

Conspecific alarm cues affect interspecific aggression in cichlid fishes

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Abstract Individuals have to respond simultaneously to different environmental factors often making trade-offs between conflicting demands necessary. Many freshwater ecosystems are resource-limited and both intra- and interspecific competitiveness is a common requirement to gain and defend resources necessary for reproduction. Although predation risk is an important selective force affecting behavioral decisions, little is known about the impact of predation risk on interspecific competition. Here, we investigate whether chemically mediated predation risk affects interspecific territorial aggression by the freshwater cichlid *Pelvicachromis taeniatus*. In our experiments, territorial *P. taeniatus* males were visually confronted with a territorial intruder: a heterospecific, sympatric cichlid (*Benitochromis nigrodorsalis*) which generally induced aggression in *P. taeniatus*. Predation risk for *P. taeniatus* was simulated by a concurrent release of conspecific chemical alarm cues. In control treatments,

no chemical cues, dissolved heterospecific alarm cues, or aliquots of distilled water were provided during these aggressive encounters. The results show that interspecific aggression of territorial male *P. taeniatus* is significantly decreased under predation risk compared to the control treatments. This suggests that interspecific competition becomes less intense under concurrent predation risk. As this process could hinder competitive exclusion, predation risk may indirectly promote and stabilize biodiversity in natural ecosystems.

Keywords *Pelvicachromis taeniatus* · *Pelvicachromis kribensis* · Alarm cues · Interspecific aggression · Interspecific competition · Predation risk

Introduction

In natural ecosystems, animals have to handle numerous interspecific interactions which act as factors in natural selection and accordingly affect phenotype evolution (Kneitel & Chase, 2004; Leibold et al., 2004). In order to maximize fitness, individuals are assumed to respond in an optimal way towards coexisting species. Two major classes of coexisting species to which individual animals should adapt are heterospecific competitors and predators.

Interspecific competition has been suggested to be one of the driving forces of biodiversity in many

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ecosystems (Schluter, 1994; Huisman & Weissing, 1999; Begon, et al., 2005). Sympatric species interact competitively when they have similar ecological demands or when space is limited (Grether et al., 2013). Consequently, outcompeting heterospecifics has been suggested to be beneficial for individual fitness (Schoener, 1982; Bengtsson, 1989). Accordingly, interspecific competition can drive phenotypic changes like behavioral adaptation (e.g., Bourke et al., 1999), morphological character displacement (e.g., Schluter, 1994; Pritchard & Schluter, 2001), and life-history change (e.g., Persson, 1990 but see Jackson et al., 2001; Crow et al., 2010). Interspecific competition consists of indirect exploitative competition and direct interference competition (Grether et al., 2013). Interspecific aggression as a form of direct interference competition is the predominant form of interspecific competition but surprisingly its role has been often neglected in eco-evolutionary studies (Grether et al., 2009, 2013). One of the best researched contexts of interspecific aggression is interspecific territoriality (Peiman & Robinson, 2010). Interspecific territoriality is widespread in aquatic ecosystems and has consequently been reported in many different fish families, e.g., the Pomacentridae (Myrberg & Thresher, 1974), the Gasterosteidae (Peiman & Robinson, 2007) and the Cichlidae (Kohda, 1991; Genner et al., 1999; Maruyama et al., 2010). This is because interspecific territoriality is prevalent in habitats where access to resources and mating opportunities is limited (Schoener, 1987) which is the case for many freshwater ecosystems. In such habitats, the defense of space by interspecific territoriality is critical to secure access to resources even if heterospecifics do not exploit the same resources (Grether et al., 2013).

In addition to competition, predation is a driving force in evolution (Lima & Dill, 1990; Nosil & Crespi, 2006). Predation risk often fluctuates both on a temporal and spatial scale due to changing predator abundances and species compositions (Sih et al., 2000). Hence, antipredator phenotypic plasticity is common (Adler & Harvell, 1990; Brönmark & Miner, 1992; Clark & Harvell, 1992). Such plasticity can either be irreversible developmental plasticity, seasonal polyphenism, seasonal life-cycle staging, or reversible phenotypic flexibility (Piersma & Drent, 2003). As a form of phenotypic flexibility, behavioral decisions are strongly dependent on current predation risk (Lima & Dill, 1990; Lima, 1998). For instance,

