The Effects of Size Differential on Aggression in Female Convict Cichlids (Archocentrus nigrofasciatus)

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Abstract

Convict cichlids are highly aggressive tropical fish, exhibiting complex behaviors and adaptations. Studies suggest that environmental conditions, such as resource availability, individual development, trait variation, and activity of other individuals, affect these factors. Examining aggressive behavior in laboratory-raised females under different pairing situations, the researcher hypothesized that an individual paired with an equally-sized individual would display more aggression than the same individual paired with a smaller opponent. Aggression was measured by scoring attack behavior, namely the number of bites, number of chases, and chase lengths. Individuals in the equally-sized treatment exhibited more and longer chases than those placed with an unequally-sized opponent. This study is beneficial in leading to further understanding of the field of behavioral ecology of fishes. Analyzing ways in which fish respond to different situations at an individual level can inform us about ecological and evolutionary factors, such as survival and reproduction, at higher levels of organization.

Environmental factors including temperature, chemicals/nutrients in the environment, and resource availability can have drastic effects on animal behavior. The characteristics and behavior of other animals within the same population may also have an effect on the behavioral ecology of organisms. An apparent behavior that is affected by these factors is aggression, which is defined as "an animal's tendency to act with a goal of protecting its individual fitness and reproduction efficiency" (Brown 1964, 160). In other words, any form of agonistic behavior used to increase an organism's chance of survival or attractiveness is considered aggressive behavior. Individuals may exhibit aggressive behavior when competing for resources or mates, which allows them to live and pass on their genes to offspring in the most effective way possible. The evolution of traits and strategies that allow organisms to better compete are favored by natural selection (Dingemanse and Wolf 2011). The traditional theory of aggression and other animal behavior is that flexibility in behavior is centered on an adaptive mean, the most favorable level of a certain behavior, with extreme levels acting as outliers (Conrad et al. 2011). However, a new theory is beginning to emerge as recent studies have shown that differences in aggression and other behaviors are organized at the individual level. Each animal

can display various levels of behavior based on environmental factors, variation in traits, temperament, and specific situations.

Cichlids are popular fish used in behavioral studies due to their aggressive nature and extensive parental investment in offspring (Barlow 2000). They are a model subject in many behavioral studies because many species are easily accessible and maintained (Barley and Coleman 2010). The convict cichlid (*Archocentrus nigrofasciatus*) is perhaps the most commonly studied New World cichlid (Galvani and Coleman 1998). Due to their active and bold nature, convicts have become a widely studied species as researchers examine the function and ecological significance of their complex behavior. Various studies have explored the different factors that influence aggressive behavior by convict cichlids (e.g., Barley and Coleman 2010).

Barley and Coleman (2010) found that a dense habitat structure decreases levels of aggression in this species. The researchers paired female convict cichlids in aquaria and compared attack frequencies under different amounts of habitat structure by manipulating the number of plants and ceramic pots present. Their study suggests that with more habitat structure, there is less competition over resources due to a decrease in the chance of encounters and the increase in territory; this results in less aggression. Similarly, studies have found that food abundance and dispersion of resources can also affect aggression levels of convict cichlids (Grant et al. 2000; Noel, Grant, and Carrigan 2005). Noel, Grant, and Carrigan (2005) manipulated the competitor-to-resource ratio in social groups of fish, and found that aggressive behavior was significantly altered when food abundance was decreased. Grant et al. (2000) found that fish changed their feeding behavior when food dispersal patterns were manipulated, suggesting that fish adjust their behavior under different environmental conditions.

Characteristics of individuals, such as size, are also likely to play a role in aggression levels. Leiser, Gagliardi, and Itzkowitz (2004) examined the differences in aggression in small and large size-matched pairs of convict cichlids (i.e., a small fish matched with a small fish, or a large fish matched with a large fish), but found that aggression levels were similar in both groups. They found that large and small fish display similar behavior patterns in contests, yet larger male fish tend to escalate to more risky behavior sooner than smaller males. However, few research studies have investigated the importance of size asymmetry between opponents in pair situations.

