

## REVIEW

# On closer inspection: Reviewing the debate on whether fish cooperate to inspect predators

A. Li Veiros<sup>1</sup>  | Manon K. Schweinfurth<sup>2</sup>  | Michael M. Webster<sup>1</sup> 

<sup>1</sup>School of Biology, University of St Andrews, St Andrews, Scotland

<sup>2</sup>School of Psychology & Neuroscience, University of St Andrews, St Andrews, Scotland

## Correspondence

A. Li Veiros, School of Biology, University of St Andrews, St Andrews KY16 9TS, Scotland.

Email: [av90@st-andrews.ac.uk](mailto:av90@st-andrews.ac.uk)

## Funding information

EASTBIO DTP

Editor: Wolfgang Goymann

## Abstract

Cooperative behaviours, which benefit a recipient, are widespread in the animal kingdom; yet their evolution is not straightforward. Reciprocity, i.e., cooperating with previously experienced cooperative partners, has been suggested to underly cooperation, but has been contested throughout the years. Once a textbook example of reciprocity was cooperative predator inspection, where one or several individuals leave their group to approach a potential threat. Each can at any point stop or retreat, increasing the risk for its partner. It was suggested that inspecting individuals follow a specific reciprocal strategy called tit-for-tat, i.e., cooperating on the first move and then copying the partner's last move. Numerous studies provide evidence to support the claim that fish cooperate to inspect predators, including three-spined sticklebacks (*Gasterosteus aculeatus*), guppies (*Poecilia reticulata*) and minnows (*Phoxinus phoxinus*). However, over the past few decades some scholars have expressed scepticism whether predator inspection is indeed a cooperative behaviour or rather a case of by-product mutualism, which describes behaviours that benefit a partner as a corollary of an otherwise selfish behaviour. For instance, it has been shown that pairs of fish moving in unfamiliar environments appear to coordinate movements even in the absence of predators. Many studies have also used coarse measures of overall approach rates towards predators rather than the fine-grained analyses necessary to infer tit-for-tat in cooperative inspections. Now is the time to return to the question of cooperative predator inspection with new tools and approaches to resolve a decades-old debate.

## KEYWORDS

by-product mutualism, cooperation, fish, predator inspection, reciprocity, tit-for-tat

## 1 | INTRODUCTION

Cooperation is behaviour, involving two or more individuals, that benefits the recipient and has been (at least partially) selected for that purpose (Davies et al., 2012; West et al., 2007). Cooperative behaviour can evolve via different mechanisms (see Table 1 for

definitions). Kin selection can explain cooperation, if individuals help those that share genes with them (Hamilton, 1964). Reciprocity can lead to cooperation, if individuals are more likely to help those that helped them before (Schweinfurth & Call, 2019; Trivers, 1971). However, it is important to disentangle cooperative interactions from by-product mutualisms, which are behaviours that appear to

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Ethology* published by Wiley-VCH GmbH.

TABLE 1 Definitions.

Term	Definition
By-product mutualism	Behaviour, involving two or more individuals, that is beneficial to the recipient as a by-product, having been selected for the benefits to the actor (Brown, 1983).
Cooperation	Behaviour, involving two or more individuals, that benefits the recipient and has been at least partially selected for that purpose (West et al., 2007).
Coordinated predator inspection	Predator inspection behaviour conducted by a minimum of two individuals, that maintain closer proximity than in regular shoaling throughout.
Leading	Being closer to the potential threat when the inspecting pair/group is approaching the threat.
Partner choice	Avoiding cheaters and selectively approaching cooperators (Noë & Hammerstein, 1995).
Partner control	Controlling cheaters' future behaviour through withdrawing help or active punishment (Trivers, 1971).
Predator inspection	One or more individuals approaching a possible threat, typically leaving a larger group to do so, and usually slowly and visually oriented towards said possible threat (Dugatkin & Alfieri, 1991b), probably with the purpose of gathering information.
Reciprocally cooperative predator inspection	Coordinated predator inspection in which individuals reciprocate risky behaviour and take turns.
Reciprocity	Cooperation preferentially with previously cooperative partners, with an exchange of goods or services that depends on the partner's behaviour (Schweinfurth & Call, 2019).
Snowdrift game	Social dilemma two-player game with two possible moves: cooperate or defect. Both players can access the benefit of cooperation, whose cost is divided between them when the opponent cooperates as well. This makes cooperation advantageous when rare, leading to a mixed-state equilibrium. In this case, mutual defection has a lower individual pay-off than the "sucker's payoff", for an individual that cooperates when its partner defects. Snowdrift is equivalent to the Hawk-Dove and Chicken games (Doebeli & Hauert, 2005).
Tit-for-tat	Strategy that involves cooperating on the first move and then copying the partner's behaviour (Axelrod & Hamilton, 1981).

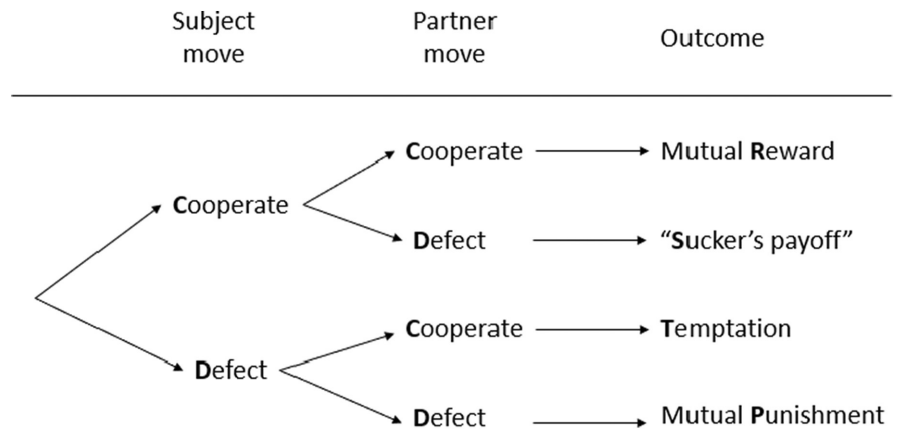
be cooperative but arise as a by-product of an otherwise selfish act (Brown, 1983; Connor, 1995; Dugatkin, 2009). The importance of kinship in cooperative interactions has been widely acknowledged (e.g., Clutton-Brock, 2009). However, the occurrence of reciprocity in non-human animals has been challenged multiple times (e.g., West et al., 2007).

