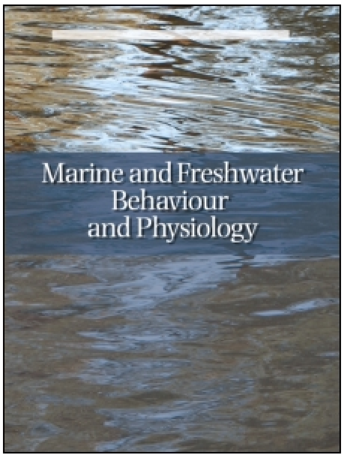

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Behavioral response of Nile tilapia to an allopatric predator

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We investigated interaction of the Nile tilapia, *Oreochromis niloticus*, paired with either a predator, spotted sorubim, *Pseudoplatystoma corruscans*, or a non-predator, threespot leporinus, *Leporinus friderici*. Fish behaviors were quantified 5 min before pairing and 15 min during pairing (a heterospecific fish introduced into the Nile tilapia aquarium). Distance from the heterospecific fish, frequency, and time spent in dorsal-fin display, and frequency of agonistic interactions were registered. Agonistic interaction occurred mainly between Nile tilapia and threespot leporinus. Pairing increased frequency and time spent in dorsal-fin display, mainly when tilapia was paired with the threespot leporinus. Tilapia kept further away from spotted sorubim than from threespot leporinus. We concluded that Nile tilapia discriminates a predator from a harmless nonpredator allopatric heterospecific, suggesting a genetically-based ability. The dorsal-fin display is interpreted as both anti-predatory (displayed to the predator spotted sorubim) and intimidator behavior (displayed to the threespot leporinus).

Keywords: tilapia; *Oreochromis niloticus*; behavioral response; predator species; *Pseudoplatystoma corruscans*; non-predator species; *Leporinus friderici*; genome-based preference

Introduction

Anti-predator strategies have been described in fish mostly for schooling species (Pitcher and Parrish 1993), although anti-predatory mechanisms are also necessarily expected to occur in territorial species. For instance, in the territorial fish stickleback, dorsal-fin display is considered sufficient to prevent the predator to swallowing the prey (Wootton 1976 in FitzGerald and Wooton 1993).

Anti-predator behaviors are assumed to evolve in prey–predator organisms sharing the same geographical and temporal area. In such conditions, predator recognition by prey has been described in some species (Chivers and Smith 1993; Mathis et al. 1993; Jordão and Volpato 2000). However, predators evolving in different regions should share some traits that could be recognized by prey so that the prey can reduce predation risk when exploring new habitats. Catfishes are a group of ferocious predators, which share a conspicuous body appearance (body shape and barbells), thus being expected to be identified by prey not sharing the same environment. Therefore, in the present study we investigate whether a territorial predator-naïve fish is able to recognize a predator fish to

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which they are evolutionary naïve. We studied a naïve-predator Nile tilapia, *Oreochromis niloticus* (L. 1758), an African species that was introduced in Brazilian waters about 50 years ago (Jalabert and Zohar 1982). Despite the fact that this is a very short time for evolutionary consequences, recognition of native predators is expected to explain the reported widespread distribution of the Nile tilapia in Brazilian rivers. In this way, the response of predator-naïve Nile tilapia to the spotted sorubim, *Pseudoplatystoma corruscans*, a ferocious native predator fish shall be investigated. As a methodological control, these responses with those to a nonpredator harmless South American fish, the threespot leporinus, shall also be contrasted.

Material and methods

We studied Nile tilapia, *O. niloticus*, juveniles provided from a monoculture fishery and held for 3 months before the experiment and without any heterospecific contact, socially isolated in glass aquaria ($40 \times 20 \times 25$ cm; 12 L). On the 10th isolation day, the tilapia were video recorded for 5 min (basal value) and then a heterospecific fish (the South American catfish spotted sorubim, *P. corruscans*, or the South American threespot leporinus, *Leporinus friderici*) was introduced into the aquarium and behavior was continuously video-recorded for 15 min. Distance between fish in each pair, Nile tilapia dorsal-fin display (frequency and total time spent) and frequency of social interactions were quantified. To compare the values obtained in a 15-min period with basal values, we calculated the means within the period from the values divided by 3. Seven pairs (tilapia and heterospecific fish) were registered for each heterospecific species.

Mean body-weights (BW) of the Nile tilapia were 6.8 ± 1.9 and 5.3 ± 0.7 g, respectively to the predator and nonpredator conditions (Student's *t*-test: BW, $t = 2.00, p = 0.07$). Intruder heterospecific fish were similarly smaller than the Nile tilapia: 1.8 ± 1.9 and 2.4 ± 1.0 g lighter than the respective Nile tilapia, for spotted sorubim and threespot leporinus, respectively (Student's *t*-test: $t = 0.69, p = 0.51$). During the experimentation and holding conditions, water temperature was about 24°C and photoperiod was set up from 06:00 to 18:00 h daily.