The current research evaluates the impacts of size differential on aggression levels in pairs of convict cichlids. The researcher hypothesized that contests between individuals of obviously different size are likely to be resolved more rapidly and with less aggression because the outcome is more obvious to the participants, i.e., the larger one would likely win should the contest escalate to physical encounters. However, the outcome is less obvious when contestants are closer in size; therefore, we are likely to witness longer and more intense aggression to determine the outcome. This study aims to test this hypothesis to determine if fish in equally-sized pairings exhibit more aggression than fish in pairs where the individuals differ substantially in size.

Rationale

This study will expand our knowledge about the degree to which factors like size asymmetry can affect aggression in animal contests. Recent studies have found that environmental factors such as resource abundance, temperature, and body size are associated with aggression levels in fish. However, determining whether the magnitude of size differences between two individuals affects levels of aggression will tell us more about the competition in the forms of contests and fighting present in convict cichlids and also behavioral variation happening at the individual level. In addition, studying behavior is important in determining ecological and evolutionary aspects of fish behavior and how variation in aggression can alter their ability to perform in certain situations (Conrad et al. 2011).

This research evaluates aggression patterns in aquarium-raised fish, which is a common technique used in cichlid research because controlling conditions and assessing behavior in the wild is challenging due to confounding factors such as the presence of predators, disturbance, and other influences. However, it is equally as important to gather information on the behavior of wild fish in other studies to compare and contrast behavior of domestic and wild populations of fish.

Literature Review

Animal behavior has been of great interest in the scientific field, and becoming familiar with the behavioral ecology of certain species or populations of animals can give us insight into different conservation techniques and what influence certain environmental factors are having on animals (Bell 2007). Fish are considered model subjects for research in behavioral ecology because different studies have demonstrated consistent behavioral associations across different populations and taxa of fish (Conrad et al. 2011). For example, cichlid behavior has been studied extensively in the last decade, and results have frequently demonstrated the complexity of aggressive behavior shown by this group of fish. By developing a clear idea of which biotic (living organisms) and abiotic (nonliving) factors are affecting agonistic behavior in different fish species, researchers can determine which strategies are most suitable for domesticated fish populations, and those being released back into the wild (Carere and Eens 2005). Aggression is a behavior that requires individuals to act in ways that result in substantial energy costs, physiological depletion, and altered overall fitness (Briffa and Sneddon 2007; Copeland et al. 2011). Other than applications for

fisheries management, research on fish behavior gives us insight into social and evolutionary dynamics by investigating animal conflict between individuals, and these findings may be applied to any population of animals (Conrad et al. 2011).

Contests and Fighting

Current literature in behavioral ecology shows evidence that animal conflict and aggression are universal issues impacting humans and other populations; research on this topic has shown that agonistic behavior influences, and has implications for, both human and animal social dynamics (Filby et al. 2010). Behavior can affect other individuals in an animal's population as well as the community dynamics of an ecosystem in the form of intraspecific (within the same species) and interspecific (between species) competition. An example of aggressive behavior common across many species comes in the form of contest competition, in which animals directly compete for resources to increase their chance of survival by gaining certain payoffs (Davies, Krebs, and West 2012). Contests involve injurious fighting and other types of direct physical aggression and communication (Briffa and Sneddon 2007). These conflicts are usually over competition for territory, mates, and other resources (Chatterjee, Reiter, and Nowak 2012; Reddon et al. 2011).

Evolutionary Game Theory

A prominent theory that suggests different patterns or rules present in animal conflicts is known as Evolutionary Game Theory, which was developed by Maynard Smith in 1982 (Davies, Krebs, and West 2012). Several explanations and models were used, involving strategies for fighting and contests, including the 'Hawk-Dove model', the 'War of Attrition model', and the organisms' ability to use 'evolutionarily stable strategies' and assess the 'resource holding potential' of themselves and others in the population (147). Game theory suggests that instead of using models of 'optimal behavior' (where organisms behave in a way that results in the greatest chance of survival) to explain animal conflict, the theory reveals that organisms should adjust their behavior depending on what other organisms in the population are doing (Davies, Krebs, and West 2012).

