Predation Effect of *Belostoma dentatum* (Hemiptera: Belostomatidae) on the Predator Perception and Behavioral Response of *Moenkhausia sanctaefilomenae* (Pisces: Characidae)[1]

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Abstract Predation is an important interaction for the regulation of population dynamics due to the effect caused by the direct consumption of prey. However, some populations present strategies to detect risk of predation and react to the predator. Our objective was to evaluate the effect of the predation risk of *Belostoma dentatum* (Mayr), under the behavioral response of the red-eye tetra fish, *Moenkhausia sanctaefilomenae* (Steindachner), to the availability of refuge and the density of prey. We tested the hypothesis that the distance between prey and predator decreases if there is refuge and if the individual is in a group. We observed the position of *M. sanctaefilomenae* in relation to the water slide. In the first treatment, we added a predator; in the second, we included refuge; and in the third, we added two more fish. The occupation pattern inside the container was only detected in the presence of the predator. With the addition of the predator, the prey was restricted to the refuge. With the removal of refuges, the distance between predator and prey remained the maximum. On the other hand, when the two new individuals were added, the occupancy pattern was no longer detected, indicating the dilution effect on group behavior. These aspects indicate that in the face of the risk of predation by *B. dentatum,* the individual *M. sanctaefilomenae* may adopt different behavioral strategies, suggesting that they are able to perceive the predator and, thus, modify prey behavior. Prey are apparently interpreting environmental cues to increase chances of survival.

Key Words defense behavior, predatory behavior, group effect

The dynamics between predator and prey is usually described based on the abundance of prey populations as a consequence of direct predator consumption. For this reason, many organisms can develop defensive strategies that reduce the chance of encounter and predator interest, such as camouflage, apostasy, and/or Batesian and Mullerian mimicry (Krebs and Davies 1993, Gnaspini and Hara 2007). These strategies act independently of the presence of the predator and are called primary strategies (Edmunds 1974). However, the indirect effects caused by the

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predator's perception may be more important in community dynamics than direct consumption (Abrams 1990, Anholt and Werner 1995, Lima 1998).

The presence of the predator represents a risk of predation, which may result in the development of behavioral, morphological, or physiological strategies that increase prey performance only when the predator is present (Schmitz et al. 2004). These defenses are secondary strategies and are displayed only after detection of predation risk or after predator attack (Edmunds 1974, Scott 2005). Therefore, they involve actions with higher energy expenditure, such as tanatosis, attack deflection, retreat or escape, and blunt responses such as retaliation (Gnaspini and Hara 2007, Chelini et al. 2009). There are also defense mechanisms that can function as primary or secondary as, for example, group defenses or defensive aggregations (Edmunds 1974).

The way prey and predator detect the presence of one another can be influenced by the environment in which they are inserted (Edmunds 1974). Habitats may be selected according to the availability of refuge, food, possibility of mating, competition, and the presence of predators (Leibold 1989, Stamps 2009). Thus, variation in spatial structure tends to influence the outcome of predation (Hughes and Grabowski 2006).

In aquatic environments, macrophytes increase the complexity of the environment and may reduce potential predation (Srivastava 2006, Padial et al. 2009). Therefore, different strategies are used in waters with and without vegetation (Saha 2009). In the absence of macrophytes, prey become susceptible to predators.

Belostomatidae spp. (Hemiptera) are large insects that occur worldwide among the main aquatic predatory insects in lentic environments, feeding primarily on other invertebrates such as mollusks, other insects, and crustaceans, as well as small vertebrates such as fish and anurans. Being important in the structure of aquatic communities (Schuh and Slater 1995, Pereira and Melo 1998, Armúa and Estévez 2006, Rafael et al. 2012, Toledo 2003, Brahma et al. 2014, Boersma et al. 2014, Tara and Kour 2014, Wojdak et al. 2014)

Therefore, some groups, such as fish, use aggregation strategy as one of the main secondary defenses to avoid predators. This strategy includes the effect of confusion and dilution, which reduces the attack and, consequently, the potential rates of predation (Wrona and Dixon 1991, Uetz et al. 2002). In this way, all individuals in the groups are equally safe, because each individual has a lower chance of being attacked (Bertram 1980); therefore, these individuals tend to present reduced vigilance (Studd et al. 1983, Lendrum 1984). When detecting the risk of predation, the defense strategies used will depend on environmental conditions. However, the result of successive changes in the environment under the behavioral modification of prey is not known.

Thus, we examined some predator–prey interactions by using the red-eye tetra fish, *Moenkhausia sanctaefilomenae* (Steindachner) (Pisces: Characidae) as prey and *Belostoma dentatum* (Mayr) (Hemiptera: Belastomatidae) as predator. Our objectives were to determine if prey behavior was altered by the presence of the prey, in the absence of refuge, and by group formation. We test the following hypotheses: (1) In the presence of the predator, prey will seek a refuge to avoid predation; (2) In the absence of refuge but in the presence of predator, prey will locate at the furthest distance from the predator as possible; and (3) prey will gather in groups to create a dilution effect of predation.