under predation risk, safety has to be traded off against foraging opportunities (Pettersson & Brönmark, 1993; Strobbe et al., 2011), against optimal mate choice (Forsgren, 1992; Bierbach et al., 2011) and against intraspecific aggression (Wisenden & Sargent, 1997; Brick & Jakobsson, 2002). The prerequisite for an optimal antipredator response is an accurate determination of predation risk. For this purpose, aquatic animal species commonly use chemical cues, which reliably signal predator presence from a distance (Dodson et al., 1994; Brown, 2003; Ferrari et al., 2010; Steiger et al., 2011; but see Kats & Dill, 1998), because they readily dissolve and disperse in water (Wisenden, 2000; Mirza & Chivers, 2002). In fishes, predation risk can be estimated by detecting either predator-specific chemical signatures (Kats & Dill, 1998) or substances emitted from prey in response to a predation event. Such substances can be actively released disturbance cues (Brown et al., 2008, 2012) or alarm cues that are passively set free by injured conspecifics and reliably signal predator-unspecific predation risk (Mathis & Smith, 1993; Brown et al., 1995; Chivers & Smith, 1998; Vøllestad et al., 2004; Chivers, et al., 2012).

Predators and interspecific competitors often occur concurrently in a habitat and the optimal responses to each of them strongly conflict with each other (Tilman, 2000). For example, the appropriate behavioral response during elevated predation risk (e.g., decreasing activity in order to reduce conspicuousness) conflicts the optimal behavior during the presence of a competitor (e.g., increasing activity and aggression in order to gain or retain access to resources). Hence, optimal antipredator responses, which are exhibited by animals even under concurrent intraspecific competition, are costly (Leibold, 1996; Relyea, 2002; Uriarte et al., 2002; Relyea & Auld, 2005; Teplitsky et al., 2005; Lakowitz et al., 2008). Accordingly, intraspecific aggression as a form of intraspecific competition was also shown to be reduced in the face of predation (e.g., Wisenden & Sargent, 1997; Brick & Jakobsson, 2002; Kim et al., 2004). Despite that, little is known about how animals handle the conflicting demands of interspecific competition and predation. It might be intuitive to assume that similarly to intraspecific competition, animals should respond primarily to predation risk rather than to interspecific competitors when both factors are present. Testing whether this is truly the case is

important to understand the impact of predation risk on interspecific competition. While intraspecific competition drives evolution by causing cycles in the abundance of populations (Schoener, 1973; Pomerantz et al., 1980; Bjørnstad & Grenfell, 2001) and by inducing disruptive selection as a starting point for sympatric speciation (Seger, 1985; Bolnick, 2004; Bürger et al. 2006), interspecific competition was similarly suggested to cause cycles in the abundance of sympatric species (Huisman & Weissing, 1999) and to induce morphological character displacement in individual species, thereby driving the formation of different ecological niches (Grether et al. 2013). Moreover, interspecific aggression includes fighting over space with individuals that can be larger and more dominant (Grether et al., 2013) which accordingly may favor different adaptations than intraspecific aggression which is restricted to competition among individuals with similar phenotypes. Therefore, understanding the ecological consequences of altered interspecific competition— independent of whether the frequency or intensity of competition is affected—is similarly important as understanding intraspecific competition.

Here, we investigate how interspecific competition in a territorial context is influenced by chemically mediated predation risk in a cichlid. Many cichlid species live in resource-limited ecosystems and accordingly display high levels of territoriality (Peeke et al., 1971; Peeke & Peeke, 1982; Oliveira & Almada, 1996; Matsumoto & Kohda, 2004). As competition over breeding territories and food is fierce in many cichlid habitats, territories are also defended against interspecific competitors (Kohda, 1991; Genner et al., 1999; Maruyama et al., 2010). Cichlids feature a fine-tuned olfactory system (see Meuthen et al., 2011 and references therein). They are sensitive to conspecific alarm cues, which are released through injuries (Foam et al., 2005; Barreto et al., 2010) and which have been shown to affect cichlid intraspecific aggression (Wisenden & Sargent, 1997; Kim et al., 2004). In our experiments, we examined the interspecific aggression in males of a territorial West African river cichlid, *Pelvicachromis taeniatus* (Boulenger), which was confronted with a heterospecific, sympatric cichlid species *Benitochromis nigrodorsalis* (Lamboj). *B. nigrodorsalis* occurs in sympatry with *P. taeniatus* in the natural habitat (Linke & Staeck, 2002), their diet is similar and they act aggressively towards each other in a laboratory setting. Therefore, in nature, both species

may compete over feeding habitats and *B. nigrodorsalis* may therefore be a common intruder into *P. taeniatus* territories. In the present experiments it was tested how predation risk alters the interspecific aggression of *P. taeniatus* towards *B. nigrodorsalis* by concurrently adding conspecific alarm cues which were shown to simulate predation risk to *P. taeniatus* (Meuthen et al., 2014). In control trials, we (1) presented *B. nigrodorsalis* with no simulated predation risk (2) concurrently added heterospecific alarm cues to control for a generalized response to injured fish irrespective of species, and (3) concurrently added distilled water to control for the water disturbance caused through introduction of the chemical stimuli.