There are different factors that determine the types and intensity of behavior present in contests, such as the costs and benefits of the situation (Barley and Coleman 2010). Engaging in aggressive behavior may be difficult and costly due to the potential loss of time and energy for participating in other activities and the risk of injury or death (Briffa and Sneddon 2007). The intensity of fighting behavior also relies on the value of the desired resource because it influences the motivation of the individuals fighting for it. A factor that may influence the motivational state of opponents in a contest is 'prior residency'. Prior residency refers to one individual occupying a particular piece of territory before another, which is thought to affect both the outcome and intensity of a contest over that territory (Harwood et al. 2003).

Wazlavek and Figler (1989) investigated whether there is a residence advantage during contests between male and female convict cichlids. Sex was not controlled in this experiment because the researchers expected males and females to both display aggressive behaviors during resource contests. In this study, researchers expected a prior resident to display more aggression than an intruder because the prior resident may have a sense of ownership over the territory. Results showed a significant residence advantage during the contests, which supported their hypothesis. Researchers found that size asymmetry played a bigger role in contest success than prior residency. However, when convict cichlids were both larger and held prior residence, they displayed the most aggression and advantage over intruders. This group also exhibited less escalation of aggression, suggesting that the intensity of animal behavior can be affected by their motivational state; in this case, the fish with prior residence and a size advantage were more motivated to defend the resource over intruders.

Other studies have investigated costs and benefits of contests in relation to body size of opponents and found that other factors such as physiological constraints and metabolic costs may affect aggression and decisions made by fish (Briffa and Sneddon 2007; Copeland et al. 2011). Copeland et al. (2011) investigated the metabolic costs and behavior involved in fights between male convict cichlids. They found that size asymmetries affected contest outcomes between larger fish more so than smaller fish. Results also showed that larger fish engaged in more costly behavior. The researchers suggested that larger cichlids engaged in more risky behavior because they had more tolerance for metabolic and energy costs; meaning they were able to better withstand lactic acid accumulation and have more energy available to last longer in fights. These findings were consistent with evolutionary game theory because larger fish were able to successfully assess their chances of winning fights.

Beeching (1992) did a study on the attack behavior of oscar cichlids, examining differences in opponent body sizes, which were modeled by artificial fish (dummy models). The study used a game theory approach and expected that the intensity of attacks would be correlated to the size of opponents. Results concluded that the most aggression was displayed when opponents were around 75% of the subject's body size; this finding suggests that the fish are able to assess the relative body size of opponents and to adjust their behavior to reflect the most evolutionarily stable strategy. In this case, it was most reasonable to be more aggressive toward an opponent that was moderately smaller because that individual had a higher resource holding potential compared to a significantly smaller fish, and the risks of losing were low for the larger fish. This study demonstrates the importance of body size in contest competition, as well as a fish's capability of evaluating the fighting ability

of another fish through visual assessment. Because body size plays a large role in fighting ability, reproduction and resource defense, natural selection is expected to favor the evolution of strategies that allow a fish to visually measure the resource holding potential of its opponents (Beeching 1992).

The War of Attrition Model

A paradigm of the evolutionary game theory is the war of attrition model, also known as the 'waiting game', in which contest opponents wait for different periods of time to achieve a certain resource. Chatterjee, Reiter, and Nowak (2011) describe these waiting competitions as biological auctions because the desired resource is being auctioned to the animal with the most favorable wait time. The authors discuss the evolutionary dynamics and evolutionarily stable strategies present in biological auctions.