Here, we will revisit one classic, but highly debated, example of non-human reciprocity, i.e., the turn-taking of individuals that leave their group to approach a potentially dangerous threat (Connor, 1996; Dugatkin & Alfieri, 1991b). Once a textbook example of reciprocity (Beauchamp, 2014; Dugatkin, 2009; Ostlund-Nilson, 2007), coordinated predator inspection has more recently been described as one of the most contested claims of reciprocity (Carter, 2014). Predator inspection is a widely-documented behaviour that exists in a wide range of taxa, including mammals (FitzGibbon, 1994), birds (Koboroff et al., 2009; Nocera et al., 2008), reptiles (Leal & Rodríguez-Robles, 1997) and invertebrates (Zaguri & Hawlena, 2019); but mostly it has been studied in small prey fish (see Table S1 for a list of examples), such as sticklebacks (*Gasterosteus aculeatus*) (Milinski, 1987) and guppies (*Poecilia reticulata*) (Dugatkin, 1991). If those fish spot a potential predator, some individuals leave their group and swim together towards the threat to inspect it. Approaching a predator might seem like a maladaptive strategy because of increased risk of being captured (Walling et al., 2004). However, there are benefits involved with approaching predators. Always fleeing when faced with a threat results in

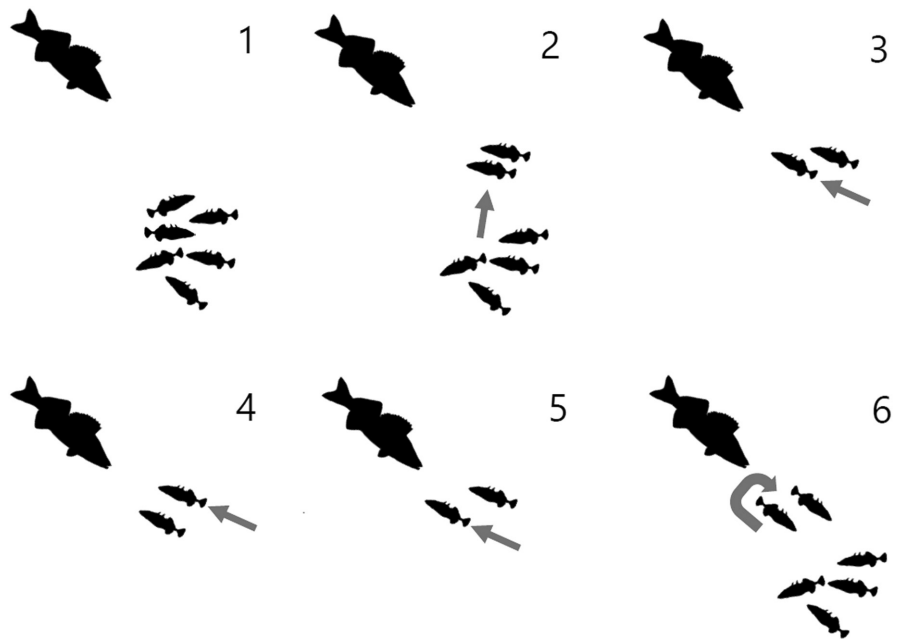
energy expenditure and opportunity costs such as lost chances to feed (Dugatkin, 1991) or court mates (Dugatkin & Godin, 1992). By inspecting a threat, prey fish can confirm whether it is indeed a predatory species, gain information on the predator's precise location, and determine whether it is actually hunting or merely resting (Milinski, Pfluger, et al., 1990). This information may influence decisions to flee or remain. Other fish in the shoal are able to recognize changes in the behaviour of fish that have detected predators and respond by reducing their foraging behaviour and hiding (Magurran & Higham, 1988). Predator inspection can also have an attack deterrence effect (FitzGibbon, 1994), although evidence to support that hypothesis has been conflicting for fish (Milinski et al., 1997, but see also Godin & Davis, 1995). Among the inspecting fish there is a dilemma in that any one fish would be better off staying behind and letting others inspect the predator, so long as it is able to benefit from the information that they acquire about the level of risk posed by the predator. However, if no fish inspects the potential threat, none can gain from the associated benefits of gathering information about the risk it poses.

This dilemma can be illustrated in an iterated Prisoner's Dilemma Game (iPDG) (Kastampolidou et al., 2020). If each inspection run is considered as a move in the repeated game, each individual can choose to either cooperate, i.e., move with the other fish towards the potential predator, or defect, i.e., stay behind (Figure 1). If the two fish cooperate with each other, they both swim together towards the threat to gain information while diluting the risk of

**FIGURE 1** Game tree for one run of a PDG, with payoffs for the subject's perspective. Bold letters highlight common abbreviations for each term (for example, "R" to stand for mutual reward). For an iPDG, the same options would be repeated sequentially.



**FIGURE 2** Schematic representation of a typical coordinated predator inspection event. The numbers show order (left-to-right and top to bottom). The larger fish in the top left corner of each panel represents a potential predator, the smaller fish represent prey fish. Fish silhouettes designs from PhyloPic (2023).



predation. Although both individuals benefit from the interaction, one individual might be tempted to cheat. Here, the cooperative individual approaches the predator and takes the risk of predation, while the uncooperative individual lacks behind and thereby does not take the risk of predation although it still receives the benefit of knowledge gain. The dilemma is that while individuals benefit from cooperation, the individual that exploits a cooperater by staying behind is better off than the cooperater. Yet, if all defect none of them gain information about a potential predator. There are however other frameworks with less strict assumptions, like the Snowdrift or Hawk-Dove game (Doebeli & Hauert, 2005), in which both the benefits of cooperation and the risks of defection are shared between the two players. A solution to the iPDG problem is reciprocity, where individuals only cooperate with previously experienced cooperators.