Distance between fish in a pair was analysed by calculating the distance of the eye of the fish from each other. Thus, fish eye positions were registered for each fish on a squared grid (3.5×3.5 cm, placed on the frontal glass of the aquarium) every 20 s, as described in Jordão and Volpato (2000). Each position was then plotted on a Cartesian axes (X and Y) and the distance between each coordinates (fish eye positions) was calculated for each 20 s time point. For each pair, a mean of these distances was calculated for each 5 min in the 15 min period and compared over time and between each heterospecific condition (Nile tilapia – spotted sorubim vs. Nile tilapia – threespot leporinus) by profile analysis (Morrison 1976).

The dorsal fin of Nile tilapia was registered as erect or not. When erect, the spines are easily observed. Otherwise, the dorsal fin is retracted to some degree (the spines are almost or completely parallel to the dorsal body part). Both frequency and time spent displaying with the dorsal fin completely erect was quantified for each period (basal and pairing).

Nile tilapia agonistic interactions were based on Alvarenga and Volpato (1995), Giaquinto and Volpato (1997), Barki and Volpato (1998) and quantified as (i) *nipping*: the Nile tilapia bites any body part of the opponent; (ii) *chasing*: the Nile tilapia swims towards to the opponent, which flees in the opposite direction (a course never

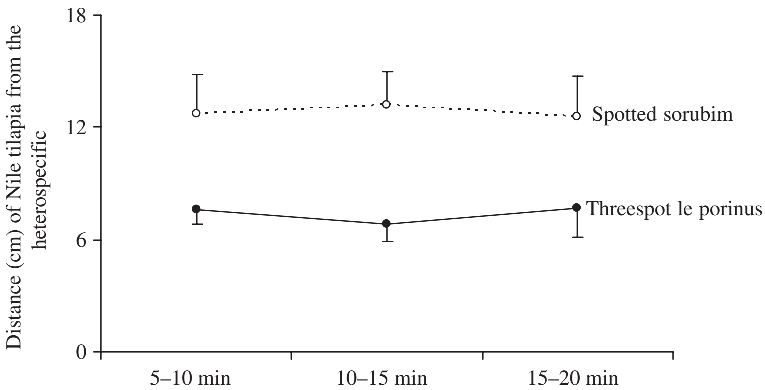

Figure 1. Distance of the Nile tilapia from heterospecifics. Mean values (±SEM, $N = 7$). Profile analysis showed higher distance from spotted sorubim than from threespot leporinus in each time point ($F = 18.83, p < 0.05$), but no changes over time for both heterospecific fish ($F = 0.23, p > 0.05$).

shorter than 3 cm); (iii) *lateral fight*: the Nile tilapia stays close to and laterally positioned near the heterospecific fish, moving its tail sideways.

Exploratory data analyses revealed outlier values, which were replaced by the mean values, as referred to in Tukey (1977), and are shown in the following section.

Results

Nile tilapia maintained a longer distance from the spotted sorubim than from the threespot leporinus, irrespective of time (Figure 1). The spotted sorubim stayed most of the time at the bottom, almost motionless, while threespot leporinus and tilapia occupied mainly the middle area between bottom and surface and were more active.

Mean basal number of Nile tilapia's dorsal-fin displays was similar between the two heterospecific conditions (threespot leporinus in Figure 2(a) × spotted sorubim in Figure 2(b); *U*-test: $U = 16$, $p = 0.28$). Also, no difference occurred for mean basal time spent by the tilapia in dorsal-fin displays between these two conditions (threespot leporinus in Figure 2(d) × spotted sorubim in Figure 2(e); *U*-test: $U = 13$, $p = 0.14$). These similar basal values were validated by comparing these variables after pairing. Pairing with a heterospecific fish increased the number of Nile tilapia's dorsal-fin display in the presence of either spotted sorubim or threespot leporinus (Figure 2a, b, c). The total time spent in dorsal-fin display by tilapia was also increased when paired with heterospecific fish (Figure 2d and e); however, a more pronounced increase occurred when tilapia was paired with threespot leporinus (Figure 2f).

No heterospecific fish attacked the Nile tilapia. Tilapia, however, bit the opponents' body more frequently than the threespot leporinus bit the spotted sorubim. Only three tilapias exhibited nipping to the predator (spotted sorubim), even though at lower frequencies (2, 5, and 5). On the other hand, all the tilapia paired with threespot leporinus were more intensely involved in agonistic interactions. Mean (±SD) frequencies were: nipping = 24.29 ± 10.92, chasing = 11.00 ± 5.20, and lateral fight = 1.86 ± 2.85 (Kruskal-Wallis: $H = 14.89, p < 0.01$). The complementary Nemenyi test revealed that nipping was more frequent than lateral fight ($q_{calc} = 5.42 > q_{0.05,\infty,3} = 3.31$), but both these agonistic