Materials and Methods

We collected fish and insects from a pond (approximately 1.5 ha) in a wetland near the Miranda River, located at the Pantanal Study Base of the Federal University of Mato Grosso do Sul, Brazil (S 19°34′38.19″, W 57°01′01.39″). The Pantanal is the largest floodplain in the world, with an approximate area of 150,000 km^2 (Junk and Cunha 2005). It has a well-defined seasonality with two distinct seasons. During the flood period, river waters overflow into the plain and aquatic fauna easily disperse among floodplains, lakes, and permanent and temporary ponds (Oliveira and Calheiros 2000). Prey and predators, captured using the active trawl method, were transported to the laboratory for the studies conducted in July 2015.

Belostoma dentatum was used at the predator in these models because it is abundant in the region (Ribeiro 2007, Floriano et al. 2013), is a predator that uses a sit–wait predation strategy, and preys upon invertebrates (e.g., aquatic insects, crustaceans, and mollusks) and vertebrates (e.g., fish and amphibians) (Kehr and Schnack 1991, Toledo 2003). These predators usually hide in aquatic plants waiting for the opportunity to attack their prey. We used *M. sanctaefilomenae* as the prey in our model because this species is abundant in lotic and lentic habitats in the region, exhibits aggregation behavior to dilute predation (Lourenço et al. 2012), and is omnivorous, feeding mainly on insects and algae (Tófoli et al. 2010, Casatti et al. 2001).

Biological models occur in sympatry, so both prey and predator are able to interact naturally in the predator–prey relationship. At the end of the experiment, the organisms were returned to their habitat, except for the fish that were preyed upon during the experiment.

Experimental design and statistical analysis. In the laboratory, the fish were placed in a plastic tray with filled with water from the pond for 1 h to allow for acclimatization. The same was done with the predators, in a separate container. Prey specimens of a similar size (3.38 ± 0.17 cm) were selected to avoid the effect of body size on the prey behavioral response. The same was done for selection of predators (3.9 ± 0.3 cm) to avoid behavioral responses of fish in response to predator size (Fig. 1).

Ten spatially and visually separated containers with a water column height of 15 cm (Fig. 2) were used. Four stages of predator–prey conditions were observed: step 1, a control of fish in the presence of plant refuge composed of *Eichhornia crassipes* (Commelinales: Pontederiaceae); step 2, fish, plant refuge, and the addition of a predator; step 3, removal of the plant refuge; and step 4, placement of two additional fish in the water column.

In each of the steps, five observations were conducted per container, each lasting 1 min with a 5-min interval between the observations. In step 1, the position of the fish in the water column was noted. In stages 2, 3, and 4, the positions of the fish and the insect in the water column were noted. The observation in step 1 was then used

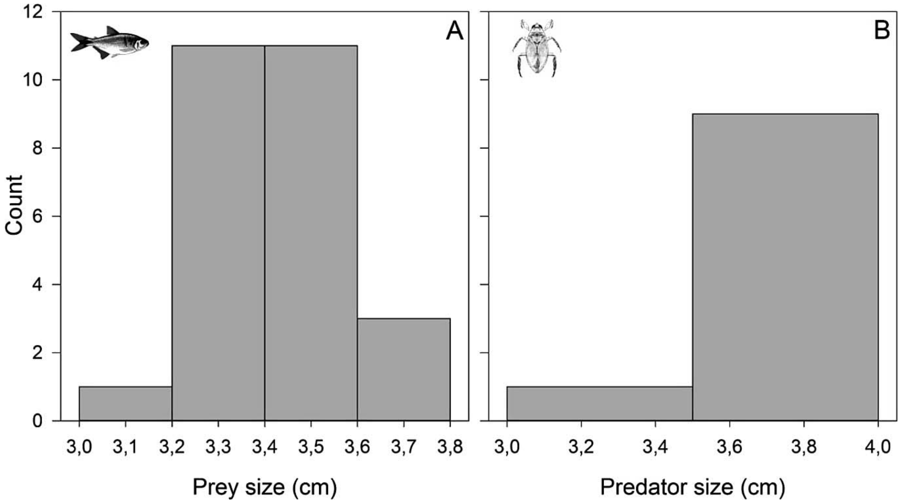

Fig. 1. Distribution of the body size (cm) of *Moenkhausia sanctaefilomenae*/ prey (head length/tail) (A) and *Belostoma dentatum*/predators (face length/abdomen) (B) used in the experiment.

to verify the behavior of the prey in response to the predator. All measurements were taken in centimeters, based on the scale attached to the vessel.