Indeed, it has been suggested that inspecting fish show a specific reciprocal strategy to ensure cooperation and avoid exploitation (Milinski, 1990a), which is called tit-for-tat (Axelrod & Hamilton, 1981), even within a single coordinated predator inspection event. Here, one fish starts the interaction by swimming

towards the predator, i.e., it cooperates (Figure 2). This decision to initiate an approach can be reciprocated by their inspection partner, who takes over and thereby cooperates as well. The subject responds by doing the same, and so on. Thus, the two fish cooperate by taking turns and thereby jointly approach the predator while spreading the costs between them (Milinski et al., 1997). If one fish behaves uncooperatively by staying behind, the other fish can directly retaliate and stay behind. In other words, one individual starts cooperatively by approaching the predator and thereafter each fish copies the previous move of the other. This reflects tit-for-tat, which is defined by the rule "start cooperatively and copy the partner's last move".

To date, several studies have provided evidence for reciprocated cooperative predator inspection, following the tit-for-tat strategy (Dugatkin, 1991; Milinski, 1987; Milinski, Külling, & Kettler, 1990; Milinski, Pfluger, et al., 1990). Yet, it has been argued that coordinated predator inspection is not a cooperative behaviour, but should be better described as a by-product mutualism, resulting from an otherwise selfish behaviour (Connor, 1996). Furthermore, it was argued that even if coordinated predator

inspection is cooperative, there is no strong evidence for tit-for-tat as most studies have not analysed individual moves of the inspectors in order to confirm that they do match each other's lead turn-taking, and punish each other's defections, necessary conditions to support a claim of tit-for-tat (Lazarus & Metcalfe, 1990). In this review, we firstly synthesize what is known about predator inspection in fish. We then discuss whether this behaviour can be described as cooperative and whether it meets the criteria for the reciprocal cooperation strategy 'tit-for-tat'. Based on this discussion, we propose future research directions, including proposing refined analyses, adding control conditions, and gathering more data on natural inspection events.

## 2 | EXPERIMENTAL STUDIES OF COOPERATION IN PREDATOR INSPECTION

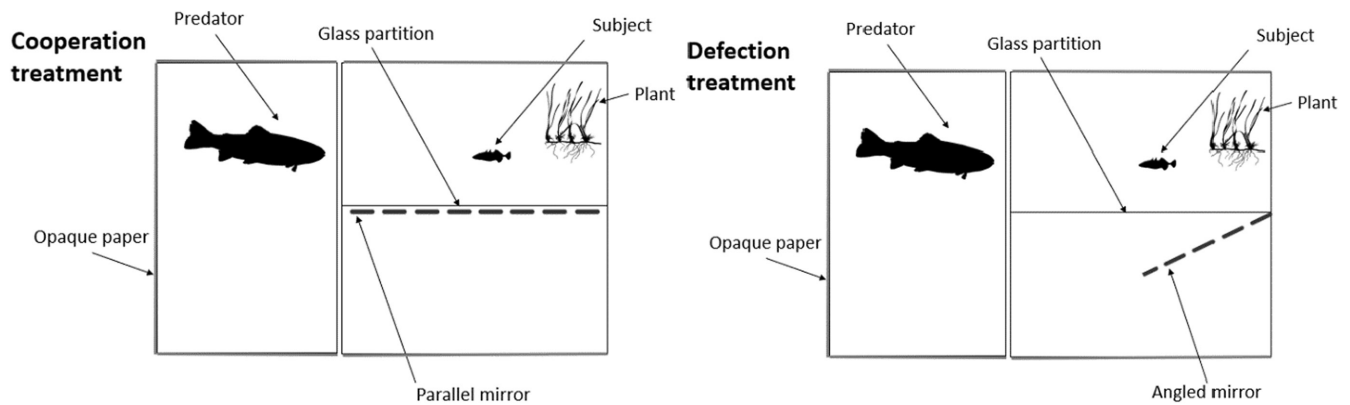
Several approaches have been used to study tit-for-tat strategies within fish coordinated predator inspection. Live predators have been used to induce predator inspection (Milinski, Külling, & Kettler, 1990) in addition to physical models of predators (Magurran & Girling, 1986), although these do not always work (Magurran & Seghers, 1990), and computer animations (Pimentel et al., 2021). In those studies, fish have been shown to cooperate conditionally with others when inspecting predators (Dugatkin, 1991; Dugatkin & Alfieri, 1991b; Milinski, Külling, & Kettler, 1990). To causally study inspection, the behaviour of the inspecting partner needs to be manipulated to determine how the test subject responds to cooperation and defection. One way to achieve this is to use mirrors to simulate cooperative or uncooperative partners from the subject's own image (Figure 3). With this method, subject fish are exposed to a mirror parallel to their approach path, so that when they inspect a predator, it simulates a cooperating partner approaching simultaneously and keeping pace. Alternatively, the mirror can be angled away from the subject's approach path, so that as subject fish carry out an inspection, their image will seem to move progressively further from them and then disappear, simulating a defecting partner (Dugatkin, 1988; Milinski, 1987).

Another way of manipulating partner behaviour is to train partners to appear to be cooperative or uncooperative (Figure 4). Milinski, Külling, and Kettler (1990) achieved this by training partner fish to swim towards a green light, placed close to the predator. This light was visible to the partner fish, but not to the test subject. Hence, the subject experienced an apparently cooperative partner, who readily approached the predator. To simulate defection, another partner trained in the same way was not seen approaching the predator due to an opaque partition blocking only that partner's side, in the half of its tank that was closest to the predator. This made it seem like that partner suddenly disappeared in the most dangerous section of an inspection.

