Predatory developmental environments shape loser behaviour in animal contests

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Abstract

High predation risk during development induces phenotypic changes in animals. However, little is known about how these plastic responses affect signalling and competitiveness during contests. Herein, we have studied the consequences of anti-predator plasticity during the intra-sexual competition of *Pelvicachromis taeniatus*, a cichlid fish with mutual mate choice. We staged contests between adult size-matched siblings of the same sex derived from different environments: one fish was regularly exposed to conspecific alarm cues since the larval stage (simulating predator presence), the other fish to control conditions. Rearing environment did not affect the winner of contests or total aggression within a fight. However, contest behaviour differed between treatments. The effects were especially pronounced in alarm cue-exposed fish that lost a contest: they generally displayed lower aggression than winners but also lower aggression than losers of the control treatment. Thus, perceived predator presence modulates intra-sexual competition behaviour by increasing the costs associated with fighting.

Keywords

Pelvicachromis taeniatus, alarm cues, signal honesty, intra-sexual competition, sexual selection, predation risk, predator-induced phenotypic plasticity.

1. Introduction

Animal contests during intra-sexual competition are a central aspect of sexual selection (Earley & Hsu, 2013; McCullough et al., 2016). These contests often follow ritualized behavioural sequences whose underlying principles

are similar across diverse taxa (Archer & Huntingford, 1994): contests start with the exchange of low-cost aggressive behaviours such as displays that signal individual strength. If individuals greatly differ in competitiveness, then the weaker contestant will often withdraw at this early stage. Otherwise, the fight will escalate and include overt aggression such as attacks that can cause severe injuries. At this stage, the individual that is able to maintain its level of aggression is predicted to win the fight by the war-of attrition model (Maynard-Smith, 1974). In contrast, the loser will stop displaying any aggressive behaviour, and instead show submissive behaviour and retreat so as to avoid further damage. Such fight patterns have been observed in multiple species, for example in cichlids (Jakobsson et al., 1979; Mosler, 1985), in lizards (Rand & Rand, 1976; Bradbury & Vehrencamp, 2011) and in crickets (Hofmann & Schildberger, 2001). Still, recent research revealed substantial variation in animal signalling during contests, and the underlying mechanisms remain a puzzle in biology (Field & Briffa, 2013; Tibbetts, 2014). Environmental variation may affect the perceived costs and benefits of signals and developmental plasticity has been suggested as a mechanism that breaks down signal reliability (Ingleby et al., 2010; Hunt & Hosken, 2014). Although contest behaviour has evolved in fluctuating natural environments, few studies have considered the effect of different developmental environments on contest behaviour later in life (Royle et al., 2005; Palaoro et al., 2017).

One of the best-studied cases of adaptive plasticity comes in the form of behavioural and morphological changes resulting from exposure to predator-related cues. Increased vigilances and the development of morphological defences are beneficial in the presence of predators but they may conflict with fitness-enhancing activities such as foraging, competition and mate choice, generating a trade-off between investment in anti-predator responses and other activities (Sih, 1980; Helfman, 1989; Houston et al., 1993; reviewed in Kishida et al., 2010). Accordingly, anti-predator plasticity leads to competitive disadvantages against non-plastic individuals in animal contests. Predator-exposed *Rana sylvatica* tadpoles are worse competitors (Relyea, 2002) and high-risk wild-caught damselfish (*Pomacentrus amboinensis*) have competitive disadvantages against low-risk individuals in a predator-free environment (Ferrari et al., 2019). This trade-off is modulated by cognitive rules that follow the threat-sensitivity hypothesis. This hypothesis postulates that the level of predation risk alters the costs and benefits of

fitness-related behaviours. Thus, with increasing risk, animals should invest more in costly anti-predator strategies and less into other behaviours (Helfman, 1989).