We used the one-sample signed rank test to determine statistical significance of the position of the fish in the water column in comparison to the control. Differences in prey–predator distances among the treatments were compared by analysis of variance followed by Tukey's honest significant difference for mean separation ($\alpha = 0.05$).

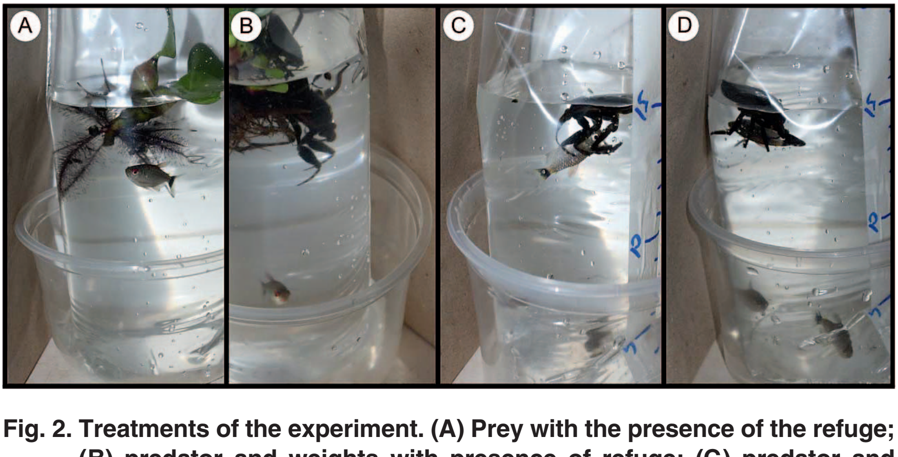

Fig. 2. Treatments of the experiment. (A) Prey with the presence of the refuge; (B) predator and weights with presence of refuge; (C) predator and prey without refuge (detail of prey being consumed); (D) predator and group without refuge (detail of prey being consumed).

Results

This represents the first report of observations of the predatory behavior of *B. dentatum*. In the absence of the predator, the red-eye tetra fish (prey) occupied a variety of locations in the water column, with mean ($\pm$ SD) differences in position among replicates of 11.4 ($\pm$3.4) cm ($Z = 6.29$; $P < 0.05$). When the predator was introduced, the prey occupancy range within the column was reduced in comparison to the control without a predator, except when prey was able to aggregate into a group ($F = 9.84$; df $= 3$; $P < 0.05$).

When the predator was added to the column, the fish prey remained in the roots of aquatic plant refuge. During the period when the plant refuge was present, no predation was observed because *M. sanctaefilomenae* remained hidden and usually on the opposite side of the column from the predator, thus exhibiting avoidance behavior. When the refuge was removed, the predator detected the presence of prey and attempted to attack and prey on the fish. However, successful predation occurred only after additional fish were added to the column.

Once the predatory hemipteran was added, the range of space occupied by the fish decreased, apparently to maintain distance from the predator. With the availability of plant refuge, the distance between prey and predator decreased (4.2 $\pm$ 2.3 cm; $P < 0.05$), apparently because of the prey's ability to remain visually obstructed from the predator. Following removal of the refuge, there was an immediate increase in the distance between prey and predator (6.0 $\pm$ 1.3 cm; $P < 0.05$). Regardless of the position of the predator, the prey moved to occupy the opposite end of the vessel. Predation events were recorded in this treatment. When we added new individuals, the occupation pattern was lost (6.4 $\pm$ 1.8 cm; $P = 0.09$), indicating that the prey no longer reacted to the presence of the predator (Fig. 3; Table 1).

Discussion

The pattern of occupation of the water column by individuals of *M. sanctaefilomenae* varied immediately at each stage of the study, indicating the existence of a decision-making capacity in the perceived risk of predation by *B. dentatum*. However, in addition to the behavioral change due to the presence of the predator, the environmental conditions in each treatment determined the response to the predator. For example, when each prey was isolated in its container without the presence of the predator, individual foraging characteristics determined the preference in occupying the space. So, no occupancy pattern was detected. The individuals were distributed throughout the water column.

The addition of a predator to the container caused the prey to use the refuge as protection, remaining hidden by the plant roots. The structural complexity of the habitat can modify prey selection and predation rate (Padial et al. 2009, Saha et al. 2009 Swisher et al. 1998, Warfe and Barmuta 2004, Hughes and Grabowski 2006). The approximation of the prey to the predator is indicative of its immediate ability to perceive it and recognize the risk associated with it by promoting behavioral changes based on the characteristics of the environment. The roots of the aquatic macrophyte serve as a base of fixation for the predator to remain in