The Sequential Assessment Model

Another important pattern that plays into the characteristics of contests and fighting is the sequential assessment model, which was developed by Enquist and Leimar in the 1980s (Briffa and Sneddon 2007). Sequential assessment is the idea that "contests escalate through a series of phases of increasing intensity" (Briffa and Sneddon 2007, 629). These differing intensities of behavior represent the animal's tendency to evaluate the fighting ability and health of its opponent at different levels to avoid investing too much energy into unnecessary physical contact. Koops and Grant (1993) investigated whether assessment patterns were present in convict cichlids by staging contests between pairs of male fish that varied in weight ratio. As predicted by the sequential assessment model, individuals engaged in a consistent sequence of behavior (from visual displays to physical fighting). Contests lasted longer when the weight ratio between individuals was low (closer in size). As predicted by other researchers, the more symmetric the pairs were, the more intense were the contests (Eshel 2005).

Most studies on fish aggression and conflict focus on group dynamics or male combat, rather than individual behavior. This study aims to evaluate individual behavior patterns and strategies occurring in contests and fighting. Various theories have been developed regarding contest behavior and resource defense. This study aims to investigate the validity of those theories and look at the patterns of behavior in female convict cichlids.

Methods

The Study Organism

Convict cichlids are small tropical freshwater fish inhabiting lakes and streams ranging from Guatemala to Panama (Galvani and Coleman 1998). They are substrate-spawning fish, most frequently found in habitats with shelter in the form of rocks or sunken branches (Wisenden, Lanfranconi-Izawa, and Keenleyside 1995). The convict cichlid is considered a model organism in behavioral ecology because it is easily bred and maintained in the laboratory environment, with spawnings occurring every 4-6 weeks (Barley and Coleman 2010). Various studies of convict aggression have been performed in natural and laboratory environments because of their distinct fighting behavior (Galvani and Coleman 1998; Leiser, Gagliardi and Itzkowitz 2004; Reddon and Hurd 2009). By studying the complex traits that convicts cichlids display, researchers can develop a better understanding of animal conflict and territoriality.

Experimental Design

In the current study, female convict cichlids were placed in different pairing situations within aquaria, the difference being the relative body size of opponents. The goal was to observe aggressive behavior depending on the body size of opponents. The experiment was conducted in the main fish room of the Evolutionary Ecology of Fishes Laboratory at California State University, Sacramento. The room is subjected to 12:12 hours light: dark with minimal human traffic. All experiments were performed in 75-liter experimental aquaria (30cm x 30 cm x75 cm) containing a standard set up. Aquaria contained approximately 3 centimeters of grey gravel coating the bottom, a sponge filter, a ceramic flowerpot that was 8 cm in diameter (turned on its side to serve as shelter), an artificial *Hygrophila* plant, and a heater to keep temperatures at 26°C. Aquaria were cleaned using algae scrubbers and a gravel siphon before fish pairs were placed into them for each trial.

To avoid courtship and gender influences (see Methods section in Barley and Coleman 2010), the researcher only used females; females were differentiated from males because of the bright orange coloring on the belly region of females. The juvenile and adult females used were no smaller than 32 mm in total length (TL) and were chosen from three available stock aquaria, each containing 10-14 convicts of mixed genders. Fish in stock aquaria were fed daily on a mixture of Hikari micro wafers and TetraMin flake food. For each experimental trial, one female fish was selected and subjected to two treatments. This fish was referred to as the focal female. No two females were previously housed in the same aquarium before being paired together in an experimental aquarium.

Treatment 1

In the equally-sized treatment, the focal female was paired with an equally-sized individual in an aquarium. All females in the equally-sized treatment were less than 10% different from each other in total length (see Methods section in Leiser, Gagliardi, and Itzkowitz 2004). The two fish were added to separate Lustar plastic isolation baskets (16.5cm x 12cm x 13.3cm) at opposite ends of the same aquarium to acclimate for 24 hours. Fish were fed approximately 10 Hikari micro wafers per individual within a few minutes of being placed in the isolation baskets. The acclimation period allowed the fish to adjust to the new environment and undergo similar experiences before being released into the aquarium, and also mitigated the aggressive effects of prior winning or losing in fighting contests (Hsu, Earley, and Wolf 2006).