Our first hypothesis is that individuals growing up in a predatory environment should be worse competitors and less likely to win intra-sexual contests. Second, following the threat-sensitivity hypothesis, we hypothesize that growing up in the presence of alarm cues should alter the costs and benefits of fighting, leading to a lower investment in contests. To test these hypotheses, we study the effect of a predatory developmental environment on fighting behaviour during intra-sexual competition. Our study species is *Pelvicachromis taeniatus*, a small, socially monogamous Western African river cichlid with mutual mate choice and intra-sexual competition in both sexes (Thünken et al., 2011, Baldauf et al., 2011) that responds with adaptive plasticity to perceived predation risk (Meuthen et al., 2016, 2018a).

2. Materials and methods

2.1. Experimental fish

In 2007 we collected adult *P. taeniatus* from the Moliwe river (Cameroon, 04°04'N, 09°16'E) as a breeding stock. *P. taeniatus* becomes sexually mature at an age of approximately one year and lives up to six years. In 2012, 12 different adult F1 pairs were bred to generate the clutches used in this study. Clutches were then split into two equally-sized groups that were, from hatching onwards for five days a week over three years, exposed to two different chemical cues. These were either a control treatment of distilled water ('control fish') or chemical alarm cues derived from ground whole conspecifics ('alarm cue-exposed fish') in a concentration of 7.2 mg/l, which induces clear behavioural and morphological anti-predator responses in *P. taeniatus* (Meuthen et al., 2016, 2018a; Meuthen et al., 2018b) and in other fish (Chivers & Smith, 1994a). Conspecific alarm cues are innately recognized cues (Chivers & Smith, 1994a,b) and the effects of prolonged exposure to them mirror findings from natural water bodies where predators are present (Stabell & Lwin, 1997; Laforsch et al., 2006; Meuthen et al., 2019b). Also, in contrast to predator odours, fish do not appear to habituate to conspecific alarm cues even after repeated exposure (Imre et al., 2016). In 2015, three-year-old adult fish derived from this split-clutch design were then tested in intra-sexual competition trials where alarm cues were absent.

2.2. Competition experiment

Preliminary trials revealed that the presence of alarm cues inhibits any competitive interaction between *P. taeniatus*. Theoretically, the absence of alarm cues during trials may represent a predator-free environment and thereby alter the behavioural response. However, following the risk allocation hypothesis, not only current risk but also the proportion of time at high risk is what shifts individual decision-making to a focus on anti-predator responses (Lima & Bednekoff, 1999; Ferrari et al., 2009). This hypothesis has been confirmed in many empirical studies on fish, ranging from the cyprinid *Pimephales promelas* (Meuthen et al., 2019a,b) to *P. taeniatus* (Meuthen et al., 2016). Here, we staged contests between siblings of the same sex that were raised in different treatments; hence individual contests were always between an alarm cue-exposed fish and a control fish. Because alarm cue exposure did not affect individual morphology in our fish at the age of testing as outlined in Meuthen et al. (2018a), we size-matched fish to a <5% total length difference so as to mitigate size-based contest resolution (sensu O'Connor et al., 2015). As there was substantial between-family variation in body size, only by using siblings we were able to obtain fish similar in body size. Moreover by using siblings, we were able to control for genetic effects that may lead to differences in competitiveness. To ensure that fish competed with each other in a context of sexual reproduction and to minimise inter-individual variation in behaviour arising from differences in social status ('winner/loser effects'), we isolated individual fish for one week prior to trials and stimulated them (by placing smaller tanks in front of the isolation tanks) daily first for 15 minutes with a fish of the same sex and thereafter for 15 minutes with a fish from the opposite sex (see e.g. Thünken et al., 2014). Then, fish were transferred to the experimental set-up, which consisted of a 20 × 30 × 20 cm (length × width × height) tank that was separated into two equally sized compartments (20 × 15 × 20 cm each) by a retractable grey opaque plastic sheet and acclimated overnight. Afterwards, we removed the sheets via a pulley-rope system and allowed fish to freely interact with each other; we recorded interactions between competitors for a period of up to three hours (QuickCam 9000, Logitech, Suzhou, China). The time until winners and losers were determined differed between pairs (median, interquartile range (IQR): 731.0, IQR 393.5–1354.0 s), but the treatment of the winning fish did not affect this duration (independent

