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The behavioral mechanism of competition for food between tilapia (*Oreochromis* hybrid) and crayfish (*Cherax quadricarinatus*)

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ABSTRACT

Studies on polyculture have usually investigated the consequences of this widespread culture method for growth and survival of the cultured species. However, research into the behavioral mechanism underlying competition between co-cultured species is lacking. For the first time in co-cultured fish and crustaceans, this study explored experimentally the behavioral interaction between red tilapia and red-claw crayfish in the context of food competion. The effects of the presence of heterospecifics (absent or present), the size of fish relative to crayfish (larger or smaller) and the number of food patches available for the fish (one- versus two-patch conditions) on the foraging decisions and aggression of fish and crayfish were tested. Time spent by fish in the bottom food patch (accessible for fish and crayfish) was shorter in the presence of crayfish, for small but not large fish and when there was an alternative patch for the fish (accessible only for fish). Time spent by crayfish in the bottom food patch was reduced in the presence of large, but not small, fish and when there was no alternative food patch for the fish. Fish were most aggressive towards conspecifics whereas interspecific aggression was exhibited only by crayfish. At the individual level, the dominant fish and crayfish spent more time in the bottom patch and performed more aggressive actions than the other conspecifics. In fish, this was not altered in the presence of crayfish. In crayfish, the overall reduction in foraging duration and aggression was due to an effect of large fish on the dominant individual. The implication of these findings for fish–crayfish communal culture is discussed.

1. Introduction

The farming of tilapia is the most widespread type of aquaculture in the world, with more than 135 producer countries and territories worldwide (FAO, 2014). Tilapia are most commonly cultured in semi-intensive polyculture with one or more species of fish and/or crustaceans (Wang and Lu, 2015). The basic idea of polyculture is growing species with complementary or minimal competing feeding habits and different ecological requirements that can utilize different trophic niches in the pond (Milstein, 2005). However, with densities currently applied in polyculture practices, supplementary artificial food is usually added to meet the energetic requirements for optimal growth. This might introduce a resource for which the different cultured species compete. When competition ensues, one species may be more successful than the other, causing a reduction in growth of the inferior species from what might be obtained in monoculture.

Numerous studies over the last 3 decades have investigated polyculture of tilapia with other species, including crustaceans (Wang and Lu, 2015). These studies were conducted under varying degrees of intensification and at different species compositions. For instance, tilapia was investigated as a major species (alongside common carp) in combination with freshwater prawns in semi-intensive polyculture ponds (Wohlfarth et al., 1985), as a secondary species added to freshwater prawns' periphyton-based ponds (Asaduzzaman et al., 2009) or to marine shrimp intensive culture tanks (Muangkeow et al., 2011; Tian et al., 2001; Yuan et al., 2010), and as a principal species in intensive co-culture with crayfish (Karplus et al., 2001). These studies have investigated effects on growth performance and survival of influencing factors such as species composition, stocking rates, feeding and manure regimes and environmental (water quality) parameters. In contrast to the wealth of studies on these aspects, research into the behavioral mechanism underlying competition between co-cultured fish and crustaceans is lacking.

Unlike tilapia polyculture with freshwater prawns (e.g., Cohen et al., 1983; García-Pérez et al., 2000; Wohlfarth et al., 1985) and marine shrimps (Muangkeow et al., 2011; Tian et al., 2001; Wang et al., 1998), studies on tilapia–crayfish polyculture have usually demonstrated a negative effect on growth and survival of tilapia on crayfish (Karplus et al., 2001; Rouse and Kahn, 1998) or of crayfish on tilapia (Brummet and Alon, 1994). Thus, investigation of the behavioral mechanism of interspecific competition in the context of polyculture is particularly pertinent for tilapia and crayfish.

The current study focused on interspecific competition for food between red tilapia (*Oreochromis* hybrid) and red-claw crayfish (*Cherax quadricarinatus*). Both species are omnivorous, however, while crayfish

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are bottom feeders the red tilapia feeds from both the bottom and the water column. Most studies have considered fish and crayfish in the context of predator–prey relationships (e.g., Stein, 1977; Stein and Magnuson, 1976). However, owing to their large size, hard shell and powerful weapons, crayfish are no easy prey for fish and they may compete directly with bottom feeding fish for food (Carpenter, 2005) and for shelter (Griffiths et al., 2004). Furthermore, under certain circumstances each omnivorous fish and crayfish might harm heterospecifics (Neveu, 2001); fish might harm vulnerable crayfish at molting, and the nocturnal crayfish might harm diurnal fish at night when the fish are less active. Thus, fish–crayfish relationships appear to be complex; it involves both competition and predation (Dorn and Mittelbach, 1999; Reynolds, 2011) and it can be reversed, depending on relative size (Keller and Moore, 2000).

In a previous study we investigated the consequences of food competition between red tilapia and red-claw crayfish for growth (Barki et al., 2001). We demonstrated that tilapia grew better in the presence of crayfish, possibly by consuming part of the feed ration intended for the crayfish, whereas the growth of crayfish was adversely affected by tilapia. The magnitude of this effect depended on the relative size of the fish. That this was a consequence of food competition was evident by the finding that feeding the crayfish at night, when the fish are less active, reduced the impact of large fish on small crayfish and increased their growth by 32%. In the current study we investigated the foraging decisions and aggressive interactions of the fish and crayfish under intra- and interspecific competition. Specifically, we investigated the interplay of several factors in influencing the foraging decision of fish and crayfish, namely the presence of heterospecific competitors, heterospecific relative size and the number of food patches available for the fish. To the best of our knowledge, this is the first attempt to delve into behavioral details of competition for food between co-cultured crustaceans and fish, up to the individual level.