Just prior to release, the fish were fed again. Once released from the baskets, the fish underwent another 24 hour acclimation period of free swimming in the aquarium to encounter each other and establish their relationship before aggressive behavior was recorded. The researcher then sat 1.5m across from the aquarium to observe aggressive behavior for a 30-minute period. The behavior which was recorded included the number of bites and chases, as well as chase lengths, made by the focal female. Other behavior, such as lateral and frontal displays, was present, however, the researcher chose to record only biting and chasing because they were distinct. An action was considered to be a bite when a focal female touched her mouth to the body of her opponent. A chase was defined as occurring when the focal fish swam towards and came within 10cm of her opponent. The combined time duration of chases during the 30-minute trials were also recorded to account for variation in chase lengths. Once behavior was recorded, the fish pair was fed a final time.

Treatment 2

Immediately after recording behavior in the first treatment, the focal female was placed with a significantly smaller female in a different aquarium to acclimate for 24 hours in isolation baskets. The fish then underwent the same procedures as in treatment 1, with the difference being the size of her opponent, which was from 5-10 millimeters shorter in standard length.

Statistical Analysis

Ten trials consisting of a total of 30 females were recorded. Biting and chasing behavior data from treatment 1 (equally-sized pairs) and treatment 2 (unequally-sized pairs) were compared using paired student's t-tests. By comparing the three measures of aggression (number of bites, number of chases, and chase lengths) within the two treatments, the researcher determined if and to what degree body size was affecting female aggression.

Results

The experiment was repeated ten times, i.e., each of the ten focal females was paired with an equally-sized and an unequally-sized opponent. The total length (TL) of fish ranged from 32.0-74.0 millimeters, and weight ranged from 0.80-8.5 grams. Data were collected over a five-week period.

To test the degree to which individuals were willing to engage in aggressive activity, the researcher compared the frequency of bites, chases, and chase durations between the two treatments (equally-sized versus unequally-sized). The focal females spent more time and engaged in more aggressive activity when paired with a fish of equal size in comparison to an unequally-sized individual. There was a significant difference between focal female behavior in total number of chases between fish paired with equally-sized versus smaller-sized opponents (see Figure 1); the number of chases were higher when fish were equally sized (two-tailed paired t-test, $t=3.38, df=9, P<0.01$). Likewise, total chase times (see Figure 2) for the entire 30 minute periods were significantly higher in the equally-sized treatment (two-tailed paired t-test, $t=2.62, df=9, P<0.05$). There was no difference between the number of bites made by focal fish in the equally-sized versus unequally-sized treatments (see Figure 3). Average chase times also showed no difference between the two treatments (see Figure 4).

Figure 1

The number of chases made by the focal female during the 30-minute observation period