Wilcoxon test, $W = 125$, $p = 0.830$). Refuges were not available during trials as they also inhibited any interaction between fish during preliminary experiments; moreover we planned to terminate trials as soon as one fish suffered visible injury. However, this scenario never occurred throughout experiments, suggesting that the staged competition did not negatively impact fish welfare. After each trial, individual fish were measured on graph paper to an accuracy of 0.5 mm. Each fish was used only once; in total we tested 62 fish in 31 staged competitions (16 male–male competition, 15 female–female competition).

2.3. Data analysis

A naïve observer scored individual fish behaviour until 5 minutes after the competition was resolved (as indicated by one fish assuming typical loser behaviour where they turn black, fold their fins and behave submissively by not retaliating towards the other fish, see Enquist & Jakobsson, 1986; Barlow, 2000). Agonistic behaviours were scored as displays or attacks as defined in previous studies of cichlids (Jakobsson et al., 1979; Enquist et al., 1990; Barlow, 2000). Afterwards, we calculated the number of displays and attacks per minute because as opposed to analysing raw behaviours, this allowed us to statistically compare behavioural frequencies between contests of unequal length. Moreover, we identified winner and loser identity (with the ‘loser’ being the individual that turns black, folds its fins, behaves submissively and does not retaliate against further attacks by the ‘winner’ for a period of 5 minutes).

2.3.1. Statistical analysis

Male and female competitions did not differ in the frequency of lateral displays (independent Wilcoxon test, $W = 88$, $p = 0.213$) or in the frequency of attacks (independent Wilcoxon test, $W = 90.5$, $p = 0.251$). Because of these results and due to our small sample size per sex/treatment combination that would lead to over-parameterized models (thereby substantially increasing the likelihood of a false positive result), we pooled results between sexes for analysis. Results were then analysed based on exact binomial tests and $\log_{10}$ -transformed data (with an added constant value of 1 so as to achieve normal distribution) with linear mixed-effect models from the ‘nlme’ package (Pinheiro et al., 2018) of R 3.2.5 (R Core Team, 2016). Here we entered winner/loser identity and treatment as fixed factors and trial (dyad identity) and fish family as random factors and studied their interaction. By

including trial as a random factor in the model, we accounted for the fact that the behaviour of the two contestants within a dyad is not independent. Across models, all tests of statistical significance were based on likelihood ratio tests (LRT; $\chi^2 = -2 * (\log_{10}(\text{likelihood_model_1}) - \log_{10}(\text{likelihood_model_2}))$), which assessed whether the removal of a variable caused a significant decrease in model fit according to the Aikake information criterion; degrees of freedom differed by one in all models. The reported p values refer to the increase in deviance when the respective variable was removed.

3. Results

Treatment did not significantly affect the proportion of fights won (alarm cue-exposed fish won 14 times in 31 staged competitions, exact binomial test, $p = 0.720$). Independent of treatment, winners displayed towards (LRT, $\chi^2 = 7.156$, $p = 0.008$) and attacked (LRT, $\chi^2 = 6.426$, $p = 0.011$) losers significantly more often, but we did not find evidence for general treatment effects independent of winner/loser identity for displays (LRT, $\chi^2 = 0.018$, $p = 0.894$) or attacks (LRT, $\chi^2 = 0.643$, $p = 0.423$). However, we found that alarm cue-exposed winners and losers behaved differently than controls as shown by a significant interaction between winner/loser identity and treatment for displays (interaction winner/loser identity $\times$ treatment, LRT, $\chi^2 = 4.248$, $p = 0.039$, Figure 1a) and a non-significant interaction for attacks (interaction winner/loser identity $\times$ treatment, LRT, $\chi^2 = 2.826$, $p = 0.093$, Figure 1b). Within control fish, there were no significant differences between winners and losers for displays (LRT, $\chi^2 = 1.117$, $p = 0.291$) or attacks (LRT, $\chi^2 = 0.051$, $p = 0.821$). However, losers that grew up in the presence of alarm cues displayed towards (LRT, $\chi^2 = 6.674$, $p = 0.010$) and attacked (LRT, $\chi^2 = 6.892$, $p = 0.009$) their opponents significantly less often than alarm cue-exposed winners. Within losers, alarm cue-exposed fish displayed towards (LRT, $\chi^2 = 4.502$, $p = 0.034$) and attacked (LRT, $\chi^2 = 3.358$, $p = 0.067$) their opponents less often than fish from the control treatment. Moreover, when control fish won, the losers that were exposed to alarm cues during development displayed towards (LRT, $\chi^2 = 4.717$, $p = 0.030$) and attacked (LRT, $\chi^2 = 4.949$, $p = 0.026$) their opponents less often. In contrast, alarm cue-exposed winners tended to display more towards their opponents than control winners (LRT, $\chi^2 = 3.196$, $p = 0.074$) but did not attack them more often (LRT, $\chi^2 = 1.347$, $p = 0.246$). At the same time,