Materials and methods

Experimental fish

Pelvicachromis taeniatus is a stream-dwelling, socially monogamous and cave breeding cichlid from Western Africa with biparental brood care (Thünken et al., 2007, 2010). Sexes display a pronounced size and color dimorphism (Baldauf et al., 2009, 2011). Males compete for breeding territories, which they defend aggressively (Lamboj, 2004). Large males outcompete smaller ones (Thünken et al., 2011). As in other cichlid species, olfaction is highly sensitive in *P. taeniatus* (Thünken et al., 2009; Meuthen et al., 2011; Hesse et al., 2012), and females of this species respond to conspecific alarm cues with a reduction in swimming activity (Meuthen et al., 2014). *P. taeniatus* used in the experiments were either F₁- or F₂-offspring of wild-caught fish collected in June 2007 from the Moliwe river (04°04'N, 09°16'E) near Limbe, Cameroon; a recent study suggests *Pelvicachromis kribensis* (Lamboj) as an revalidated species name for several *P. taeniatus* populations including the studied one (Lamboj, 2014). Prior to experiments, fish were kept in mixed-sex sibling groups of 10 up to 50 individuals (in total 36 groups; tank sizes were 60 × 45 × 30 cm (L × W × H) or 50 × 50 × 30 cm). Rooms were illuminated in a 12:12 h L:D cycle (light from 9 am to 9 pm) and room air temperature was kept constant between 26 and 27°C. Fish were fed daily ad libitum with a mix of defrosted mosquito larvae of the genera *Chironomus*, *Culex*, and *Chaoborus* as well as *Artemia* sp. in a ratio of 2:1:0.25:1. Experiments were

conducted between June 2010 and February 2011. *B. nigrodorsalis*, another cichlid species within the tribe Chromidotilapiini (Linke & Staack, 2002; Schwarzer et al., 2015), was used as heterospecific competitor during experiments. *B. nigrodorsalis* is the only other territorial cichlid species present in the natural habitat of our *P. taeniatus* population (Thünken T., personal observation). In the laboratory, *B. nigrodorsalis* displays aggression towards *P. taeniatus*, making it likely to be a direct competitor and common intruder into *P. taeniatus* territories in nature. The six adult *B. nigrodorsalis* used during the trials were concurrently caught in the same location of the Moliwe river as the parental F_0 generation of *P. taeniatus* in June 2007. Prior to the experiment, *B. nigrodorsalis* were kept individually in $40 \times 21.5 \times 25$ cm tanks under similar conditions as *P. taeniatus*. All *B. nigrodorsalis* were of similar size (total length $10.92 \pm \text{SD } 0.37$ cm, standard length $8.27 \pm \text{SD } 0.34$ cm, body mass $22.00 \pm \text{SD } 1.74$ g), no sexual dimorphism was perceivable and thus they were assumed to constitute heterospecific competitors of similar quality.

Experimental setup

The experimental setup consisted of three tanks (Fig. 1). The central tank ($40 \times 21.5 \times 25$ cm) contained the heterospecific competitor (*B. nigrodorsalis*) and was adjacent to two smaller tanks ($20 \times 30 \times 20$ cm). These smaller tanks (referred to

as ‘experimental tanks’ from now on) contained one focal fish each (*P. taeniatus*). During acclimation, all tanks were visually separated from each other by removable 20×30 cm opaque, gray plastic sheets. Each of the experimental tanks contained a standard breeding cave (RA-1 ceramic cave with one opening, Kerola, Germany), positioned in the corner next to the front pane that was furthest away from the competitor tank. The opening of the cave was facing towards the central tank with the heterospecific competitor in all cases. In the opposite corner of the same end, a plastic plant fixed on artificial rocks was offered as an additional refuge. Throughout acclimation and the trials, aeration was provided via a gently bubbling $1.5 \times 1.5 \times 3$ cm airstone at the same position as the plant. All tanks were provided with 100 ml gravel sand to cover the ground. A second replicate of the 3-tank experimental setup which was visually separated by a 100×39 cm opaque gray plastic sheet from the original setup allowed four trials to be run at the same day. Furthermore, the outermost sides of the experimental tanks except the front were encased by opaque gray plastic sheets to prevent interaction with adjacent tanks.

