



Social cichlid fish change behaviour in response to a visual predator stimulus, but not the odour of damaged conspecifics



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ABSTRACT

Predation is one of the primary drivers of fitness for prey species. Therefore, there should be strong selection for accurate assessment of predation risk, and whenever possible, individuals should use all available information to fine-tune their response to the current threat of predation. Here, we used a controlled laboratory experiment to assess the responses of individual *Neolamprologus pulcher*, a social cichlid fish, to a live predator stimulus, to the odour of damaged conspecifics, or to both indicators of predation risk combined. We found that fish in the presence of the visual predator stimulus showed typical antipredator behaviour. Namely, these fish decreased activity and exploration, spent more time seeking shelter, and more time near conspecifics. Surprisingly, there was no effect of the chemical cue alone, and fish showed a reduced response to the combination of the visual predator stimulus and the odour of damaged conspecifics relative to the visual predator stimulus alone. These results demonstrate that *N. pulcher* adjust their anti-predator behaviour to the information available about current predation risk, and we suggest a possible role for the use of social information in the assessment of predation risk in a cooperatively breeding fish.

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1. Introduction

Predation has direct costs in terms of loss of life or injuries sustained during unsuccessful predation attempts (Beauchamp et al., 2007; Nonacs and Blumstein, 2010). Predation can also carry substantial indirect costs in terms of the time and energy required for anti-predator behaviours, which can detract from other important activities such as foraging and reproduction (Lima and Dill, 1990). Because anti-predator behaviour is in itself costly, there should be strong selective pressure for individuals to closely match their anti-predator responses to the current risk of predation in the environment (Helfman, 1989). Information regarding the presence and threat level of a predator can come from visual, olfactory, auditory, and tactile cues emitted directly by the predator, or indirectly

through information about predation produced by conspecifics or heterospecifics (Thorson et al., 1998).

In the aquatic environment, chemical cues are often used to assess predation risk (see reviews by Smith, 1997; Wisenden, 2000, 2015; Ferrari et al., 2010). These may include disturbance cues (i.e. chemical cues released by nearby individuals that have detected a predator; Hazlett 1990; Chivers and Smith, 1998; Ferrari et al., 2010; Wisenden, 2000), kairomones (i.e. chemical cues that are directly released by a predator, Kats and Dill, 1998; Ferrari et al., 2010) and damage-released cues (Chivers and Smith, 1998; Dalesman et al., 2007; Ferrari et al., 2010). Damage-released cues appear to be a particularly salient chemical cue of predation risk, as these cues are released during the attack and capture stages of the predation sequence, and indicate that a predator is actively foraging nearby (Brown, 2003). Thus, damage-released cues are a good predictor of a clear and imminent risk of predation, and concordantly, elicit intense anti-predator responses (Ferrari et al., 2010; Wisenden, 2015). Hundreds of studies have investigated the importance of these cues in mediating predator–prey interactions (see reviews by Chivers and Smith, 1998; Wisenden, 2000, 2015; Ferrari et al., 2010; Chivers et al., 2013), and a wide variety of aquatic taxa, including fishes, respond to damage-released cues (reviewed by

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Chivers and Smith, 1998), suggesting a widespread benefit to the use of damage-released cues by prey animals (Ferrari et al., 2010; Wisenden, 2015).

By making use of multiple sensory inputs, and relying on both direct and indirect sources of information about predation risk, individuals can increase their accuracy of risk assessment, and optimise their anti-predator behaviour (Dalesman and Inchley, 2008). In aquatic environments, turbidity or habitat complexity may reduce the utility of visual cues in assessing predation risk (Wisenden, 2015), while variable water currents may confound chemical information about the direction or proximity of a predator. Therefore, the reliability of individual cues in predator assessment may be reduced (Chivers and Smith, 1998). As a result, aquatic organisms in particular are expected to use multiple sources of information in order to accurately assess predation risk and respond appropriately.