Figure 1. (a) Displays and (b) attacks per minute (mean $\pm$ SE) during *P. taeniatus* intra-sexual competition. Competing fish were raised either under perceived predator presence (alarm cue-exposed) or in a control environment (distilled water). Shown is the frequency of attacks (butts, nips, tail-beats, approaches) for alarm cue-exposed (dashed bars) and control (open bars) winners and losers, respectively. Asterisks denote statistically relevant differences and the topmost line in each figure indicates the significance of the interaction. ** $p < 0.01$; * $p < 0.05$; (*) $p < 0.1$; ns, $p > 0.1$.

when fish that grew up in the presence of alarm cues won, they displayed tendentially more than their losing control opponents did (LRT, $\chi^2 = 2,771$, $p = 0.096$) whereas the frequency of attacks was comparable between the contestants in a dyad (LRT, $\chi^2 = 2.119$, $p = 0.146$).

4. Discussion

To determine the consequences of anti-predator phenotypic plasticity in animal contests, we staged fights between same-sexed pairs of adult size-matched sibling *P. taeniatus* that were obtained from different environments. Within each dyad, one fish was exposed to high perceived risk (i.e., alarm cues) during development and the other fish to a control developmental environment. In contrast to the expected costs associated with anti-predator plasticity, the alarm cue developmental environment did not directly cause competitive disadvantages that influenced the outcome of intra-sexual contests. However, fish that grew up in the presence of alarm cues differed from control fish in their contest behaviour. This effect was especially pronounced in alarm cue-exposed fish that lost: they displayed less agonistic behaviour than winners from both treatments but also lower aggression than losers of the control group. In contrast, fish from the control treatment behaved the same independent of whether they won or lost.

Our finding that alarm cue-exposed losers displayed and attacked their opponents less than winners is consistent with the war-of-attrition model, which predicts that the loser of a contest is the individual that is unable to match the display and attack frequency of its opponent (Maynard-Smith, 1974), a pattern that has also been shown in many empirical studies (Rand & Rand, 1976; Jakobsson et al., 1979; Mosler, 1985; Hofmann & Schildberger, 2001; Bradbury & Vehrencamp, 2011). This is related to the energetic and injury-related costs associated with performing displays and attacks, which makes the maximum frequency of these behaviours a reliable indicator of individual quality and strength. The cost of these signals are further increased in predatory environments because conspicuous signallers (Zuk & Kolluru, 1998) and exhausted individuals (Yachi, 1995) are more prone to attacks by predators. Consequently, exposure to alarm cues during development appears to have modulated the perceived costs of fighting in accordance with the threat-sensitivity hypothesis (Helfman, 1989). In predatory environments, low-quality fish that eventually emerge as losers are unable to compensate

