Effects of group size, space, and 3-D structure on behavior in captive Midas cichlids

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Abstract. Animals may perform elevated levels of aggression in captivity, which may be a response to the modified costs and benefits of resource defense imposed by their artificial environments. The Midas cichlid (*Amphilophus citrinellus*) is a species whose patterns of aggression appear to fit predictions of resource defensibility. Two experiments were performed to test the effects of small-scale changes in group size, available space, and habitat complexity on aggression to determine if juvenile Midas cichlids modify behavior under different conditions of defensibility. Proportions of time spent in aggression were not associated with group size or available space, but submissive behavior performed by subordinates and the amounts of body damage they received were. Aggression was lower in the presence of 3-D structure. Behavior in the experiments was then compared to that observed in a large zoo exhibit (large group size) and in nature (large available space) to investigate the effects of large-scale differences in defensibility. Aggression was highest under the more defensible, experimental conditions. Midas cichlids increased aggression under defensible conditions, but were unable to maximize net benefits by adjusting aggression according to fine-scale changes in defensibility in artificially small group sizes and enclosures, which resulted in aberrantly detrimental effects on subordinates. Captive aggression in the absence of food or mating motivation suggests that space was defended as a resource, but it may result as a default due to restrictive artificial conditions that do not provide opportunities for alternative activities. Regardless, it has serious animal welfare implications. Some alternative housing tactics that do not promote aggression may nevertheless be suboptimal as they restrict behavioral diversity.

INTRODUCTION

Captive fishes are known to exhibit elevated levels of aggression [e.g. Okuno 1963, Buchanan 1971], which may be due to artificial ecological conditions that promote resource defense. Resources that are commonly guarded include food, mates, and shelter. Costs of aggressive defense might include injury, expended energy, vulnerability to predators, and time not spent exploiting the resource.

A captive environment may be more defensible than a natural environment due to decreased number of competitors and decreased amount of available space. Against large numbers of competitors the costs required to defend a resource may exceed its benefits [reviewed by Grant 1993]. A small amount of available space will encourage resource defense because less swimming will be required to deliver attacks [Schoener 1983]. Maximum aggression is expected at intermediate densities. 3-D structure may serve as territory boundaries or block visual contact and result in fewer opportunities for aggression [Breau and Grant 2002].

The Midas cichlid, *Amphilophus citrinellus* (Günther, 1864), is known to be aggressive and difficult to house in groups in aquaria [Barlow 1976]. To determine if Midas cichlids optimize benefits with small-scale changes in defensibility aggression was observed in small captive groups. Aggression was expected to decrease as number of competitors increased and as available space increased. To determine if behavior differs with larger-scale differences in defensibility, results were compared to behavior observed in a large zoo exhibit (large group size) and under natural conditions (large available space).

TABLE 1. Midas cichlid behavior recorded at periodic intervals

Behavior	Description
aggression	attack (nip, chase, charge) or display (lateral display or operculum flare) [Baerends and Baerends van Roon 1950].
cowering	any two of the following: accelerated beating of pectoral fins, accelerated respiration, in contact with wall of aquarium, near water surface, body held obliquely in water.

EXPERIMENTS

- Observations of juvenile fish prevented mating motivation from influencing aggression.
- Aggression expected to be lower in complex environments [Barlow and McKaye 1982].
- Simple environments: gravel substrate and sponge filter
- Complex environments: simple environment plus one stone, Java moss (*Vesicularia dubyana*), two clay tiles forming two caves.
- n ≈ 8 for each treatment.
- Super-complex environment: extensive 3-D structure (380 l aquarium only) (Fig. 1).
- One trial = three days. Data collected for 5 min. each day.
- Numbers of aggressive bouts performed by dominant fish recorded.
- Time budgets established by recording at 30-second intervals.

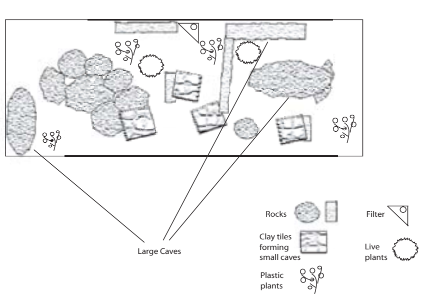

Fig. 1. Super-complex environment erected in 380 l aquarium (top view).

