.72
26	1.03	1.15	1.12	1.33	1.30	1.31	1.30	1.33	1.39
28	1.13	1.28	1.36	1.41	1.39	1.39	1.38	1.40	1.38
29	0.64	0.74	0.77	0.81	0.82	0.80	0.82	0.81	0.79
30	1.10	1.23	1.38	1.40	1.44	1.41	1.42	1.46	1.43
31	1.07	1.27	1.40	1.61	1.68	1.81	1.81	1.95	2.10
32	1.42	1.65	1.75	2.05	2.15	2.23	2.20	2.17	2.16
33	0.87	0.98	1.03	1.14	1.15	1.19	1.25	1.30	1.41
34	0.85	0.99	1.02	1.04	1.01	1.00	1.01	0.98	0.99
36	0.78	0.79	0.84	0.93	0.88	0.89	0.85	0.88	0.83
37	1.12	1.19	1.26	1.33	1.31	1.33	1.31	1.33	1.34
38	0.91	0.97	0.97	0.97	0.95	0.94	0.96	0.98	0.88
39	0.95	1.04	1.07	1.08	1.03	1.03	1.04	1.02	1.02
40	1.18	1.32	1.35	1.35	1.30	1.28	1.27	1.25	1.23
41	1.11	1.28	1.43	1.54	1.52	1.55	1.53	1.50	1.50
42	0.97	1.07	1.08	1.09	1.05	1.04	1.03	0.98	1.01
43	0.71	0.75	0.79	0.86	0.85	0.89	0.91	0.90	0.88
44	0.72	0.92	1.06	1.32	1.39	1.51	1.59	1.73	1.78
45	0.71	0.93	1.02	1.18	1.27	1.36	1.34	1.24	1.04
46	1.02	1.16	1.20	1.17	1.13	1.15	1.13	1.14	1.09
47	1.47	1.69	1.78	1.99	1.92	1.93	1.94	1.93	1.85
48	1.24	1.51	1.58	1.90	1.90	2.00	1.95	1.96	1.91
50	1.02	1.11	1.14	1.26	1.12	1.19	1.16	1.18	1.12
51	1.15	1.34	1.40	1.53	1.48	1.52	1.58	1.65	1.70
52	0.87	0.92	0.94	1.00	1.03	1.08	1.07	1.08	1.08
53	0.75	0.84	0.85	0.89	0.86	0.89	0.87	0.91	0.88
54	1.24	1.49	1.53	1.61	1.55	1.55	1.54	1.56	1.49

Appendix B – Replicate Aggression Measurements

Latency to display to a conspecific is given in seconds to approach and perform a lateral display. Aggression scores are ln-transforming values of the averages of the two fastest replicates.

	Time to Display (s)				
Fish ID	**Day 1**	**Day 2**	**Day 3**	**Average of 2 fastest replicates**	**LN(ave)**
1	105	24	28	26	3.26
2	57	22	103	39.5	3.68
3	31	600	600	315.5	5.75
4	16	9	22	12.5	2.53
6	424	310	81	221.5	5.40
8	51	20	28	24	3.18
9	106	134	230	120	4.79
11	25	600	251	138	4.93
12	49	33	4	18.5	2.92
13	66	105	348	85.5	4.45
14	36	29	235	32.5	3.48
15	16	55	116	35.5	3.57
16	97	45	119	71	4.26
20	42	16	40	26	3.26
21	48	97	213	72.5	4.28
22	147	177	282	162	5.09
23	28	550	21	24.5	3.20
24	47	43	41	42	3.74
25	18	6	10	8	2.08
26	18	3	46	10.5	2.35
28	23	16	26	19.5	2.97
29	49	9	10	9.5	2.25
30	97	22	21	21.5	3.07
31	26	45	40	33	3.50
32	17	11	25	14	2.64
33	40	9	8	8.5	2.14
34	23	32	7	15	2.71
36	36	64	62	49	3.89
37	15	14	40	14.5	2.67
38	46	600	75	60.5	4.10
39	36	15	50	25.5	3.24
40	36	134	111	73.5	4.30
41	94	201	600	147.5	4.99
42	28	35	52	31.5	3.45
43	134	118	24	71	4.26
44	42	31	29	30	3.40
45	19	13	5	9	2.20
46	24	12	30	29.5	3.38
47	24	6	128	15	2.71
48	29	18	17	17.5	2.86
50	86	23	36	29.5	3.38
51	33	38	600	35.5	3.57
52	600	600	24	312	5.74
53	213	600	600	406.5	6.01
54	16	32	26	21	3.04

Appendix C – Replicate Stamina Measurements

Stamina is measurement in seconds to exhaustion. Speed at which each fish was tested is based on individual swimming ability and standard length (measured from the front of the fish to the caudal peduncle). The highest time to exhaustion is used as the stamina score for each fish.

