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Habitat structure directly affects aggression in convict cichlids *Archocentrus nigrofasciatus*

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Abstract Aggressive behavior can be an important factor in determining how animals use and divide space and resources. Previous studies have shown that aggression in fishes can be influenced by a variety of factors, including water temperature and resource levels. In this study, we tested if the amount of habitat structure in the environment affected aggression levels in female convict cichlids *Archocentrus nigrofasciatus*. We performed a laboratory experiment in which we placed female convict cichlids into an aquarium with low or high amounts of habitat structure and monitored the dominant female's behavior toward the subordinate female. Aggressive behavior in convict cichlids primarily consists of chases and bites. We found that the total time the dominant female spent chasing the subordinate female was greater when there was a low amount of habitat structure as compared to when there was a high amount of habitat structure. We also found that both the average duration of a chasing bout and the number of bites directed at the subordinate fish increased when there was a low amount of structure, but the number of chases did not. These results indicate that increased habitat structural complexity decreases aggressive behavior in convict cichlids [*Current Zoology* 56 (1): 52–56, 2010].

Key words Neotropical, Life-history, Female-female competition, Fish, Resource competition

Aggression in fishes can be the result of a variety of factors, including intrasexual selection, resource competition, and resource defense (Ratnasabapathi et al., 1992). The level of aggressive behavior that is displayed in response to these factors can vary as a result of the environmental conditions in a fish's habitat. This has been extensively studied in a variety of taxa, particularly cichlid fishes (Barlow et al., 1975; Barlow et al., 1986; Kim and Grant, 2006; Oldfield et al., 2006; Lehtonen and Lindstrom, 2008). Aggression levels in convict cichlids *Archocentrus nigrofasciatus* have also been shown to change in response to temperature, prior residence, conspecific density, risk of predation, and even time since last mating (Fitzgerald and Keenleyside, 1978; Cole et al., 1980; Ratnasabapathi et al., 1992; Wisenden and Sargent, 1997; Kim et al., 2004). Noel et al. (2005) found that aggression in juvenile convict cichlids changed significantly in response to an increase in competitor-to-resource ratio when food was the resource being contested.

Aggression levels in fish can be important to individuals and populations. Aggression can have profound impacts on how fish partition space. Larger, more aggressive fish utilize larger areas and consequently have access to more resources (e.g., Praw and Grant, 1999). Smaller, less aggressive fish have a harder time competing for resources, which can directly and indirectly affect an individual's ability to mate and successfully reproduce. The amount of energy a fish expends on aggression impacts the amount of time and energy it has available for other demands (Schoener, 1987). It can also be an important factor in reproduction and parental care in fishes such as convict cichlids. Previous studies of aggression have primarily focused on male-male interactions. For example, Leiser et al. (2004) examined contests between pairs of male convict cichlids of matched sizes and showed that size mattered, i.e., small males fought differently than did large males. Aggression among females is also important in some cichlids and plays a key part in nest site selection and possibly mate choice (Tobler, 2007). For example, Lehtonen and Lindstrom (2008) recently showed that convict cichlids in Lake Xiloá (Nicaragua) exhibit density-dependent reproduction such that they avoid breeding close to each other. Lehtonen and Lindstrom (2008) stress the importance of understanding the distribution and abundance of resources for breeding individuals. Furthermore, the importance of intrasexual aggression in both sexes in

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convict cichlids is highlighted by the fact that pair formation appears to occur prior to nest-site selection (Gumm and Itzkowitz, 2007) and that both individuals are subsequently involved in obtaining and maintaining the nest site (Alonzo et al., 2001).

Aggression may be affected by habitat structural complexity (Schoener, 1987). A complex habitat may reduce aggression for two reasons. First, complexity may reduce the frequency with which two individuals in a population encounter each other. This may reduce the total number of aggressive interactions that occur during a given period of time. Second, increased habitat complexity within the same total space may provide an increase in resources, e.g., an increase in hiding places. This could affect the level of aggressive behavior that is displayed during an encounter. These two factors may operate in concert or independently; however, the effect of habitat structural complexity has not been extensively studied in fishes. Kelley et al. (2006) found that increased habitat structural complexity decreased aggression level in the butterfly splitfin *Ameca splendens* (Family Goodeidae); however, this result only occurred when fish were kept at very high densities (0.26 fish/l).

The purpose of this study was to test the hypothesis that manipulating habitat structural complexity would alter aggression levels in convict cichlids. Our hypothesis is that an increase in the amount of habitat structure, i.e., an increase in habitat complexity, will lead to a decrease in aggressive behavior.

1 Materials and Methods

The convict cichlid is a small fish native to freshwaters of Central America from Guatemala, El Salvador, Nicaragua, Costa Rica, and Panama. This fish has been studied extensively in behavioral research because it is well-suited to captive maintenance, reproduction, and manipulation (Galvani and Coleman, 1998; Snekser and Itzkowitz, 2009) and has been studied in the field as well (Wisenden, 1995; Alonzo et al., 2001). We used a total of 30 laboratory-raised convict cichlids, and all experiments were performed at California State University, Sacramento. Fish from different aquaria that had not previously been housed together were divided into two large stock aquaria (60 × 60 × 30 cm^3 high). Each aquarium contained a total of 15 male and female convicts. Although males were present in these stock aquaria, only females were used in the structural treatment experiment in order to control for differences in aggression levels between the sexes (Cole et al., 1980; Coleman, 1993) and to avoid introducing courtship into the experiment.