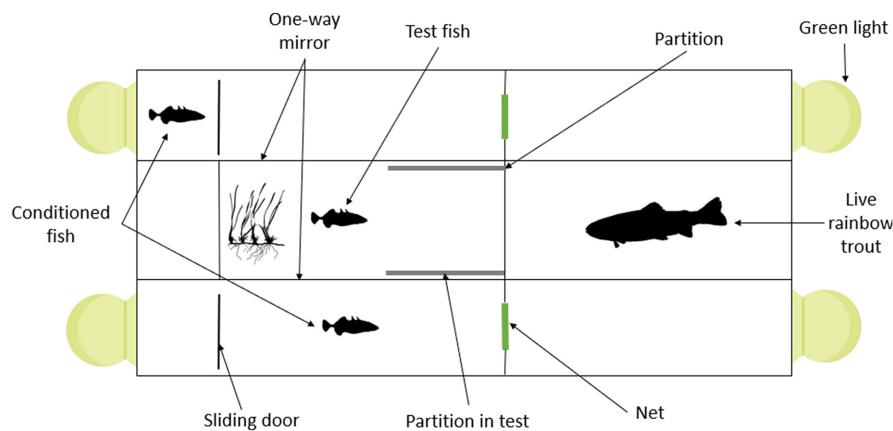
Several studies demonstrated that fishes are more likely to inspect predators with cooperative partners that had joined them in

previous trials compared to uncooperative partners that had not (Dugatkin, 1988; Dugatkin & Alfieri, 1991a), both in the studies using mirrors (Dugatkin, 1988; Milinski, 1987) and live partners (Dugatkin & Alfieri, 1991a; Milinski, Külling, & Kettler, 1990; Milinski, Pfluger, et al., 1990). Specifically, fish were on average 1–5 cm (less than their average body length of 5.1 cm, according to Fishbase, 2023) closer to the predator in the trials with simulated cooperative partners, although this was not consistent or always significant throughout trial runs (Milinski, Külling, & Kettler, 1990). Overall, fish responded similarly to mirror images and to live partners in those studies and hence mirror studies seem a good predictor of behaviour in live partner trials (Dugatkin & Alfieri, 1991b). While inspection behaviour is consistent over time, there is large inter-individual variation in this behaviour, i.e., some fish are more and some are less cooperative (Dugatkin & Alfieri, 1991b). Social shoaling partner preferences may also affect inspection partner choice. In fact, social network analyses have revealed that guppies, for instance, prefer to inspect predators with partners with which they shoal close to frequently, compared to partners that they spend less time shoaling near (Croft et al., 2006).

Additionally, there has been some work exploring the risks and benefits involved in a predator inspection. In particular, inspecting fish have been shown to reduce the risk to themselves by avoiding a predator's anterior end, in what is known as "attack cone avoidance" (Brown et al., 2001; Magurran & Seghers, 1990). This demonstrates that inspectors are aware of undertaking predation risk, which is supported by the fact that this behaviour is more common in what are perceived as higher risk scenarios (Brown et al., 2001). Regarding the information benefits of inspecting, there is some evidence suggesting that closer inspections provide more reliable information, which the fish can then apply to optimize their own foraging (Häberli et al., 2005). Both chemical cues, which fish have been shown to also use for information during inspections (Brown & Magnavacca, 2003), and visual cues are likely to be more reliable in closer inspections. This might affect the equilibrium and strategy used. There might also be a plateau effect, with some critical minimum distance being reached after which the information benefit no longer outweighs the risk of predation. The cost of leading might increase substantially after a certain point in an approach, when the inspectors can be detected by the predator or approach its strike distance. A sudden increase in danger might make cooperation for the risk dilution benefits more important in the closer phases of an inspection. Although being closer to a potential predator is likely to lead to higher predation risk (Milinski et al., 1997), it could however be counter-balanced by diluting risk with larger inspecting groups (van der Bijl et al., 2015), for the overall benefit of gaining higher quality information. This information on risk can then be transmitted to the remaining shoal members, even if they are not in direct visual contact with a potential predator (Magurran & Higham, 1988). Therefore, evidence on the involved risks and benefits is important to understand how animals can navigate this dynamic and adjust their behaviour to the environment, which can influence whether and how they cooperate.



**FIGURE 3** Simplified version of the experimental set up in mirror experiments (based on e.g., Milinski, 1987). Subjects were placed in a compartment in front of the predator, with a plant refuge on the other end of their tank. Subjects were presented with one of two mirrors, either the parallel mirror (cooperation treatment) to simulate a cooperating conspecific or the angled mirror (defection treatment) to simulate defection.—Fish silhouettes and plant from Phylopic (2023).



**FIGURE 4** Set up for conspecific experiments (e.g., Milinski, Külling, & Kettler, 1990) viewed from the top. Before the experiment, partner fishes were trained to approach the green lights. During the experiment, the subject was placed in the centre in front of a predator, with a plant refuge on the opposite end of its tank. In the testing phase, cooperative partners would swim towards the green light on the predator's end of the tank, while uncooperative partners were not seen completing the approach due to an opaque partition. Both conditioned partners were on the outside compartments. The side on which a conditioned fish would be seen to swim forward (cooperator) was alternated. One-way mirrors ensured that the subject could see its partners, but the partners could not see the subject. Fish silhouettes and plant from Phylopic (2023).

### 3 | DEBATE: COOPERATION OR BY-PRODUCT MUTUALISM?

The controversy surrounding predator inspection is not about whether this behaviour exists but whether the inspector and its partner actually cooperate with each other, and if so whether this is a form of reciprocal cooperation and more specifically a tit-for-tat like strategy. One concern is that coordinated predator inspection is not an altruistic behaviour because the behaviour is immediately beneficial for the inspector and its partner. Hence, it is not straightforward to understand whether it has evolved to benefit the partner as a form of cooperation or is the by-product of an otherwise selfish behaviour.

Another concern is that not all studies have included predator absence/presence controls (Lazarus & Metcalfe, 1990; Reboreda & Kacelnik, 1990). This is crucial, however, since if there is no specific threat, then what looks like cooperation might just be a by-product

of other behaviours, like shoaling. Indeed, one study found that guppies showed the same inspection behaviour regardless of whether there was a predator present or absent in the mirror set-up (Masters & Waite, 1990; but see for opposite results Dugatkin & Alfieri, 1991a, 1991b). Although this might speak towards inspection behaviour being the result of shoaling, it should be noted that many populations of guppies have coevolved with many predators (Magurran, 2005), and when placed in a new and therefore potentially risky environment, they might have perceived a risk even without the presence of a predator (Milinski, 1990b). This suggests that inspection behaviours are not limited to situations in which a predator is clearly visible, but that the unfamiliarity of the environment is enough to elicit turn-taking in a situation perceived as risky by the fish (Harcourt et al., 2010).