EXPERIMENT I – CHANGING GROUP SIZE

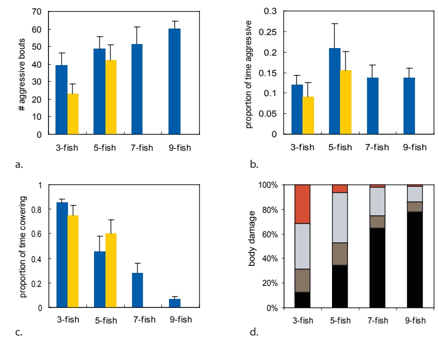

Fig. 2. Mean (+SE) numbers of (a) aggressive bouts performed by alpha fish and (b) proportion of time spent behaving aggressively in simple (blue bars) and complex (yellow bars) environments. (c) Time subordinate fish spent cowering. (d) Superficial damage received by subordinates in simple environments. Black – no damage, brown – one tear in fin, gray – two or more fin tears, red – fin damage and scale loss. Damage was not beyond what is commonly seen in captive fishes and no illness or death occurred. For statistical analysis the three classes of damaged fish were combined and damaged compared to not damaged.

	group size	complexity	statistical test
Dominant fish			
# aggress. bouts	p = 0.031	p = 0.179	2-way factorial ANOVA
% time aggress.	p = 0.789	p = 0.528	2-way factorial ANOVA
Subordinate fish			
Cowering	p < 0.001	p = 0. 803	2-way factorial ANOVA
Body damage			
simple	p = 0.038	3-fish p = 0.164	Chi-square
complex	p = 0.617	5-fish p = 0.379	Chi-square

Rate of aggressive bouts increased with group size, but proportion of time spent behaving aggressively did not. Dominant fish were stimulated to attack consistently in all of the treatments, but when faced with greater numbers of competitors the dominant fish apparently switched targets more frequently which resulted in an increased rate of aggressive bouts. To minimize the costs of aggression, it should have been performed only at a level sufficient to maintain dominance over competitors. Instead, alpha fish performed similar levels of aggression against different numbers of competitors. Effects on subordinates varied by treatment, further indicating that alpha fish were not capable of adjusting aggressive behavior under differing conditions of defensibility.

EXPERIMENT II – CHANGING AVAILABLE SPACE

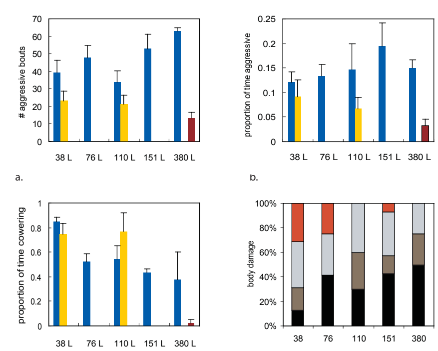

Fig. 3. Data as in Fig 2, above. Maroon = super-complex treatment.

	tank size	complexity	statistical test
Dominant fish			
Without super-complex			
# aggress. bouts	p = 0.091	p = 0.002	2-way factorial ANOVA
% time aggress.	p = 0.502	p = 0.052	2-way factorial ANOVA
With super-complex			
# aggress. bouts	p = 0.075	p < 0.001	2-way factorial ANOVA
% time aggress.	p = 0.478	p = 0.006	2-way factorial ANOVA
Subordinate fish (w/out super-complex)			
Cowering	p = 0.008	p = 0.173	2-way factorial ANOVA
Body damage			
simple	p = 0.647	38 l: p = 0.164	Chi-square
complex	p = 0.894	110 l: p = 0.740	Chi-square
380 l, simple vs. super-complex p = 0.509			Chi-square

Dominant fish exhibited similar levels of aggression at different density treatments, which resulted in a high level of variability in the effects on subordinates. Aggression was higher in simple than in complex environments in total numbers and nearly significantly higher in proportion of time. When the 380 l super-complex treatment was included proportion of time spent behaving aggressively also became highly affected by complexity. Addition of 3-D structure may have provided barriers to visual communication and reduced the rate of reception of sign stimuli that could lead to aggression [Bronstein 1983]. However, in some replicates of the super-complex treatment fish swam in close proximity with one another with little aggression and sometimes shared a cave. This suggests that fish cease defense when enough complexity is offered.