Convict cichlids exhibit a great deal of aggressive behavior related to territoriality, resource defense, and parental investment (Breau and Grant, 2002; Grant et al., 2002). Aggression in convict cichlids manifests itself primarily in biting and chasing (bursts of increased swimming speed directed at other individuals), and aggression in cichlids is known to be strongly dependent on body size (Barlow, 1983). For each trial, one female fish was taken from each of the stock aquaria and placed into the experimental aquarium (76 × 30 × 30 cm^3 high). Females were selected such that one was slightly larger than the other. This eased the process of scoring aggression because it provided a predictable way of determining which female should be more aggressive (Barlow, 1983). All trials were run in the same 68-l experimental aquarium.

Fish were introduced into the aquarium containing one of two structural treatments. Structure was set up in the aquarium using plastic *Hygrophila* (30 cm tall) plants and clay flowerpots (10-cm diameter) with the bottoms knocked out, lying on their sides. Flowerpots are used by convict cichlids in aquaria as spawning sites and constitute a defendable resource. Plants provide visual protection from predators and competitors. The low-structure treatment consisted of one flowerpot and one plant. The high-structure treatment consisted of five flowerpots and twelve plants evenly distributed about the aquarium. We did not place a filter into the aquarium because we did not want to introduce additional structural effects. Instead, we placed a small air stone on one side of the aquarium to oxygenate the water, and we replaced half of the water between trials. The bottom of the aquarium was covered in a layer of fine aquarium gravel approximately 3 cm deep. An aquarium heater was also placed in the back corner of the aquarium to keep the water temperature at 26°C. The back and two sides of the aquaria were covered by white plastic to ensure that fish were not disturbed by activities outside the aquarium. The experimental aquarium was situated in a portion of the laboratory with little to no human traffic. A plastic cover placed over the top of the aquarium kept fish from jumping out.

Fish were given 24 h without the presence of humans to acclimate to the apparatus and to establish a dominance hierarchy. We then returned and monitored the behavior of the fish for a 30-min period. During this period, we recorded the number of chases, the duration of each chase, and the number of bites by the dominant fish. A chase was considered to have occurred if the dominant fish rapidly moved towards the subordinate fish and came within 10 cm. A bite was considered to have occurred if the dominant fish made contact with the body of the subordinate fish with its mouth. After the 30-min observation period, we removed the fish and changed the aquarium to the alternate structural treatment. We then placed the same pair of fish back into the aquarium and again gave them a 24-h acclimation period. We then returned and again scored the dominant fish's behavior as done previously. Both fish from each trial were then removed from the experimental aquarium, placed into a third stock aquarium, and never used again in the experiment. All observations occurred between 12:00 h to 17:00 h to control for temporal variation in the activity level of the fish.

The order of structural treatments was alternated to control for the effect of which treatment fish first encountered. These treatments were repeated for 10 pairs of fish. The larger, more aggressive fish that was used in each trial was also taken alternately from each of the stock aquaria to control for potential differences between the stock aquaria.

The data were analyzed using paired t-tests to compare the two treatments. To compare the effects of the two levels of habitat structure on aggression levels between treatments, we analyzed the total number of chases, the total time spent chasing, the average duration of each chase, and the number of bites in each treatment.

2 Results

The dominant (larger) fish was always the more aggressive of the two and spent substantial time and effort chasing the subordinate fish away from the flowerpot(s). We found that the total time the dominant female spent chasing was significantly greater in the low-structure treatment than in the high-structure treatment (paired t-test; $t = 3.48$, $df = 9$, $P < 0.01$; Fig. 1A). The average duration of an individual chase was significantly greater in low-structure treatments as well (paired t-test; $t = 7.19$, $df = 9$, $P < 0.001$, Fig. 1B), but the total number of chases during the observation periods was not significantly different between treatments (paired t-test; $t = 2.02$, $df = 9$, $P = 0.07$). We also found that the total number of bites by the dominant fish was significantly greater in the low-structure treatments (paired t-test; $t = 3.44$, $df = 9$, $P < 0.01$, Fig. 2).

The number of bites by the dominant fish correlated with the total chase time for both the low-structure (Pearson correlation; $r = 0.82$, $n = 10$, $P < 0.01$) and high-structure (Pearson correlation; $r = 0.71$, $n = 10$, $P < 0.05$) treatments. Similarly, the number of bites correlated with the number of chases for both the low-structure (Pearson correlation; $r = 0.68$, $n = 10$, $P < 0.01$) and high-structure (Pearson correlation; $r = 0.83$, $n = 10$, $P < 0.01$) treatments.