If coordinated predator inspection were the by-product of any selfish behaviours, it would be unlikely to be conditional on the

partner's behaviour. However, there is evidence that fish preferentially associate with those group members that showed cooperative predator inspection in the past (Dugatkin & Alfieri, 1991a, 1991b). Specifically, after an inspection trial, 80% of the guppies chose to spend more time (about 70% of the trial) near the side of their tank that was adjacent to (another tank that contained) the fish that had been on average closer to the predator, suggesting some partner choice (Dugatkin & Alfieri, 1991a). Furthermore, fish inspect more with partners that are more strongly socially associated with them (Croft et al., 2006). Additionally, fish that were on average closer to the predator than their partner, in paired trials, approach instead their partner's average position in subsequent trials (Dugatkin & Alfieri, 1991b). Hence they are adapting their cooperation levels in response to their partner's behaviour, suggesting some partner control. Although this provides evidence that inspecting fish consider previous cooperation levels and bonding status, it has been argued that fish are simply more likely to shoal with those partners, rather than cooperatively inspect predators (Connor, 1996). For example, the dilution effect can explain the benefits of a joint approach while at the same time being part of the reason fish shoal in the first place (Ward & Webster, 2016). In addition, fish might just be bolder in the presence of other fish (Lazarus & Metcalfe, 1990), which would explain closer approaches to predators when with perceived or actual partners. In other words, partner choice and partner control mechanisms can be present and stable in scenarios where interactions are repeated, without implying that the repeated behaviour itself was selected to be cooperative. Disentangling those effects empirically in non-verbal species is however difficult.

#### 4 | DEBATE: PREDATOR INSPECTION AS AN EXAMPLE OF TIT-FOR-TAT?

Several studies showed that fish choose to interact with cooperative partners, i.e., partner choice (Dugatkin & Alfieri, 1991a), and act conditionally upon previous experienced cooperation levels, i.e., partner control (Dugatkin, 1988; Dugatkin & Alfieri, 1991a; Milinski, 1987; Milinski, Külling, & Kettler, 1990; Milinski, Pflugger, et al., 1990), providing evidence for reciprocal cooperation (Trivers, 1971). It is important to disentangle reciprocal cooperation from tit-for-tat. Reciprocal cooperation is an umbrella term, which describes contingent cooperative exchanges between individuals (Trivers, 1971). Tit-for-tat is just one reciprocal strategy among many others, like "win-stay, lose-shift" (Bshary & Bergmüller, 2008). Hence, tit-for-tat is one, but not the only form of reciprocity and should consequently not be equated with reciprocal cooperation more generally (c.f. Carter, 2014). Tit-for-tat is a strategy that has been shown to be evolutionary stable and cognitively relatively simple (Axelrod & Hamilton, 1981). Yet, there has been limited evidence for this strategy in the animal kingdom, except for fishes (but see for a later example Krama et al., 2012). Those studies have attracted much criticism (Lazarus & Metcalfe, 1990; Masters & Waite, 1990; Turner & Robinson, 1992). Especially whether predator inspection resembles

an iPDG structure and whether as a result the fish indeed show tit-for-tat (Reboreda & Kacelnik, 1990). To demonstrate evidence for fish to show tit-for-tat, several pieces of evidence are needed.

First, fish need to repeatedly interact to be able to take turns in between moves. However, multiple interactions between the same individuals might be rare in nature because fish shoals are commonly fairly large, temporary, and variable in composition (Croft et al., 2003). Despite those fission-fusion dynamics, there is evidence that some fish can maintain stable partner associations in the wild, which increases the chance of repeated interactions with the same individuals (Croft et al., 2005; Ward et al., 2002). Additionally, tit-for-tat moves can take place between different or within the same approach, the latter making turn-taking much more likely. If the entire inspection event is considered as a move in the game, initiating and/or leading it would be the cooperating option, which could be reciprocated with partners alternating roles between inspection runs. On the other hand, during predator inspection fish commonly move multiple times (Dugatkin & Alfieri, 1991b), with each being an opportunity to cooperate or defect. However, it has been argued that a single inspection event cannot be considered as a repeated game in itself because of the implication that the fish would need to re-evaluate their options after every move (Noë, 2006).

Second, tit-for-tat is a very specific strategy, i.e., start cooperatively and then copy a partner's move, for which detailed analyses on every move are required. This would be particularly important to support the claim that a single inspection event can be considered a repeated game. Yet, past studies have often analysed whether subjects approached predators overall more with certain partners (Lazarus & Metcalfe, 1990; Reboreda & Kacelnik, 1990). Hence, there is rather limited evidence that fish respond to single moves in a tit-for-tat strategy. It has also been suggested that this is a cognitively challenging strategy which easily breaks down if memory errors occur (Stevens et al., 2011). However, cognitive demands can be lowered, if fish show reciprocally cooperative predator inspection only with a subset of all available partners (Dugatkin & Alfieri, 1991a). In this case, there would be less information to remember, for example only having to recall a past interaction with a few partners as opposed to all shoal members or a larger populational social network. This is found in guppies, who are more likely to inspect predators with partners that they were more strongly socially associated with (Dugatkin & Alfieri, 1991a). This likely lowered memory demands, and fish could remember previous cooperation levels for at least 4 h.