Phase I: interspecific aggression under conspecific alarm cues and absence of additional cues

First, we investigated interspecific aggression of focal *P. taeniatus* towards a visually present *B.*

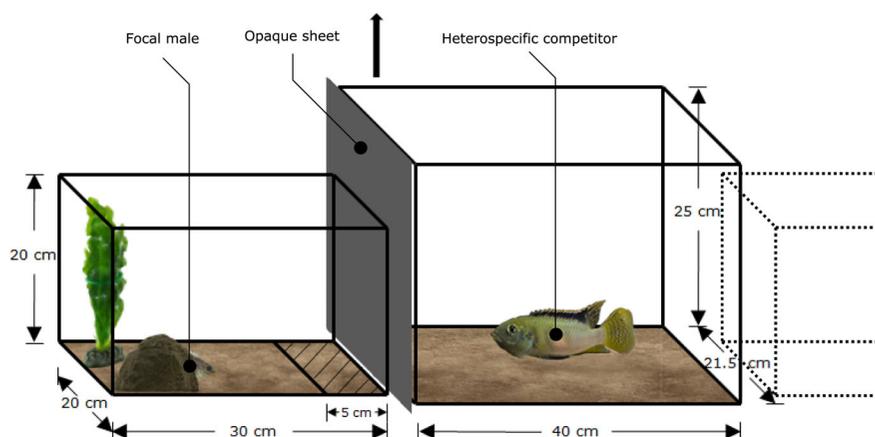


Fig. 1 Experimental setup. During trials, the opaque sheet was removed and the aggressive behavior of the territorial focal *P. taeniatus* male in the front area (hatched region) recorded. Each central heterospecific competitor tank was adjacent to two

experimental tanks housing focal fish that were used in sequence only after an intermission period of at least 90 min (second experimental tank indicated by dotted lines)

nigrodorsalis in the presence or absence of predation risk. In the predation risk treatment ($N = 30$) conspecific alarm cues were added to the *P. taeniatus* tank (see next paragraph for a description as to how they were obtained). Conspecific alarm cues are known to strongly and reliably signal predation risk (Mathis & Smith, 1993; Brown et al., 1995; Chivers & Smith, 1998; Vøllestad et al., 2004; Chivers et al., 2012). In a control treatment without predation risk, we studied the interspecific aggression of the focal *P. taeniatus* while presenting *B. nigrodorsalis* visually without additional cues (no predation risk, $N = 30$).

Chemical cues

Conspecific alarm cues were derived from ten unrelated donor *P. taeniatus* from our laboratory stock (mean \pm SD standard length 3.87 ± 0.27 cm, even sex ratio). Similar to an earlier study on *P. taeniatus* (Meuthen et al., 2014), whole body extracts were used in order to account for the possibility that the putative alarm cue of our particular cichlid species is not only part of the skin. While some previous studies have shown a response towards skin-based alarm cues in a few cichlid species (e.g., Wisenden & Sargent, 1997; Brown et al., 2004) other studies have suggested that in different cichlid species the putative alarm cue might be another substance which is released upon injury such as e.g., blood (Barreto et al., 2013). To prepare alarm cues, the donor fish were euthanized by a blow to the head followed by severing the spinal column according to § 4, § 8b, and § 9(2) of the German animal welfare act (BGB I. I S. 1207, 1313). Subsequently, fish were cut into smaller pieces, placed into a mortar and ground with a pestle so that the putative alarm cues were released. Tissues were then diluted in chilled distilled water so that the concentration each fish was exposed to during trials was 4 mg/l donor fish wet body mass. This concentration is comparable with the concentration of 3.6 mg/l which has been shown to induce significantly different activity in *P. taeniatus* (Meuthen et al., 2014). Afterwards, the liquid phase was stored in 1 ml aliquots (Eppendorf Varipette 100–1000 μ l, Eppendorf, Germany) inside 1.5 ml microcentrifuge tubes at -20°C until use. This temperature allows alarm cues to retain the capacity to elicit fright responses over a long period (Lawrence & Smith, 1989).