3 Discussion

These results indicate that increased habitat structural complexity decreases aggression levels in convict cichlids as we had predicted. The total time the dominant female spent chasing during the observation period was considerably greater in the low-structure habitat treatment, as was the average duration of individual chases. The number of bites by the aggressive fish correlated with both the total time spent chasing, and the number of chases and was also significantly higher in low-structure habitats. Bites can be important factors in aggressive behavior because they can result in serious injury to individual fish.

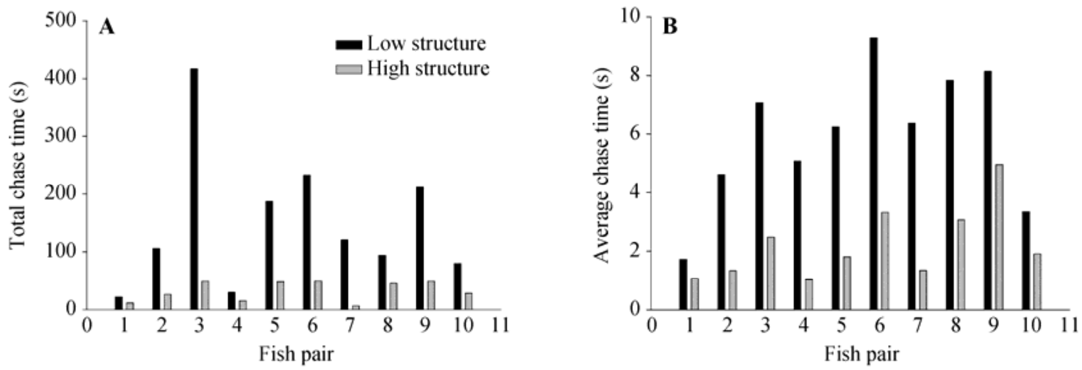

Fig. 1 The total time the dominant fish spent chasing the subordinate fish (A) and the average duration of chases by the dominant fish (B)

The dominant fish spent significantly more time chasing in the low-structure treatment than in the high-structure treatment.. The average chase duration was significantly longer in the low-structure treatment.

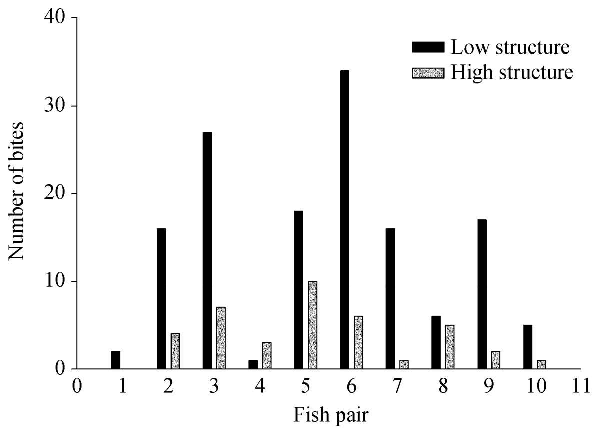

Fig. 2 The total number of bites by the dominant fish towards the subordinate fish
The dominant fish bit significantly more often in the low-structure treatment.

Although the average number of chases during the observation period tended to be greater in low-structure environments, this was not significant. However, we do not believe that the total number of chases during a time period is necessarily a good indicator of aggression level. The total number of chases is more a function of how often the two fish come into close contact during the observation period. This can be due to a variety of factors other than aggression levels, such as how active the fish are and how much time the subordinate fish spends hiding. If there are many chases, but they are short and not intense, they may be of little significance to the subordinate fish. Longer, more intense changes are much more energetically expensive, and also have a greater risk of injury.

How organisms use and divide space and resources is a complex issue and will likely be affected by many species-specific parameters. In this experiment, we attempted to distill the parameters down to a very simple, highly controlled system that has demonstrated the importance of the amount of structure on aggression. Our results are similar to those found in other aquatic systems. Laboratory studies such as ours allow researchers to manipulate the structural complexity directly. For example, Baird et al. (2006) studied aggression in the freshwater crayfish *Cherax destructor*. Using a laboratory setup with low- and high-structure treatments, they found that the number of agonistic interactions and the total time spent interacting was reduced in the high-structure habitat compared to the low-structure habitat. Basquill and Grant (1998) found that zebra danios *Danio rerio* showed less aggression in a complex habitat with simulated vegetation than in a simple habitat with no vegetation. Similarly, in their experiments on Atlantic salmon *Salmo salar*, Blanchet et al. (2006) argued that the complexity of riffle habitats in an artificial stream experiment resulted in reduced aggression compared to more homogeneous pool habitats. In un-manipulated field studies, we might expect a different manifestation of the same underlying phenomena, with organisms adjusting territory size to compensate for potentially higher levels of aggression. For example, Semmens et al. (2005) compared space use and behavior of the blue tang *Acanthurus coeruleus* on territories with low versus high structural complexity. They did not find differences in aggression within these territory types, but they did find that low-structure territories were four times larger than high-structure habitats, suggesting that occupants had resolved the aggression issue by increasing territory size; in fact, resource acquisition on both territory types was the same. Future field studies will be important for understanding how the results of our study are related to population structuring and behavior of individuals in nature.

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