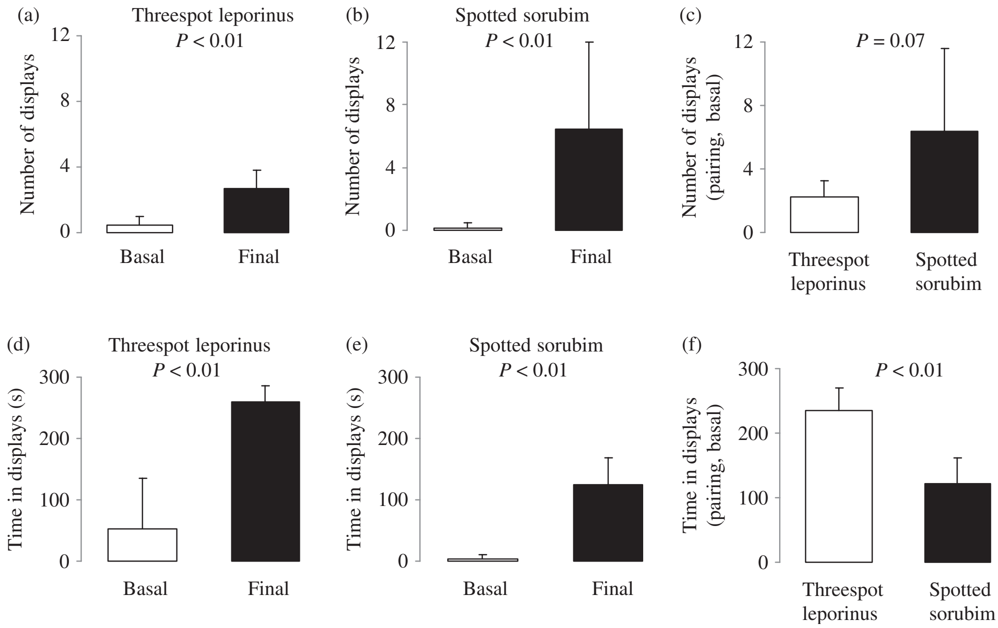

Figure 2. Nile tilapia's dorsal-fin behavior displayed to either a predator (spotted sorubim) or a nonpredator (threespot leporinus) heterospecific. Means (±SD) of seven fish in each condition. U-test: (a) $U = 3.00$; (b) $U = 0$; (c) $U = 10.5$; (d) $U = 0$; (e) $U = 0$; (f) $U = 0$.

types were equal to chase (nipping = chasing, $q_{\text{calc}} = 2.44 < q_{0.05,\infty,3} = 3.31$; lateral fight = chasing, $q_{\text{calc}} = 2.98 < q_{0.05,\infty,3} = 3.31$).

Discussion

This study showed that the African Cichlidae Nile tilapia discriminates South American fishes, the predator, spotted sorubim from the nonpredator fish, threespot leporinus. Behavioral reactions indicated that Nile tilapia retreated from the predator spotted sorubim and attacked the threespot leporinus, thus suggesting a risk-mediated behavioral trade-off by the Nile tilapia.

As the three species investigated were naïve to each other (reared in monoculture from hatching), the different responses of the Nile tilapia may express a genetic-based ability to discriminate a predator fish, as also reported to the Characin fish pacu (Jordão and Volpato 2000). The Nile tilapia's response to the heterospecific fish cannot be attributed to the novelty of a first stimulus (the conspecific) because tilapia reacted to each heterospecific species differently, thus reinforcing discrimination between the harmless threespot leporinus and the predator spotted sorubim. Nile tilapia were reported to respond to the view of spotted sorubim by increasing ventilatory rate, a response interpreted as an alert to a predation risk (Barreto et al. 2003). In the present study, tilapia maintaining distance from spotted sorubim might also be a defense mechanism. Prey's distance from the predator has been recognized as an antipredator defense mechanism in other fish species (Abrahams 1995). As spotted sorubim is a species to which the tilapia is evolutionary naïve, a tentative explanation assumes that recognition might be based on some traits shared among the catfish predators (e.g. body shape), but this deserves further investigation.

For the interaction of the Nile tilapia with the threespot leporinus, the short distance between them is likely to be a consequence of territorial disputes. Nile tilapia and threespot leporinus remained active in the water column, and thus interactions were expected. Supporting this, the agonistic profile exhibited in these interactions is very similar to those displayed by the Nile tilapia during intraspecific hierarchical and territorial disputes (Alvarenga and Volpato 1995; Barki and Volpato 1998). Moreover, the dominance of the Nile tilapia over threespot leporinus in all studied pairs may also result from a prior-residence effect (the owner of the territory wins combats against intruders, Huntingford and Turner 1987).

Another conspicuous behavior studied was the dorsal-fin display. Nile tilapia increased dorsal-fin display to both heterospecifics, thus reinforcing that they were not ignored (despite the low diurnal activity of the nocturnal fish spotted sorubim). Dorsal-fin displays have been assumed to be a defense response in other species because the spines are extended and may hurt the predator (Wootton 1984 in FitzGerald and Wootton 1993; Colgan 1993). On the other hand, in the territorial context of aggression displayed by the Nile tilapia to the threespot leporinus, dorsal-fin display may be an intimidation behavior as it enlarges body size. Thus, Nile tilapia's dorsal-fin displays may be involved at least in three contexts: interspecific predation risk (this study), interspecific territorial disputes (this study), and intraspecific disputes (Baerends and Blokzijil 1963; Barki and Volpato 1998).

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