Fourth, it has been criticized whether the iPDG actually captures the predator inspection scenario (Connor, 1996; Noë, 2006). While pay-offs are relatively easy to quantify in economic games, this is much more difficult to quantify in biological settings. Both costs and benefits can be influenced by multiple possible factors. Furthermore, costs and benefits might differ for each individual and even within an individual over time. For example, cost-benefit ratios can be influenced by reproductive state (Frommen et al., 2009), subject's size relative to its partner's (Walling et al., 2004) and personality type (Murphy & Pitcher, 1991). Yet, iPDGs usually assume players have exactly the same options and

resources (Raihani & Bshary, 2011). For a Prisoner's Dilemma to exist, the benefit of temptation (defecting when the partner cooperates) needs to be larger than the benefits when both cooperate, which in turn must be larger than the costs for when both show defection, leaving the "sucker's payoff" (cooperating when the partner defects) as the worst-case scenario from an individual perspective. This specific game structure leads to tit-for-tat being superior over other strategies (Axelrod & Hamilton, 1981). However, it has been argued that staying behind has not been proven to be more beneficial than inspecting predator (Turner & Robinson, 1992). Particularly, for the iPDG pay-offs to apply to coordinated predator inspection, the temptation (T) to stay behind must be considerably greater than the benefit (P) of both partners avoiding the costs of inspection (Noë, 2006). For  $T > P$  to be true, the benefits for cooperating and defecting individuals must be the same in terms of information. Yet, it could be argued that the iPDG is a very specific game that is unlikely to be replicated in natural settings (cf. Carter, 2014) and that its matrix is not necessarily required to explain reciprocally cooperative predator inspection behaviour (Reboreda & Kacelnik, 1990). Specifically, reciprocating cooperative moves with cooperation and uncooperative moves with defection does not require the payoff matrix of an iPDG (Dugatkin, 1988).

Finally, tit-for-tat is a solution to an iPDG with two players. While two agents are trapped in an iPDG, this is not necessarily the case for predator inspecting fish as there are often other potential partners available (Magurran & Higham, 1988). The presence of other fish enables partner choice and hence partner control mechanisms, like tit-for-tat, might be less needed. Currently, we lack information on natural inspection group sizes to evaluate individual decisions to leave the group for predator inspection with a partner. For instance, the groups might be larger than pairs (Turner & Robinson, 1992). However, fish have been shown to inspect on their own (Magurran & Seghers, 1990) with some evidence in guppies to inspect more frequently as singletons than in groups (Dugatkin & Godin, 1992). Although singleton inspections could still be reciprocated by following approaches made by other group members, it suggests that fish are not trapped in a two-player game.

## 5 | OUTLOOK: REVISITING THE QUESTION OF COOPERATION IN PREDATOR INSPECTION

Evidence for reciprocally cooperative predator inspection is mixed. On the one hand, there is evidence that fish prefer associating with previously cooperative partners and conditionally respond to previous cooperation levels (Dugatkin & Alfieri, 1991a; Milinski, Külling, & Kettler, 1990; Milinski, Pflüger, et al., 1990). These conditional partner choice and control mechanisms imply a function beyond merely maintaining a close distance to neighbours to minimize predation risk. On the other hand, aggregated

data analysis that uses broad measures of coordinated inspection, such as average time spent near a predator (Milinski, 1987), prevent us from capturing fine scale interactions such as exchanging leading and trailing positions, needed for tit-for-tat, and reciprocating cooperation or defection that must necessarily be demonstrated to support claims of (reciprocal) cooperation (cf. Lazarus & Metcalfe, 1990; Reboreda & Kacelnik, 1990).

Separating cooperative approaches from selfish shoaling behaviour (in which fish attempt to maintain close proximity to a neighbour to minimize their own predation risk) has been complicated by the lack of any clear expectation over how fish should coordinate movement and relative position to one another when inspecting a predator compared to when shoaling. We might expect that lead swapping should be more common in coordinated predator inspection approaches if the fish are cooperating, than if they were simply shoaling together. We suggest then that investigations of predator inspection should also include control conditions in which coordinated movement is quantified in the absence of predators (Lazarus & Metcalfe, 1990; Reboreda & Kacelnik, 1990) and in familiar environments, where fish are expected to be less cautious. Analyses that treat each approach phase of the inspectors within an inspection bout as an opportunity for cooperation or defection will allow us to determine whether movement decisions, such as lead-swapping, are conditional on the partner's immediately previous movement, and, crucially, whether these are seen more often in risky situations. Markov chain models could improve such an analysis, having already been applied to fish decision making in risky scenarios in other studies (Harcourt et al., 2009, 2010).

More fundamentally, there is a lack of data on inspection group sizes under natural conditions (Milinski, 1992). Subsets of individuals have been described to leave their shoals to inspect predators (Dugatkin & Alfieri, 1991b), but more information on the sizes of inspecting groups is needed in order to determine if a two-player game is an appropriate paradigm to study this behaviour. If inspections by groups of three or more individuals are common, this would have implications for the relative costs of defection and the types of models needed to capture the dynamics of cooperating.

Since predation risk increases the closer inspecting fish approach the predator (Milinski et al., 1997), future studies should assess levels of risk within inspections and whether the increase is linear. For instance, predators can have specific strike distances within which the risk of predation is considerably higher. The predation risk distribution throughout an inspection event could have interesting consequences on the payoffs: if predation risk suddenly increases in a step-like manner after a certain point, the costs of reciprocating individual moves might differ drastically. Similarly, the information used to assess predator presence through visual or chemical cues is also unlikely to be linear. For example, a closer inspection might be needed to get information on whether the predator is about to strike, which can be valuable information to avoid predation.

There is evidence that fish can transfer predation risk information to conspecifics, that then display stress behaviours even when not in visual contact with a predator (Magurran & Higham, 1988).

In this experiment, receiver fish could see transmitter conspecifics through a one-way mirror. Receivers reduced foraging and started hiding when a pike model approached the transmitters' feeding patch, even though receiver fish could not see the predator model themselves. This so gained social information might be less reliable or less valuable than personally gained information due to a delay in the information transfer process, which is crucial for a quick response. More research is needed to determine whether the information gathered in predator inspections is transmitted to other fish in real time or requires inspecting fish to return to their shoal. Those more fine-tuned analyses are likely to inform theoretical models that could as a result perhaps better model cost-benefit ratios and predict which strategies fish might use when inspecting predators.