Here, we assessed the response of the highly social cichlid fish, *Neolamprologus pulcher* to multiple indicators of predation risk. *N. pulcher* is a cooperatively breeding cichlid endemic to Lake Tanganyika, East Africa (Taborsky, 1984; Wong and Balshine, 2011). These small-bodied cichlids live in colonies containing up to 200 distinct, clustered social groups (Heg et al., 2005; Stiver et al., 2006). Each social group includes a dominant male and female that gain the majority of the reproduction within the group, and up to 20 subordinates (Balshine et al., 2001; Heg et al., 2005; Hellmann et al., 2015) that assist in communal defence and maintenance of permanent territories in the rocky littoral zone (Taborsky 1984; Wong and Balshine, 2011). *N. pulcher* is highly amenable to experimental study both in the field and in the lab, and as a result *N. pulcher* has recently emerged as a powerful model system for the integrative study of social behaviour and cooperation in vertebrates (Wong and Balshine, 2011). In the wild, *N. pulcher* live under the constant threat of predation (Balshine-Earn et al., 1998; Balshine et al., 2001). Predators of both adult and juvenile *N. pulcher* occur at high densities within and around colonies (Heg et al., 2004), and smaller subordinates have little chance of survival outside of a territory that is defended by larger group members (Taborsky and Limberger, 1981; Taborsky, 1984; Heg et al., 2004). The evolutionary drivers of social living in *N. pulcher* is an area of active research (Wong and Balshine, 2011), but there is strong evidence that high levels of predation pose a constraint to dispersal in juvenile *N. pulcher* (Heg et al., 2004), and predation therefore likely contributed to the evolution of social living and cooperative breeding in this species. Recent work supports the contention that predation pressure is likely a driver of sociality both at the group and colony level in *N. pulcher* (Jungwirth et al., 2015). Furthermore, individual *N. pulcher* show finely tuned responses to visual predator stimuli, responding differentially depending on the threat level of the presented predator stimulus (Zöttl et al., 2013; Fisher et al., 2014). To date, it has not been established whether *N. pulcher* use olfactory cues to gauge predation risk. Here, we aim to determine whether *N. pulcher* exhibits antipredator behaviour in response to odours emitted by damaged conspecifics. We seek to further our understanding of antipredator behaviour in this highly social fish by documenting the responses of individual *N. pulcher* to an indirect cue of predation risk, the odour of damaged conspecifics, to a direct visual predator stimulus and to the combination of these cues. For the direct visual predator stimulus, we used a live *Lepidiolamprologus lemairii*, a natural predator of *N. pulcher* in Lake Tanganyika (Heg et al., 2004; Heg and Taborsky, 2010; Witsenburg et al., 2010), presented behind a sealed transparent barrier.

In response to various indicators of predation risk, aquatic prey adopt a number of different anti-predator behaviours that typically involve any or all of the following: reduction in activity, movement out of the water column, seeking shelter, area avoidance, and increased grouping behaviour (Wisenden, 2000). Therefore,

we examined activity, area use, shelter-seeking, and the propensity to seek out conspecifics in *N. pulcher* in response to the direct predator stimulus, the indirect chemical cue, and both indicators of predation risk combined. Based on previous research of other cichlids' responses to indicators of predation risk (e.g. Wisenden and Sargent, 1997; Pollock et al., 2005; Ferrari et al., 2010), we predicted that both the visual predator stimulus and the chemical cue would cause a reduction in activity and exploration, increase shelter seeking, and increase the time spent shoaling. We predicted that the combination of the visual predator stimulus and the chemical cue would elicit a stronger response than either indicator alone (Wisenden, 2000, 2015; Manassa et al., 2013).

2. Methods

2.1. Study animals

All of the *N. pulcher* used in the current study were laboratory-reared descendants of wild-caught fish from Lake Tanganyika, and part of a laboratory population maintained at McMaster University in Hamilton, ON, Canada. We housed focal fish in a 527 L (183 × 48 × 60 cm) communal aquarium containing 3 cm of coral sand substrate, 4 water filters, 2 heaters, and a thermometer. Stimulus fish were housed in a separate but identical aquarium. We obtained the *L. lemairii* used as the visual predator stimulus from a commercial aquarist (Dave's Rare Aquarium Fish, San Antonio, TX), and housed them in a 189 L (92 × 40 × 50 cm) aquarium containing 3 cm of coral sand substrate, 2 water filters, a heater, and a thermometer, as well as PVC tubing and artificial aquarium plants to use as shelters. The water temperatures of all aquaria were held at 26 ± 2 °C and fish were kept on a 13:11 light:dark cycle. We fed all fish dried prepared cichlid food ad libitum six times per week.

2.2. Visual predator stimulus

Prior to the start of the experimental trials, we captured the *L. lemairii* stimulus predators ($n=3$), weighed them on an electronic balance to obtain total wet mass, and measured them for standard length (SL, the distance from the tip of the snout to the end of the caudal peduncle) using callipers. We then uniquely fin-clipped the fish for identification, allowing the individual stimulus predators to be rotated between trials while avoiding unnecessary handling and prey habituation. Fin clipping does not adversely affect the behaviour of other Tanganyikan cichlid fishes (e.g., *N. pulcher*; Stiver et al., 2004) and the removed fin tissue grows back within a few weeks. In order to maintain clear marks, all *L. lemairii* had their fin-clips redone periodically throughout the experiment. With SL = 91.3 ± 2.8 mm, and mass = 22.3 ± 1.4 g (values here and throughout the manuscript presented as mean ± standard error of the mean [SEM] unless otherwise noted), all *L. lemairii* were similar in size, and large enough to consume focal *N. pulcher* (Desjardins et al., 2008; Heg and Taborsky, 2010).

2.3. Odour of damaged conspecifics

We obtained the odour of damaged conspecifics from the skin tissue of adult *N. pulcher* housed in the communal aquaria described above, following the methods described by Pollock et al. (2005). We stunned the fish ($n=20$; SL = 75.2 ± 2.0 mm; mass = 13.1 ± 4.1 g) by submersion in an ice bath, and then swiftly euthanized them by spinal cord severance. We used a mechanical method to euthanize the fish in order to prevent any interference with the chemical cue (Hoare et al., 2004). We prepared the chemical cue in two batches, one in October 2013, and one in June 2014. For each batch, we homogenized the skin tissue harvested from both flanks of 10 *N. pulcher* (approximately 80 cm² of total skin) with 245 mL of

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