2. Materials and methods

2.1. Tanks and animals

The experiment was conducted indoors in 32 glass aquaria (25 × 50 × 40 cm). Each aquarium contained an internal biofilter with airstone and a shelter consisting of 4 tubes (10 cm in length, 2 cm in diameter) attached underneath a plastic egg tray. Thermostatically-controlled 60-Watt heaters maintained temperature between 24 and 27 °C. Lighting was provided by timer-controlled ceiling fluorescent tubes on a 12:12 h light:dark daily illumination cycle, in addition to the ambient light. Ammonium level was undetectably low, nitrite level did not exceed 0.1 mg/l, and pH ranged between 7.7 and 8.1.

The experiment was conducted with groups of 3 young red tilapia males (*Oreochromis* hybrid) and 3 redclaw crayfish (*C. quadricarinatus*). The fish were individually identified by their differing color patterns, and the crayfish were individually tagged with color plastic bands glued to the carapace.

2.2. Experimental design and procedure

The experimental design incorporated the following social and environmental factors: i) Relative size — the interspecific relative competitive ability was manipulated by means of the fish size; the 3 fish were either small (mean ± SD, 4.3 ± 1.0 g) or large (20.4 ± 3.8 g), relative to 3 similar-sized crayfish (12.1 ± 3.6 g). ii) Number of food patches — the competitive environment was manipulated by means of the number of food patches in which the food was present. Each aquarium contained two petri dishes (10 cm in diameter) in which the food could be provided through two tubes passing the flexiglass lid and ending approximately 5 cm above the petri dishes. One petri dish was situated in the bottom, attached to the left longitudinal side, and the other was mounted 12 cm above the bottom on the opposite longitudinal side at the same distance from the frontal glass and was accessible only for the fish (see supplementary video clip). The animals were fed six days a week with commercial feed pellets at a daily ration of 2% of total mass per aquarium. The food was given in either one patch (the bottom petri dish) or two patches (divided evenly between the two petri dishes). iii) Heterospecifics presence — each species was observed both in the absence and in the presence of heterospecifics. Three fish were firstly introduced for 10 days, then 3 crayfish were added for 10 days of cohabitation, and finally the fish were removed and the crayfish stayed alone for 10 days.

Intra- and inter-specific competition for food and aggressive interactions were observed. Each aquarium was video-recorded twice under each competitive condition, over two consecutive days to increase the sampling reliability, and the average values obtained served for the various analyses. The recording sessions were conducted at the end of each stage to ensure that the animals have adjusted to the specific social conditions and feeding regimes. To minimize disturbance, the video camera was located behind a black blind. Video recording lasted for 5 min before and 5 min after food supply. Based on the recorded aggressive interactions, each individual was ranked in a dominance order (see next section) and the rank factor was also included in the analyses.

2.3. Data analysis

We analyzed competitive ability in the context of competition for food by means of three measures: the total time spent in the food patch, the number of visits and the mean time per visit. A fish visit was measured when at least its snout was within the boundaries of the petri dish and approximately 5 cm above it (i.e. the level of the feeding tube opening). A crayfish visit was measured when at least the tips of its chelipeds were inside the petri dish.

Fish aggression measures were the frequencies of the following types of interactions: Overt attack, Displacement, Display and Contest (for details see Barki and Volpato, 1998). The rank order of the 3 fish (dominant, subdominant and subordinate) was determined by the relative number of their retreats in all 3 possible diads. Crayfish aggression measures were the frequencies of the following behavioral acts: Extend, Lunge, Grasp, Escalated-fighting and Displacement (for details see Karplus et al., 2003). The highest ranked crayfish was termed dominant, while the two lower-ranked individuals were similarly termed subordinates because their relative order was usually indiscernible (due to lack of interactions).

Competition measures and interspecific aggression were analyzed using PROC GLM (type III SS) of the SAS statistical package. Main and interaction effects of 4 independent variables were tested: relative size, number of food patches, heterospecific presence and dominance rank. We applied a split-plot model of ANOVA, which involved 3 error terms; size and patch were tested over the main plot error term, heterospecific presence was tested over the subplot error term and rank was tested over the residual error (Table 1). In the analysis of interspecific aggression (total number of aggressive actions) we added the feeding factor, i.e. before or after feeding, which was tested over the residual error. Frequencies were log(x + 1) transformed to increase homoscedasticity of data. In cases of significant effects ($p \le 0.05$), Tukey–Kramer HSD test was performed for multiple comparisons. Aquaria in which an animal died (due to aggression among fish or cannibalism among crayfish) were not included in the analysis.

3. Results

3.1. Fish competitive ability

Time spent by fish in the bottom food patch was overall shorter in the presence of crayfish than in their absence (main effect of crayfish, $F_{1,19} = 7.57$, $p = 0.013$; Table 1). However, significant interactions of this factor with size and patch ($F_{1,19} = 11.55$, $p = 0.009$ and $F_{1,19} =$