Finally, there is mixed evidence whether predator inspection in fish qualifies as a cooperative behaviour due to scepticism about early study designs, analyses and focus (Lazarus & Metcalfe, 1990; Masters & Waite, 1990; Turner & Robinson, 1992), such as fitting the behaviour to a model (Dugatkin, 1991; Milinski, 1987) rather than modelling the behaviour. Some studies addressed those concerns. There are however some exceptions of note in these early studies, which either explored significant aspects of this behaviour's ecological significance, like whether the risk information is transmitted or not (Magurran & Higham, 1988) or attempted to improve experiments by incorporating raised criticisms (Dugatkin & Alfieri, 1991b). Investigating whether the obtained information is transmitted is very relevant for the debate as well, since one of the main assumptions of the iPDG in this case is that the fish that stay behind still gain the benefits of inspections. There is now evidence that at least minnows modify their behaviour upon visual contact with conspecifics that were being threatened by a (model) predator, even though these receiver fish were not able to see the stressor themselves (Magurran & Higham, 1988). After some of the main critiques were published (Lazarus & Metcalfe, 1990; Masters & Waite, 1990), some subsequent experiments with guppies included design improvements, such as comparing subject behaviour with both live conspecifics and the mirror protocol (Dugatkin & Alfieri, 1991b) and no-predator control groups (Dugatkin, 1991). Still, these experiments have not yet been replicated across model systems and did not have the option to use current day analysing techniques or tracking technology. Since predator inspection behaviour has been shown to have interspecies differences in important aspects, for example whether they inspect model predators (Magurran & Seghers, 1990), replicating experiments across fish species may be particularly important to confidently generalize conclusions. Additionally, modern tracking technologies can provide detailed position information, as opposed to more qualitative measures or averages, allowing the use of more robust statistical methods. In conclusion, more research is needed to continue making progress to solve the debate, and better understand this understudied anti-predator behaviour.

## 6 | CONCLUSIONS

Numerous species of fish are known to inspect potential predators in pairs or small groups, most likely to gather information about the level of risk that they pose. Predator inspection is phylogenetically widespread and known from species in multiple families.

Inspecting fish have the opportunity to cooperate or defect on one another, by remaining close and/or taking turns to lead the approach, exposing themselves to predation risk, or by holding back or retreating, exposing their inspecting partner to more risk. Some authors have in fact claimed evidence for cooperation in predator inspection, but others have disagreed, claiming that by-product mutualism can explain coordinated approach behaviour. There has been vigorous debate over the issue, but it has yet to be satisfactorily resolved. Progress has been hampered by the use of broad measures of inspection, such as average time spent near a predator. More fine-grained measures of interaction, such as frequency of lead swapping in predator and no-predator control conditions are required if we are to determine whether fish cooperate reciprocally (or more specifically show a tit-for-tat like strategy) to share risk when inspecting predators.

The models of cooperation used to capture predator inspection make a number of assumptions about the mechanics of inspection including (with some evidence: Milinski et al., 1997) that the lead fish is at greater risk of being attacked. Further work is required to support this assumption across a range of approach distances and angles (relative to the predators' head). It is also assumed that fish typically inspect in pairs or small groups, with these leaving the larger shoal, moving away to inspect the predator and subsequently re-joining. There has been little experimental investigation of this, however, and further work quantifying inspection group size for a range of 'parent shoal' sizes is necessary to confirm this assumption. If prey fish routinely inspect predators in larger groups, this has implications for how we understand the costs and benefits of cooperating and defecting in coordinated predator inspections.

### AUTHOR CONTRIBUTIONS

A. Li Veiros, Manon K. Schweinfurth and Michael M. Webster conceived the study. AV wrote the first draft of the manuscript, which was edited by MKS and MMW.

### ACKNOWLEDGEMENTS

This work was funded by an EASTBIO DTP scholarship to A. Li Veiros. We would like to thank Allison K. Puckett, for help with updating Table S1.

### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

No new data was generated for this work.