ZOO EXHIBIT

Young individuals were observed in a pool (4500 l) in a large walk-through rainforest exhibit at Toledo Zoological Gardens (Toledo, Ohio, U.S.A.). The pool contained several breeding pairs, leaving about half of the total volume for the 87 juveniles, which formed a shoal rather than dispersing throughout the unoccupied space. Numbers of aggressive bouts and behavior at 30-second intervals were recorded from focal individuals (n = 11) . No dominant fish could be identified in the shoal. Aggression was lower than in experiments. This seemed to indicate that there was a threshold number of competitors above which individuals would not attempt to dominate others.

LAKE APOYO, NICARAGUA

Results were compared to behavior reported previously for *Amphilophus* cf. *citrinellus* in Lake Apoyo, Nicaragua [Oldfield et al. 2006]. Small juveniles (2.5 to 5 cm TL) in shallow (1 m) water were solitary but frequently came into contact and exchanged aggressive behavior.

When aggression rates were compared among the Lake Apoyo habitat (n = 32), the 380 l 3-fish super-complex environment, the 38 l 3-fish simple treatment, and the zoo pool (Table 2) there was a significant difference (Kruskal-Wallis: p < 0.001). Proportion of time (n = 29) spent in aggression was also different (Kruskal-Wallis: p = 0.035), as was foraging (Kruskal-Wallis: p < 0.001), and swimming (Kruskal-Wallis: p < 0.005). Aggression was higher under typical experimental conditions than in the zoo pool or in nature.

TABLE 2. Water volume, density, and selected behavior patterns (mean±SD) in Midas cichlids in different habitats

Habitat	Water vol. (l)	Density (# fish/m3)	Rate of aggression (#/min.)	% Time spent in aggress.	% Time spent hovering	% Time spent foraging	% Time spent swimming
Lake Apoyo	∞	1.45±1.51	0.76±1.34	4.60±9.23	21.9±19.1	20.0±17.0	33.7±19.5
super-complex	380	7.90	0.90±0.49	3.33±2.98	not recorded	0	17.8±16.8
38 l 3-fish simple	38	78.95	2.63 ±1.34	9.17±9.55	37.9±14.5	6.25±6.53	10.0±5.9
Zoo pool	2250	42.22	0.22±0.30	0.91±3.02	69.1±19.2	1.8±4.0	26.4±19.1

ANIMAL WELFARE IMPLICATIONS

Elevated aggression in small aquaria could be due to restrictions on natural behavior. In Lake Apoyo, Midas cichlids spent much of their time foraging, swimming and avoiding detection by predators, leaving little time for aggression. Although fish in the super-complex treatment and the zoo pool exhibited low levels of aggression, these environments may not have been optimal. Mellen and MacPhee [2001] argued that captive time budgets should match wild time budgets (although they acknowledged that not all natural elements are beneficial [see Dawkins 1998]). In both environments fish spent less time foraging than in Lake Apoyo and fish in the zoo spent more time hovering motionless than did wild fish. Ethological research on captive fish to improve living conditions is rare. For mammals, environmental enrichment provides objects [Schapiro et al. 1996] and furniture [Maple and Perkins 1996] that increase habitat complexity and behavioral diversity and reduce stereotypical behavior [Carlstead 1996, Mellen and MacPhee 2001]. The importance of complexity and behavioral diversity for Midas cichlids is congruent with current thinking regarding enrichment in mammals.

Juvenile Midas cichlids are common in the pet trade and are maintained in aquaria similar in size to those in experiment II, which are shown here to generally be unsuitable. Also, this species grows to 20-30 cm, at which size appropriate housing is impractical for the typical hobbyist. Perhaps zoos and public aquaria may play a role in educating the public in this matter [Marliave et al. 1995].

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