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Territorial aggression reduces vigilance but increases aggression towards predators in a cooperatively breeding fish

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In many species, aggressive individuals outcompete their less aggressive conspecifics for resources such as food and access to mates. Nevertheless, variation in aggression is maintained in populations, but the underlying mechanisms are not well understood. Here we tested the hypothesis that aggressive behaviours compromise the antipredator behaviour of prey, which would link aggressive behaviours to a cost of predation. We presented computer-animated images of predators to the cooperatively breeding cichlid fish *Neolamprologus pulcher* either during territorial contests with a group of territory intruders or when the test fish were alone. We investigated their response latencies and the behaviour directed towards predator images. We found that test fish responded to the predator images significantly later during territorial contests than when they were alone. Moreover, during territorial contests, response latencies of test fish increased with increasing levels of aggression towards conspecifics. Test fish also responded more aggressively to the predator images during territorial contests than when they were alone. During territorial contests, fish that responded later to the predator images were more aggressive towards these images. Our findings suggest that territorial contests compromised the ability of prey to respond quickly to predators. However, we propose that increased aggression towards predators might increase survival chances of prey during predator encounters in nature, and it may thus compensate for costs incurred by delayed predator responses during territorial contests. To test this hypothesis experiments under natural predation regimes that examine the relationship between predation risk, territorial and antipredator aggression are required.

Aggression is an important fitness trait in various species (e.g. Biro & Stamps, 2008; Riebli et al., 2011; Smith & Blumstein, 2008). The ability to defend a territory, compete aggressively for mates or achieve a high social rank in a dominance hierarchy is often vital for reproductive success (Peiman & Robinson, 2010; Shackleton, Jennions, & Hunt, 2005). Accordingly, there is ample evidence that aggressive individuals have a higher reproductive success than their less aggressive conspecifics (Biro & Stamps, 2008; Smith & Blumstein, 2008). Based on this, populations would be expected to become increasingly aggressive. However, studies on animal personality have revealed that the levels of aggression maintained within populations are highly variable (Sih, Bell & Johnson, 2004). The underlying mechanisms that are responsible for the maintenance of the observed variation in aggression, however, are not yet well understood.

It has been suggested that aggressive individuals suffer an increased predation risk (Carter, Goldizen, & Tromp, 2010; Quinn & Cressell, 2005; Sih et al., 2004; Smith & Blumstein, 2008). Aggressive interactions between conspecifics require a high level of attention (Brick, 1998; Jakobsson, Brick, & Kullberg, 1995), and may distract individuals from other attention-consuming tasks that are carried out simultaneously, such as vigilance (Brick, 1998; Chan, Giraldo-Perez, Smith, & Blumstein, 2010; Clark & Dukas, 2003; Dukas & Kamil, 2000; Dunn, Copelston, & Workman, 2004; Jakobsson et al., 1995). Vigilance increases the likelihood of detecting a predator before or early during an attack, reducing predation risk (Cresswell, 1994; Cresswell, Quinn, Whittingham, & Butler, 2003; Lima & Dill, 1990). Aggressive behaviour may therefore result in a cost of predation by compromising vigilance, which may contribute to the maintenance of different levels of aggression

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in a population (Sih et al., 2004; Wolf, Van Doorn, Leimar, & Weissing, 2007). However, antipredator behaviours other than vigilance are likely to influence prey survival during a predator encounter as well, such as the reaction of prey to the predator after detection (Pascual & Senar, 2014). These antipredator behaviours have received little attention, but are important to consider when examining predator-prey interactions.

In the present study we exposed the cooperatively breeding cichlid *Neolamprologus pulcher* to computer-animated images of predators and investigated how aggressive interactions during territorial contests affect predator detection. This cichlid has been shown to recognize animated two-dimensional images of the piscivorous *Lepidiolamprologus elongatus* as predators and to respond accordingly (Fischer et al., 2014). Using animated pictures allowed us to standardize predator behaviour and appearance and thereby the perceived threat posed by the predator. In the field, dominant breeder pairs of *N. pulcher* and their subordinate brood helpers defend a territory against conspecific intruders that attempt to enter the territory (Sturmbauer et al., 2008; Taborsky & Limberger, 1981). Territorial contests can be intense and can include threat displays and overt attacks (Hirschenhauser, Taborsky, Oliveira, Canario, & Oliveira, 2004). The number of attacks directed towards intruders is repeatable in this species and is an indication of an individual's inherent aggression (Schürch & Heg, 2010; Witsenburg, Schürch, Otti, & Heg, 2010). In the field, individuals are under intense predation risk, in particular by *L. elongatus*, a voracious specialized piscivore which lurks around *N. pulcher* territories (Heg, Bachar, Brouwer, & Taborsky, 2004; Hori, Yamaoka, & Takamura, 1983). *Neolamprologus pulcher* is therefore a suitable model species to study the relationship between vigilance and aggressive interactions between conspecifics.