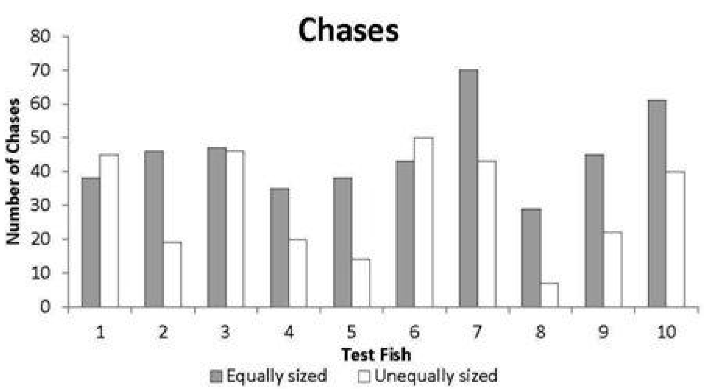


Figure 2

The total chase time by the focal female during the 30-minute observation period

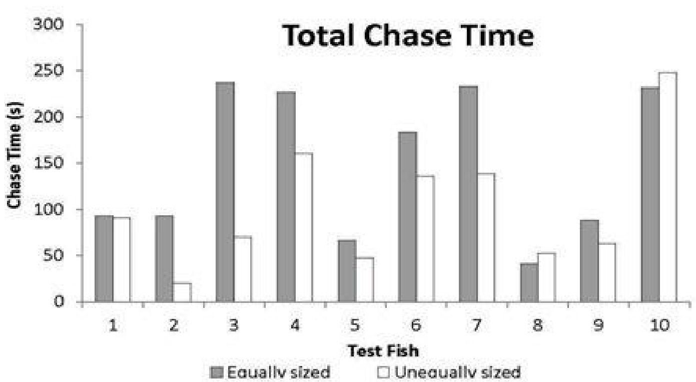


Figure 3

The total number of bites made by the focal female during the 30-minute observation period

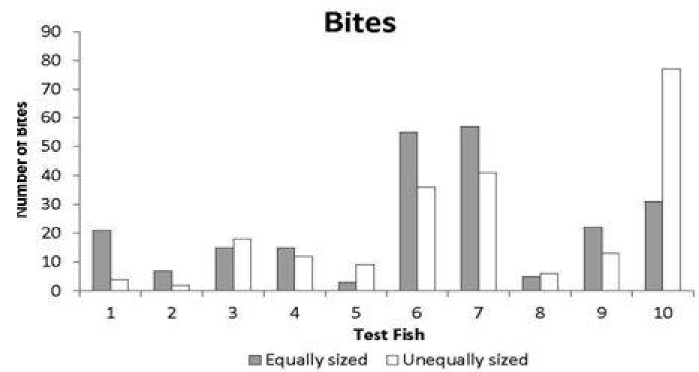
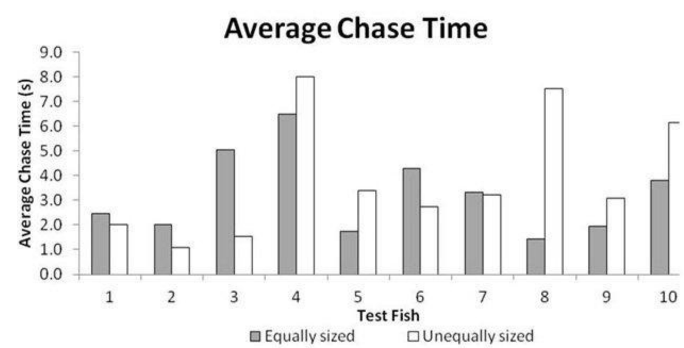


Figure 4

Average chase times by the focal female over the 30-minute observation period



Discussion

These results indicate that the level of body size asymmetry between two individuals plays a role in the amount of time and effort they are willing to exhibit in the form of aggression. Because individuals chased more and spent more time chasing when paired with equally-sized individuals compared with smaller individuals, this suggests that equally-sized individuals have similar relative fighting ability and therefore must engage in longer and more intense contests, than those which differ in size. In addition, individuals demonstrated assessment because they adjusted the intensity of their aggression depending on the size of their opponent. However, biting was not shown to increase when individuals were equally sized, and, in fact, did not change at all based on pairing situation. Therefore, biting may be considered an aggressive behavior that is very risky and is used sparingly during contests. Biting may also have been unclear to the researcher because chases usually ended in very sudden bites that were difficult to consistently monitor.

The main limitation of this study was the order of pairing of the two treatments: fish were always paired with an equally-sized fish before an unequally-sized fish, which biases the results (i.e., individuals may have been more aggressive during the first contest). The study was done in a laboratory environment, and future research in the natural habitat would be beneficial in comparing the differences in behavior of wild versus domesticated fish populations.

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