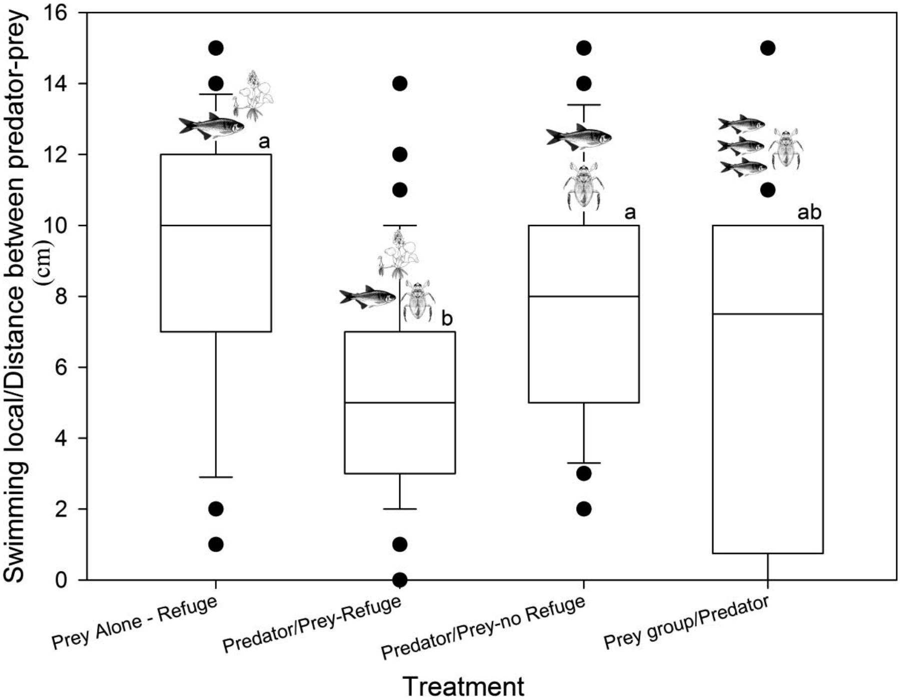

Fig. 3. Prey swimming site and distance between prey and predator in different treatments: No predator and presence of refuge; presence of predator and refuge; presence of predator and absence of refuge; and presence of predator, absence of refuge, and group formation.

the waiting position but serve as a hiding place for the prey adjacent to the predator.

The presence of vegetation reduced the effectiveness of *Diplonychus* sp. under laboratory conditions (Shaalan et al. 2007). Environmental heterogeneity affects

Table 1. **Results of paired Tukey test comparison between treatments.**

Comparison	Q	*P*
Alone versus predator refuge	7,02	0.01*
Alone versus predator no refuge	5,585	0.01*
Alone versus group	2,665	0.24
Predator refuge versus predator no refuge	4,354	0.01*
Predator refuge versus predator group	3,065	0.13
Predator no rejuge versus predator group	1,051	0.88

Significance at $\alpha = 0.05$.

the ability of predators to detect prey (Wellborn et al. 1996, Kopp et al. 2006). When the refuge was removed, the prey increased the distance from the predator as a way of avoiding the predator and the possibility of predation. This behavioral response was immediate, and the prey was able to perceive the presence of the predator and modify its behavior. When the predator moved to the bottom of the container, at the same instant, the prey moved to the highest level, always seeking to avoid it.

When we added two more prey individuals, forming a group, the individual probability of being preyed upon dropped to 33.33%, so it is possible that the prey moved by a greater amplitude and approached the predator more closely. The fact that there is no difference between any treatments indicates the effect of dilution on the behavior of the group, making the occupied position both near and far from the predator, due to the lower predation probability. This relationship was already verified for the same species (Felipe et al. 2007), where the ability of the fish to be exposed to the risk of predation was evaluated, with the fish being aggregated reducing the risk of predation. However, prediction events occurred at the time of greatest prey availability. The trade-off between the effort to perform a prediction and a greater probability of prey to compensate with the increase of nonreceptive individuals was recorded in the prevention events in 3 of the 10 replicates of the experiment at that stage.

The alteration of the prey behavior in front of the predator can also be seen in other taxa (Zanelato et al. 2010), where the strategy of tadpoles exposed to the risk of predation was observed, in which the tadpoles opted for or dispersed and confused the predator, or by remaining aggregated, also reducing the risk of individual predation.

Belostoma sp. is reported as a major predator in aquatic environments and is responsible for structuring aquatic communities due to predatory pressure (Brodie and Formanowicz 1983; Kesler and Munns 1989; Wojdak and Luttbeg 2005; Plath et al. 2011). The individual behavior reflects the variation in space occupation in that, although the individuals of *M. sanctaefilomenae* are alone in the container, the presence of refuge reduces the distance between the predator and the prey, providing a habitat in which to hide. In the absence of shelter, prey avoids the predator and the group effect dilutes the chances of predation, showing that *M. sanctaefilomenae* perceives and responds quickly to the presence of *B. dentatum*.

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