This study pursued two aims: (1) examining the influence of territorial contests between a territory owner and a group of intruders on the owner's vigilance and (2) examining the influence of territorial contests on the owner's response to predators. We used the time until the owner detected the predator (response latency) as a measure of its vigilance. We compared the owner's vigilance between a treatment allowing for territorial contests and a control situation when the territory owner was alone. We predicted that territory owners would reduce their vigilance during territorial contests, i.e. that they would detect the approaching predator later during territorial contests than when alone. We further hypothesized that responses by territory owners towards the predator will not only occur with some delay but will also be attenuated during contests.

METHODS

Study Subjects

Neolamprologus pulcher and its main predator *L. elongatus* are both lamprologine cichlids endemic to Lake Tanganyika (Konings, 1998). *Neolamprologus pulcher* inhabits sandy to rocky habitats along the shoreline from 3 to above 45 m depth (Duftner et al., 2007; Taborsky, 1984). This species typically lives in social groups of three to 25 individuals, consisting of a dominant breeder pair and subordinate brood care helpers, but in some cases single adult individuals defend a small territory (Heg, Brouwer, Bachar, & Taborsky, 2005; Taborsky & Limberger, 1981).

Ethical Note

The study was done under licence 52/12 of the Veterinary Service of the Canton Bern, Switzerland. All *N. pulcher* used in this study and the specimens of *L. elongatus* used to produce computer animations were derived from the laboratory breeding stocks kept at the Division of Behavioural Ecology, University of Bern, under standardized housing conditions (see Arnold & Taborsky, 2010). To prevent injuries, territory owners and intruders were kept in adjacent tanks and had only visual contact. Pictures of predators were used to simulate predation threat, rather than live predators, in order to reduce the number of animals used in the experiment. To avoid stress, handling time of *N. pulcher* and *L. elongatus* was kept to a minimum. At the end of the experiment, all fish were returned to their original stock tank.

Production of Animations

We used six specimens of *L. elongatus* to create animated two-dimensional predator images, following the methods outlined in Fischer et al. (2014). In brief, we took photographs (camera: Nikon Coolpix 995, 200 mm lens) of the lateral side of each *L. elongatus* and then cut out the body shape using the image editing software Gimp (Mattis & Kimball, 1995). The two-dimensional images were fitted to a size of 16 cm standard length (i.e., from the tip of the snout to the end of the caudal peduncle, excluding the tail fin) and used to create six PowerPoint presentations (one for each specimen). A PowerPoint presentation consisted of nine animations (i.e. nine different PowerPoint slides) with a greenish background resembling turbid lake water and images of stones in the front. The stones (width: 6 cm; height: 5 cm) served as a size reference relative to the fish images (Baldauf, Kullmann, & Bakker, 2008). For each of the nine animations of a given presentation, the same image of an *L. elongatus* entered the screen from the right side at a height of 5 cm, moved across the screen at a speed of 1 cm/s and left the screen on the opposite side. The image was visible for 25 s. The *L. elongatus* image of the first animation (i.e. the first PowerPoint slide) was always the most difficult to detect, with the animations in the following PowerPoint slides gradually increasing in detectability. For this purpose, we covered the fish images with an additional layer that had the same shape as the fish and a colour identical to the background. With each PowerPoint slide, the transparency value of the layer increased (<1% in the first slide, 1%, 3%, 5%, 7%, 9%, 11%, 15% and 20% in the ninth slide), imitating decreasing degrees of water turbidity and thus increasing visibility. For each transparency value all major features such as eyes, mouth, fins and body shape of the presented fish were clearly discernible. During each test, we recorded the first slide during which the test fish detected the predator (i.e. slide 1–9). The PowerPoint presentations of the six specimens were randomly assigned to the test fish.

Experimental Set-up

The experimental set-up consisted of two tanks (40 × 25 cm and 25 cm high) separated by an opaque divider (Fig. 1, divider not shown). The bottom of both tanks was covered by a 2 cm layer of gravel. The tank of the test fish (tank 1) contained a shelter, which was placed in the third of tank 1 that was closest to tank 2 and furthest away from the computer screen (further referred to as first third of tank 1; Fig. 1). The side towards the screen was covered by a paper copy of the PowerPoint slides' background to habituate the test fish to the greenish background and the stone images. The second tank (tank 2) held either a group of conspecifics or was empty, depending on the treatment (see below). All walls of tank 2, except the wall facing tank 1, were shielded by black PVC sheets.

The test fish ($N = 28$, 2.0–4.0 cm standard length) were haphazardly caught from the institute's breeding stock 1 day before the experiment started and placed in the experimental tank. One day is sufficient for juvenile *N. pulcher* to establish a territory if