for the increase in conspicuousness to predators that is associated with an increased display frequency (Zuk & Kolluru, 1998). This is because the lower energy reserves of low-quality individuals cause them to easily become exhausted during a contest. In a predatory environment, where exhausted prey are at high risk to be eaten (Yachi, 1995), such low-quality individuals face substantial predation risk when participating in a prolonged contest. Hence, the aim of low-quality losers should be to minimise competition-related costs by reduced investment into aggressive behaviour frequency and a focus on early disengagement. Alternatively, the high cost associated with fighting in a predatory environment forces losers to spend more energy on accurate sensory perception during the fight. This should cause a more accurate assessment about their own subpar and their opponent's superior fighting capabilities, leading to a quick fight resolution as soon as minimal differences between individual abilities are detected.

In our control environment, high-quality winners and low-quality losers did not differ in their behavioural frequencies. Following our hypothesis, the absence of predation risk reduces the costs of fighting and thereby allows losing *P. taeniatus* to take more risks during contests. At low predation risk, low-quality individuals should invest more energy into the fight as an attempt to win even when the probability to do so is low. Moreover, at low risk levels, losers may decide to invest more energy into repeating aggressive behaviours and less into sensory systems. This comes at the cost of a less accurate assessment of their own and their opponent's fighting capabilities.

At first glance, our results appear contrary to the finding that in the presence of predators, male sticklebacks of poor condition terminally invest into larger sexual ornaments than high-condition males (Candolin, 1999). However, we propose that the consequences of a predatory developmental environment differ from those of acute predator presence during trials (Candolin, 1999). At the same time, the results of our experiment match previous studies suggesting that losers display fewer agonistic behaviours during intra-sexual competition only when wild-caught fish, which likely experienced some degree of predation, are studied (Roy & Bhat, 2015) while this does not appear to be the case for lab-reared fish that have never experienced predation (Leiser et al., 2004). This may reflect how previous exposure to predation risk increases the perceived costs of fighting and thereby modulates loser behaviour. Hence, future animal contest research should consider

incorporating previous exposure to predation risk in their study design as this may improve our knowledge about the evolution of animal signals.

Alternatively, our results can be interpreted in a signal honesty context. Animal signals do not evolve to make information transfer accurate, but instead in a direction that maximises fitness benefits for the signaller (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984). Likewise, this should lead to the evolution of an optimal level of deceit in displays during animal contests (Bond, 1989). By exaggerating their quality when fighting against an opponent of similar or higher quality, dishonest individuals can prolong and escalate the fight and eventually win at a cost of increased exhaustion and damage. When two individuals of similar quality compete, dishonest exaggerated signalling by only one individual may appear to be able to decide a fight. However, in these circumstances, both individuals will evolve to signal dishonestly (Maynard-Smith & Parker, 1976), which escalates the fight and eventually decides the outcome by conventional means at the cost of both individuals being more exhausted. However, in a predatory environment, the costs of dishonest signalling are exacerbated. Conspicuous signallers and exhausted prey are subject to higher predation risk (see above), which should select against dishonest signalling. High-quality individuals have greater energy reserves and more muscle mass, which allows them to escape from predators even after a fight. Instead, low-quality individuals cannot do so and hence are unable to compensate for the increase in predation risk caused by dishonestly exaggerated signalling. Consistent with this alternative hypothesis, we found that alarm cue-exposed losers (which are low-quality fish) displayed and attacked less often than winners (which are high-quality fish). However, in control fish, losers (low-quality fish) did not show different frequencies of displays and attacks from winners (high-quality fish); control losers displayed almost the same frequencies of behaviours as winners, hinting at dishonestly exaggerated behavioural frequencies. Alternatively, the reduced frequencies of contest behaviour in alarm cue-exposed losers constitute a more honest signal as they are incapable of winning and thus have nothing to gain by an increased investment into exaggerated signalling. In other words, alarm cue-exposed losers did more of what is expected of losers whereas this was not the case for control fish. Nevertheless, signal honesty appears to be maintained only in alarm cue-exposed losers, suggesting that predation may be an evolutionary driver of signal honesty due to the elevated predation risk associated with signalling.

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