Experimental procedure

One day prior to trials, the holding tank of one *B. nigrodorsalis* (the center tank) was surrounded with the two experimental tanks. Afterwards, the experimental tanks were filled with 9 l of substrate-treated water to facilitate quicker acclimation (water previously mixed with gravel sand was shown to enhance activity in *P. taeniatus*, see Meuthen et al., 2011) and all objects were inserted (substrate, ceramic cave, plastic plant, and airstone). The focal *P. taeniatus* were then introduced into the experimental tanks. Subsequently, all fish were fed once with the same food as prior to the experiment and acclimated overnight.

Trials were started by removing the opaque sheet between one focal fish and the central heterospecific competitor tank. For the predation risk treatment, we simultaneously injected 1 ml of our conspecific alarm cue solution. Pre-tests with dyed water revealed that injected liquids disperse throughout the entire tank in a few seconds independent of water movement. As focal fish were neither exposed to alarm cues nor to the visual presence of *B. nigrodorsalis* prior to experiments, all trials constituted the first experience of either stimulus to *P. taeniatus*. Fish behavior was evaluated by a human observer sitting in a distance of 1.25 m to the experimental setup. Evaluation started after the focal fish crossed a reference line which marked a 5×20 cm area in direct proximity to the central heterospecific competitor tank (Fig. 1). Fish behavior was evaluated only during the first time period the focal fish spent inside this front area. Trials in which the focal fish neither entered nor left this area within 30 min, respectively, were not evaluated whereas trials in which the focal fish entered the front area but did not show any aggression were included in the analyses. Exploration activity was inferred by measuring the amount of time each fish required to enter the front area. The amount of time each fish spent inside the front area during its first visit was used as another activity variable. To investigate interspecific aggression, we scored the amount of behavioral displays in which the dorsal fin was raised, i.e., lateral displays during which the focal male positions itself sideways towards its opponent, including more extreme variants where males simultaneously open their mouths,

beat with their tail, and bend their body similar to an S (Barlow, 2000).

After the trial, the focal fish was removed from the experimental tank and its body size (standard length: from snout to the tail fin base) was measured to an accuracy of 1 mm. Subsequently, the cave, plant and substrate were removed from the tank. Except for the substrate, all objects were reused in other trials after rinsing them with hot water. Furthermore, the tank was cleaned with 3% hydrogen peroxide to remove olfactory traces (McLennan, 2004; Mehlis et al., 2008). The tank was then rinsed with clear tap water and subsequently, refilled with 9 l of substrate-treated water. Also, the cave and plant were returned to the tank and new substrate was added. Following this procedure, the next fishes were acclimated.

Four trials were conducted per day, i.e., four *P. taeniatus* males with two different *B. nigrodorsalis* as heterospecific competitors. To prevent confounding habituation effects, competitors were reused only after an intermission period of at least 90 min. Furthermore, individual *B. nigrodorsalis* were not used at two consecutive days.

Phase II: interspecific aggression under heterospecific alarm cues and distilled water

Based on the results of the first experimental phase, we decided to run two additional control treatments in the same context. In order to exclude that the response towards the conspecific alarm cue treatment was a mere response towards injured fish and not a response towards conspecific alarm cues (indicating species-specific predation risk), we investigated interspecific aggression in the presence of heterospecific alarm cues ($N = 7$, see next paragraph for a description as to how they were obtained). Furthermore, as we wanted to exclude the possibility that interspecific aggression may have been influenced by water disturbance caused by the injection of the chemical stimuli, we applied distilled water as a second control treatment ($N = 6$). We used minimal necessary sample sizes in the second phase to consider animal welfare regulations because during the first phase we noticed that visual exposition of *P. taeniatus* to *B. nigrodorsalis* is stressful for *P. taeniatus*. This became apparent by a treatment-independent stress-based melanization and by a denial of food uptake after visual exposition to *B. nigrodorsalis* (Meuthen D., personal observation).