	Speed tested		Time to exhuastion (s)		
Fish ID	**(body lengths/s)**	**(cm/s)**	**Day 1**	**Day 2**	**Day 3**
1	4	12	388	1324	1207
2	5	18	43	81	26
3	5	16	218	232	408
4	6	18	1800	1800	1800
6	4	12	26	21	28
8	5	15	67	90	48
9	5	14	66	84	1114
11	5	19	38	46	29
12	5	18	56	69	235
13	4	14	90	56	59
14	5	15	229	246	265
15	4	12	96	223	619
16	5	14	338	1800	70
20	4	12	92	1800	995
21	4	14	66	1800	1800
22	5	19	189	38	169
23	4	15	232	153	75
24	5	15	149	1800	158
25	5	18	54	72	129
26	6	20	32	27	35
28	5	17	69	36	61
29	4	12	25	1800	1800
30	5	16	129	90	58
31	5	17	140	102	141
32	5	16	24	25	18
33	6	18	251	148	127
34	4	13	21	1800	1800
36	6	17	74	249	1800
37	6	20	148	240	224
38	6	18	121	50	32
39	6	18	93	44	50
40	4	12	41	62	47
41	5	17	60	64	55
42	5	15	126	161	193
43	6	18	52	28	177
44	4	14	32	183	532
45	5	17	453	39	142
46	4	13	26	54	50
47	5	19	1800	430	225
48	4	14	118	74	53
50	4	12	1800	63	37
51	4	13	1800	1800	90
52	5	15	42	25	24
53	6	19	23	72	55
54	6	22	91	97	63

Appendix D – Replicate Maximum Swim Speed Measurements

Maximum swim speeds are measured in cm/s. An average of the three replicates is used as the aggression score for each fish.

	Max Swim Speed (cm/s)			
Fish ID	**Day 1**	**Day 2**	**Day 3**	**average**
1	28.75	25.89	31.53	32.55
2	30.40	23.65	23.65	26.68
3	16.05	21.73	26.40	22.93
4	31.53	31.53	31.53	35.35
6	20.31	23.65	27.85	25.99
8	16.05	20.31	25.36	21.78
9	15.04	18.74	16.05	16.59
11	30.40	22.40	24.24	26.60
12	28.31	30.40	29.18	31.90
13	19.54	21.03	19.54	20.19
14	29.18	25.89	31.53	32.69
15	31.16	21.03	19.54	24.06
16	30.40	31.53	31.53	34.98
20	31.16	21.03	28.75	29.40
21	21.03	28.75	21.73	24.26
22	21.03	17.89	26.90	23.64
23	17.89	30.40	30.40	29.43
24	29.59	19.54	28.75	28.38
25	17.89	23.65	24.24	22.85
26	19.54	23.65	28.75	26.40
28	30.40	18.74	22.40	24.38
29	31.16	28.31	30.40	33.16
30	16.05	15.04	30.00	23.36
31	31.53	20.31	22.40	25.28
32	21.73	17.89	18.74	19.54
33	26.90	28.75	29.18	30.88
34	21.73	19.54	18.74	20.09
36	17.00	15.04	16.05	16.01
37	31.16	23.65	30.78	31.94
38	20.31	16.05	21.73	19.78
39	20.31	19.54	15.04	18.28
40	17.89	23.04	21.73	21.31
41	17.89	19.54	31.53	26.81
42	19.54	17.89	21.73	20.14
43	26.40	23.65	30.78	30.35
44	23.04	17.89	20.31	20.64
45	17.89	20.31	16.05	18.07
46	30.00	17.89	17.00	21.63
47	30.40	30.78	21.03	27.73
48	19.54	17.89	16.05	17.81
50	16.05	17.00	15.04	16.01
51	31.53	29.59	21.73	28.04
52	31.16	18.74	31.16	30.63
53	27.38	24.24	17.00	22.87
54	26.90	20.31	18.74	22.07

Appendix E – Staged Aggressive Encounters

The raw data from 69 fights are presented below. Winners are fish that remained dominant after the fight. When a fight is over, losers relax their fins, and assume non-aggressive body coloration.