Chemical cues

We extracted heterospecific alarm cues from the swordtail *Xiphophorus helleri* (Heckel) because as other poeciliids they have a well-studied alarm cue system (Mirza et al., 2001). Furthermore, *P. taeniatus* of our “Moliwe” population live in sympatry with the african poeciliid *Procatopus similis* (Ahl) and may therefore have an evolutionary exposure to poeciliid alarm cues (Ghedotti, 2000). Moreover, alarm cues derived from *X. helleri* are a common heterospecific alarm cue control in cichlid studies (Brown et al., 2004; Foam et al., 2005; Pollock et al., 2005). Donor swordtails were obtained from a commercial fish supplier and kept in a $50 \times 50 \times 30$ cm tank at the same conditions as the donor *P. taeniatus* 1 week prior to alarm cue preparation. Subsequently, we extracted heterospecific alarm cues from the skin of seven donor swordtails *X. helleri* (standard length 3.21 ± 0.34 cm, three males and four females). We took care to avoid the inclusion of underlying muscle or visceral tissue because the alarm cues of poeciliids is located exclusively within their skin (Mirza et al., 2001). Heterospecific alarm cues were prepared with the same methods as applied for conspecific alarm cues (see phase 1) and were of the same concentration (4 mg/l donor fish wet body mass during trials, equivalent to a concentration of $0.5 \text{ mm}^2/\text{l}$ skin). This concentration is comparable with studies on the ostariophysan *Pimphales promelas* (Rafinesque) in which significant behavioral antipredator responses have been shown (Chivers & Smith, 1994a, b). As before, we stored 1 ml aliquots of heterospecific alarm cues at -20°C until use. Likewise, for the water disturbance control, we stored 1 ml aliquots of distilled water at the same temperature.

Experimental procedure

Experiments were conducted with the same methods as during the phase 1 experiments with two exceptions.

First, in phase I, $\sim 20\%$ of all test fish hid behind the airstone and did not respond to the heterospecific competitor, leading to non-evaluable experiments whose results could not be included in our data. Hence, we removed the airstones during the phase II trials, which led to a higher proportion of successful trials.

Second, due to time constraints, we replaced the human observer in phase I by a digital video camera in phase II (QuickCam 9000, Logitech, China). We recorded fish behavior from a 10 cm distance of the front pane in order to minimize experimenter-fish interaction. Records from the phase II experiments were afterwards evaluated by a naïve observer by the same methods as described before.

Statistical analysis

In our experiment, 58 trials (predation risk $N = 21$, no predation risk $N = 26$, heterospecific alarm cue risk control $N = 5$, water disturbance risk control $N = 6$) could be analyzed. These fish were derived from 30 different families but we never exposed more than two individuals from a single family to the same treatment. Focal *P. taeniatus* males were used only once. Within a single day, the same heterospecific competitor (*B. nigrodorsalis*) was subsequently presented to two males receiving the same treatment but only after an intermission period of at least 90 min.

As data were overdispersed and non-normally distributed, we could not analyze the full dataset by applying mixed models controlling for family identity. Therefore, we removed that sibling which deviated stronger from average body size (calculated over all fish) from each family contributing two fish. This approach avoids pseudoreplication due to family origin (because only one fish per family was used) and reduces random variation caused by body size which thereby increases statistical power (absolute body size and body size differences are often linked to the amount of aggression, see Taylor & Elwood, 2003). The results derived from this dataset which are reported here do not differ qualitatively from the analyses on the full dataset independent of family identity or from a dataset containing averaged data over related fish. The final sample size used for analysis consisted of 41 trials: 15 from fish under predation risk, 15 from fish with no predation risk, 5 from fish of the heterospecific alarm cue risk control and 6 from fish of the water disturbance risk control. Fish body size ranged from 4.1 to 7 cm in size but did not differ significantly among treatments (Kruskal–Wallis rank sum test, $df = 3$, $\chi^2 = 2.807$, $P = 0.422$; mean \pm SD: predation risk 5.21 ± 0.95 cm, no predation risk 5.44 ± 0.85 cm, heterospecific alarm cue risk control 5.72 ± 0.95 cm, water disturbance risk

control 5.83 ± 1.01 cm). The mean time spent inside the front area correlated significantly with the mean aggression level (Spearman's rank correlation, $\rho = 0.759$, $P < 0.001$). This was expected because these factors are inherently linked (displaying aggression requires time, which subsequently increases the time in the front area with increasing aggression). Further analyses revealed that variation in both aggression and time spent in the front area is explained by the same factors in all cases. In contrast, exploration activity (time to enter the front area) neither correlated significantly with aggression level (Spearman's rank correlation, $\rho = -0.224$, $P = 0.160$) nor with the time spent inside the front area (Spearman's rank correlation, $\rho = -0.293$, $P = 0.063$). Moreover, focusing on behavioral differences between experimental phases revealed that in contrast to interspecific aggression, exploratory activity was clearly influenced by the difference in methods rather than differences in the treatment (see Electronic Supplementary Material 1, ESM 1). Fish explored significantly faster when they were recorded by a digital video camera compared to a human observer; in contrast, interspecific aggression was not significantly affected by the change in methods between experimental phases (ESM 1). Hence, we could analyze variation in interspecific aggression among treatments independent of experimental phases which is necessary to control for all confounding factors potentially influencing interspecific aggression (see above).

All analyses were conducted using R 2.9.1 (R Core Team, 2009). Because the analysis of the aggression level was based on count data (the number of displays), we applied generalized linear models (GLM) assuming a Poisson distribution. As data showed overdispersion, we assigned quasipoisson distributions and log link functions throughout models; F values are provided. All tests of statistical significance were based on likelihood ratio tests (LRT), which assessed whether the removal of a variable caused a significant decrease in model fit; hence degrees of freedom differed by three in the full models (which include all four treatments) and by one in the post hoc models comparing two treatments each. P values refer to the increase in deviance when the respective variable was removed. Test probabilities are two-tailed throughout.

We initially created a combined dataset consisting of all four treatments (from both phases) and tested the

effect of the explanatory variable ‘treatment’ (predation risk: conspecific alarm cues, no predation risk: without chemical cues, heterospecific alarm cue risk control: heterospecific alarm cues, water disturbance risk control: distilled water) on the independent variable ‘male aggression level’ (amount of displays) and afterwards ran pairwise comparison tests between individual treatments. Furthermore, we tested the impact of *P. taeniatus* size on its interspecific aggression by entering ‘body size’ (standard length) as an additional factor to the model. Lastly, we analyzed interactive effects of body size and treatment on male aggression (‘body size’ \times ‘treatment’ interaction).

Results

The level of interspecific aggression of *P. taeniatus* males was significantly affected by chemically simulated predation risk (LRT, $df = 3$, $F = 4.274$, $P = 0.011$, Fig. 2). Under predation risk, i.e., in the presence of conspecific alarm cues, male *P. taeniatus* showed significantly less aggression than in all other treatments (all $P < 0.05$, Fig. 2). In contrast, male aggression levels did not differ significantly between the no predation risk treatment and the heterospecific

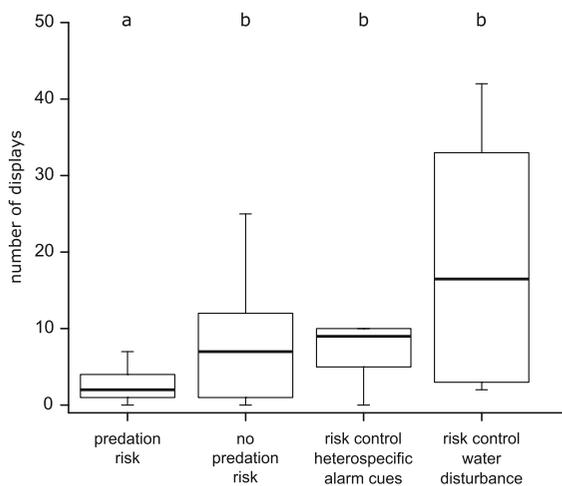


Fig. 2 Territorial aggression of *P. taeniatus* inferred by the number of displays (median \pm quartiles, whiskers indicate highest/lowest values within the range between the 1st quartile $-1.5 \times$ interquartile range and the 3rd quartile $+1.5 \times$ interquartile range) towards a heterospecific competitor in the different treatments. Different letters denote significant differences ($P \leq 0.05$)

alarm cue/distilled water risk control treatments (no predation risk vs. heterospecific alarm cues, LRT, $df = 1$, $F = 0.010$, $P = 0.922$; no predation risk vs. water disturbance, LRT, $df = 1$, $F = 1.461$, $P = 0.242$). *P. taeniatus* body size neither predicted the level of male aggression independent of treatment (LRT, $df = 1$, $F = 1.929$, $P = 0.173$) nor was the relationship between male size and the level of its aggression different among treatments (interaction body size \times treatment, LRT, $df = 3$; $F = 0.303$, $P = 0.823$).