	Winner	Loser				# of bites		Time Spent (s)			
Fight #	(Fish ID)	(Fish ID)	Ending phase[1]	First to display[2]	First to tail beat[2]	Winner	Loser	Displaying	Tail beating	Mouth wrestling	Total
1	4	3	3	L	W	5	1	16	78	226	320
2	13	31	3	L	W	3	6	87	155	51	293
3	38	1	2	L	W	0	0	8	55	0	63
4	50	2	2	W	L	0	0	13	92	0	105
5	42	39	3	W	W	3	0	58	109	184	351
6	15	43	3	W	L	6	2	8	44	270	322
7	16	53	3	L	L	2	6	31	1330	421	1782
8	36	9	3	W	L	4	1	13	36	227	276
9	44	37	2	W	W	1	0	180	281	0	461
10	40	26	2	W	L	1	4	39	149	0	188
11	21	11	2	L	L	0	0	7	23	0	30
12	51	41	3	W	W	3	1	33	86	633	752
13	23	48	3	L	L	3	5	19	49	3	71
14	40	45	2	W	W	0	0	37	79	0	116
15	32	12	2	W	W	2	0	16	84	0	100
16	46	33	2	L	L	2	0	18	8	0	26
17	6	14	3	W	L	0	0	48	45	46	139
18	29	16	1	W	0	0	0	5	0	0	5
19	53	43	2	L	W	0	0	25	588	0	613
20	52	39	2	L	W	0	0	23	13	0	36
21	3	42	3	L	L	2	2	106	46	9	161
22	37	26	2	L	W	0	0	61	9	0	70
23	11	51	3	L	W	1	3	15	27	863	905
24	23	31	3	L	W	0	0	83	101	38	222
25	4	20	2	W	0	3	2	14	66	0	80
26	22	48	3	L	W	1	2	35	202	186	423
27	2	40	3	W	W	0	0	498	284	758	1540
28	50	33	2	L	L	4	2	66	34	0	100
29	21	41	3	W	W	2	1	24	45	25	94
30	28	45	3	L	W	4	5	30	135	79	244
31	52	6	3	L	W	1	1	21	242	398	661
32	43	36	2	L	L	1	2	133	100	0	233
33	11	44	3	L	L	3	2	21	145	101	267
34	1	9	3	W	L	4	1	24	68	23	115
35	2	25	3	W	L	4	2	8	9	21	38

1. Display is referred to as phase "1", tail beating is phase "2", and mouth wrestling is stage "3".

2. Winners are referred to as "W" and losers are referred to as "L". A "0" value is reported if fights did not escate to the stage or if opponents first performed the behavior at the same time.

Fight #	Winner (Fish ID)	Loser (Fish ID)	Ending Stage[1]	First to display[2]	First to tail beat[2]	# of bites[3]		Time Spent (s)			
						Winner	Loser	Displaying	Tail beating	Mouth wrestling	Total
36	41	8	2	W	W	0	0	21	65	0	86
37	12	31	3	L	L	2	1	291	136	1733	2160
38	22	42	1	L	0	0	0	73	0	0	73
39	14	3	2	W	L	0	0	15	76	0	91
40	26	34	1	W	0	0	0	87	0	0	87
41	3	52	2	W	W	0	0	10	27	0	37
42	33	25	2	W	W	2	0	28	11	0	39
43	45	29	2	W	L	0	0	60	38	0	98
44	11	41	1	L	0	0	0	3	0	0	3
45	46	21	2	L	L	2	0	15	503	0	518
46	24	2	2	W	L	2	1	15	16	0	31
47	26	4	1	L	0	2	0	45	0	0	45
48	30	8	2	L	W	3	1	24	46	0	70
49	47	37	3	L	0	1	0	69	379	9	457
50	22	41	2	L	W	0	0	16	35	0	51
51	13	40	2	L	W	0	0	17	102	0	119
52	31	15	2	L	W	0	0	15	4	0	19
53	39	1	1	L	0	0	0	7	0	0	7
54	20	14	3	L	L	1	0	7	205	96	308
55	16	38	3	W	L	2	2	33	55	70	158
56	23	44	3	W	W	1	1	19	122	642	783
57	46	50	3	L	W	0	0	24	31	326	381
58	33	26	1	L	0	0	0	99	0	0	99
59	52	24	2	W	W	0	0	51	8	0	59
60	4	37	1	W	0	0	0	33	0	0	33
61	11	23	1	W	0	0	0	103	0	0	103
62	9	41	1	L	0	2	0	22	0	0	22
63	53	15	2	W	W	0	0	22	29	0	51
64	2	20	3	W	L	0	1	49	18	8	75
65	3	30	3	W	L	0	1	13	14	22	49
66	47	46	2	L	L	0	0	25	37	0	62
67	44	8	1	L	0	0	0	4	0	0	4
68	31	4	2	W	W	0	0	24	12	0	36
69	51	1	3	L	L	1	2	21	69	48	138

1. Display is referred to as phase "1", tail beating is phase "2", and mouth wrestling is stage "3".
2. Winners are referred to as "W" and losers are referred to as "L". A "0" value is reported if fights did not escate to the stage or if opponents first performed the behavior at the same time.