Discussion

In the present study, interspecific competition was mediated by predation risk. Interspecific aggression of male *P. taeniatus* decreased in the presence of conspecific injury-released chemical alarm cues. This result is in line with other studies which have suggested that predation risk generally causes trade-offs in behavioral decisions (Lima & Dill, 1990; Lima, 1998). More specifically, our result is in accordance with studies on intraspecific competition in cichlids, which report decreased aggression among conspecifics during elevated predation risk (Wisenden & Sargent, 1997; Brick & Jakobsson, 2002; Kim et al., 2004). Thus, predation risk affects interspecific aggression similarly to intraspecific aggression. The similar influence of predation risk on intra- and interspecific aggressiveness may seem intuitive because many cichlid species defend their territory aggressively in order to secure access to resources independent of whether they compete with conspecifics (Peeke et al., 1971; Peeke & Peeke, 1982; Oliveira & Almada, 1996; Matsumoto & Kohda, 2004) or heterospecifics (Kohda, 1991; Genner et al., 1999; Maruyama et al., 2010).

From an evolutionary perspective, reduced interspecific aggression under predation risk as in our study may indirectly promote and stabilize biodiversity in natural ecosystems. Usually, interference competition as mediated through interspecific aggression is assumed to decrease biodiversity by competitive exclusion. First, interference competition can work together with a superior capability to exploit resources—which hastens competitive exclusion when the species better at exploitation is also superior in interference competition (Amarasekare, 2002).

However, when the role of interference competition is reduced in the face of predation, the capability to exploit resources could become the primary factor for species persistence. This restriction to exploitative competition is expected to promote and stabilize biodiversity in natural ecosystems as it is assumed that exploitative competition over resources alone generates oscillations in species abundances which stabilize total community biomass while allowing the coexistence of many different species (Huisman & Weissing, 1999). Second, interference competition may also cause dominant species to limit the access to resources for sympatric species even when the former species does not require the resources itself (Grether et al., 2013). In contrast, variation in interference competition, e.g., mediated by predation risk, may allow subordinate species to gain access to resources—preventing the competitive exclusion of the subordinate species and thus stabilizing biodiversity. In fact, this indirect stabilization of species diversity in ecosystems through predation risk would be similar to what is predicted to happen when predators directly affect biodiversity (reviewed in Chesson, 2000). For example, as predators usually prey on the prey species with the highest abundance, they target different species over time which in turn causes both interference competition and exploitative competition among prey to become less significant for species persistence. This process is predicted to stabilize biodiversity (Parrish & Saita, 1970; Cramer & May, 1972; Pimm, 1984).

Another possibility to interpret our results is that *P. taeniatus* identified the heterospecific *B. nigrodorsalis* as a predator instead of a competitor through the presence of conspecific alarm cues. Other studies suggest that conspecific alarm cues drive threat-sensitivity against novel cues (Brown et al., 2013, 2014; Chivers et al., 2014), ultimately leading to novel predator recognition (Göz, 1941; Berejikian et al., 1999; Brown et al., 2001; Brown, 2003; Holmes & McCormick, 2010). However, to our knowledge only one study suggests that conditioning fish by pairing alarm cues with the visual cues of an unfamiliar, non-predator fish afterwards causes antipredator responses towards this particular fish (Chivers & Smith, 1994a). If this was also the case in our study, it would explain reduced aggression in the presence of conspecific alarm cues. Aggression requires close proximity to the

recipient and thus constitutes a high-risk behavior when the recipient is a predator. Hence, a reduction in aggression when confronting predators is likely to be beneficial for individual fitness. This hypothesis would also be in accordance with our results.

The response of our test fish towards alarm cues furthermore add to an earlier study on females of the same species, which reduced their activity in response to conspecific alarm cues (Meuthen et al., 2014). Taken together, these results suggest that *P. taeniatus* possesses an alarm cue system analogous to other cichlids (Wisenden & Sargent, 1997; Kim et al., 2004; Foam et al., 2005; Barreto et al., 2010). Furthermore, the behavioral response of *P. taeniatus* males was specific to conspecific alarm cues; heterospecific alarm cues did not cause significant changes in the level of interspecific territorial aggression. These antipredator responses to conspecific but not heterospecific alarm cues are in accordance to other studies on cichlids (Brown et al., 2004; Foam et al., 2005; Pollock et al., 2005).

Conclusion

The present study suggests that interspecific aggression and consequently interspecific competition is affected by predation risk. Our study adds to the field of interspecific interference competition which still constitutes a wide-open field for research (Grether et al., 2013). However, further studies are required to fully understand how predation risk affects interspecific competition under natural conditions. In nature, stressors such as resource limitation or injuries caused by previous fights, which were not included into our experiments, are likely to alter the impact of predation risk on interspecific competition. Such research would allow us to gain a more comprehensive insight into the relationship between interspecific competition and predation in natural communities.

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