## ORCID

A. Li Veiros  <https://orcid.org/0009-0005-2012-9121>

Manon K. Schweinfurth  <https://orcid.org/0000-0003-2066-7892>

Michael M. Webster  <https://orcid.org/0000-0001-9597-6871>

## REFERENCES

- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 211(4489), 1390–1396. <https://doi.org/10.1126/science.7466396>
- Beauchamp, G. (2014). *Social predation: How group living benefits predators and prey*. Academic Press.
- Brown, G. E., Golub, J. L., & Plata, D. L. (2001). Attack cone avoidance during predator inspection visits by wild finescale dace (*Phoxinus neogaeus*): The effects of predator diet. *Journal of Chemical Ecology*, 27(8), 1657–1666. <https://doi.org/10.1023/A:1010466410152>
- Brown, G. E., & Magnavacca, G. (2003). Predator inspection behaviour in a characin fish: An interaction between chemical and visual information? *Ethology*, 109(9), 739–750. <https://doi.org/10.1046/j.1439-0310.2003.00919.x>
- Brown, J. L. (1983). Cooperation—A Biologist's dilemma. In J. S. Rosenblatt, R. A. Hinde, C. Beer, & M.-C. Busnel (Eds.), *Advances in the study of behavior* (Vol. 13, pp. 1–37). Academic Press. [https://doi.org/10.1016/S0065-3454\(08\)60284-3](https://doi.org/10.1016/S0065-3454(08)60284-3)
- Bshary, R., & Bergmüller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. *Journal of Evolutionary Biology*, 21(2), 405–420. <https://doi.org/10.1111/j.1420-9101.2007.01482.x>
- Carter, G. (2014). The reciprocity controversy. *Animal Behavior and Cognition*, 1(3), 368–386. <https://doi.org/10.12966/abc.08.11.2014>
- Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, 462(7269), 51–57. <https://doi.org/10.1038/nature08366>
- Connor, R. C. (1995). The benefits of mutualism: A conceptual framework. *Biological Reviews*, 70(3), 427–457. <https://doi.org/10.1111/j.1469-185X.1995.tb01196.x>
- Connor, R. C. (1996). Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Animal Behaviour*, 51(2), 451–454. <https://doi.org/10.1006/anbe.1996.0042>
- Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I., & Krause, J. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, 100(3), 429–438. <https://doi.org/10.1034/j.1600-0706.2003.12023.x>
- Croft, D. P., James, R., Thomas, P. O. R., Hathaway, C., Mawdsley, D., Laland, K. N., & Krause, J. (2006). Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, 59(5), 644–650. <https://doi.org/10.1007/s00265-005-0091-y>
- Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause, J. (2005). Assortative interactions and social networks in fish. *Oecologia*, 143(2), 211–219. <https://doi.org/10.1007/s00442-004-1796-8>
- Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to Behavioural ecology*. John Wiley & Sons.
- Doebeli, M., & Hauert, C. (2005). Models of cooperation based on the Prisoner's dilemma and the snowdrift game. *Ecology Letters*, 8(7), 748–766. <https://doi.org/10.1111/j.1461-0248.2005.00773.x>
- Dugatkin, L. A. (1988). Do guppies play tit for tat during predator inspection visits? *Behavioral Ecology and Sociobiology*, 23(6), 395–399. <https://doi.org/10.1007/BF00303714>
- Dugatkin, L. A. (1991). Dynamics of the tit for tat strategy during predator inspection in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, 29(2), 127–132. <https://doi.org/10.1007/BF00166487>
- Dugatkin, L. A. (2009). *Principles of animal behavior*. W. W. Norton.
- Dugatkin, L. A., & Alfieri, M. (1991a). Guppies and the tit for tat strategy: Preference based on past interaction. *Behavioral Ecology and Sociobiology*, 28(4), 243–246. <https://doi.org/10.1007/BF00175096>
- Dugatkin, L. A., & Alfieri, M. (1991b). Tit-for-tat in guppies (*Poecilia reticulata*): The relative nature of cooperation and defection during predator inspection. *Evolutionary Ecology*, 5(3), 300–309. <https://doi.org/10.1007/BF02214234>
- Dugatkin, L. A., & Godin, J.-G. J. (1992). Predator inspection, shoaling and foraging under predation hazard in the Trinidadian guppy, *Poecilia reticulata*. *Environmental Biology of Fishes*, 34(3), 265–276. <https://doi.org/10.1007/BF00004773>
- Fishbase. (2023). Retrieved from <https://www.fishbase.se/summary/Gasterosteus-aculeatus.html>
- FitzGibbon, C. D. (1994). The costs and benefits of predator inspection behaviour in Thomson's gazelles. *Behavioral Ecology and Sociobiology*, 34(2), 139–148. <https://doi.org/10.1007/BF00164184>
- Frommen, J. G., Mehlis, M., & Bakker, T. C. M. (2009). Predator-inspection behaviour in female three-spined sticklebacks *Gasterosteus aculeatus* is associated with status of gravidity. *Journal of Fish Biology*, 75(8), 2143–2153. <https://doi.org/10.1111/j.1095-8649.2009.02408.x>
- Godin, J. J., & Davis, S. A. (1995). Who dares, benefits: Predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 259(1355), 193–200. <https://doi.org/10.1098/rspb.1995.0028>
- Häberli, M. A., Aeschlimann, P. B., & Milinski, M. (2005). Sticklebacks benefit from closer predator inspection: An experimental test of risk assessment. *Ethology Ecology & Evolution*, 17(3), 249–259. <https://doi.org/10.1080/08927014.2005.9522595>
- Hamilton, W. (1964). Genetical evolution of social behaviour I. *Journal of Theoretical Biology*, 7(1), 17–52. [https://doi.org/10.1016/0022-5193\(64\)90038-4](https://doi.org/10.1016/0022-5193(64)90038-4)
- Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., & Manica, A. (2009). Social feedback and the emergence of leaders and followers. *Current Biology*, 19(3), 248–252. <https://doi.org/10.1016/j.cub.2008.12.051>
- Harcourt, J. L., Sweetman, G., Manica, A., & Johnstone, R. A. (2010). Pairs of fish resolve conflicts over coordinated movement by taking turns. *Current Biology*, 20(2), 156–160. <https://doi.org/10.1016/j.cub.2009.11.045>
- Kastampolidou, K., Nikiforos, M. N., & Andronikos, T. (2020). A brief survey of the Prisoners' dilemma game and its potential use in biology. In P. Vlamos (Ed.), *GeNeDis 2018* (Vol. 1194, pp. 315–322). Springer International Publishing. [https://doi.org/10.1007/978-3-030-32622-7\\_29](https://doi.org/10.1007/978-3-030-32622-7_29)
- Koboroff, A., Kaplan, G., & Rogers, L. (2009). Avian anti-predator strategies: Specificity of mobbing and predator inspection in the Australian magpie (*Gymnorhina tibicen*) and the zebra finch (*Taeniopygia guttata*). [Doctoral thesis, University of New England]. <https://rune.une.edu.au/web/handle/1959.11/3059>
- Krama, T., Vrublevska, J., Freeberg, T. M., Kullberg, C., Rantala, M. J., & Krams, I. (2012). You mob my owl, I'll mob yours: Birds play tit-for-tat game. *Scientific Reports*, 2(1), 800. <https://doi.org/10.1038/srep00800>
- Lazarus, J., & Metcalfe, N. B. (1990). Tit-for-tat cooperation in sticklebacks: A critique of Milinski. *Animal Behaviour*, 39(5), 987–988. [https://doi.org/10.1016/S0003-3472\(05\)80965-0](https://doi.org/10.1016/S0003-3472(05)80965-0)
- Leal, M., & Rodríguez-Robles, J. A. (1997). Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Animal Behaviour*, 54(5), 1147–1154. <https://doi.org/10.1006/anbe.1997.0572>

- Magurran, A. E. (2005). *Evolutionary ecology: The Trinidadian guppy*. Oxford University Press.
- Magurran, A. E., & Girling, S. L. (1986). Predator model recognition and response habituation in shoaling minnows. *Animal Behaviour*, 34(2), 510–518. [https://doi.org/10.1016/S0003-3472\(86\)80119-1](https://doi.org/10.1016/S0003-3472(86)80119-1)
- Magurran, A. E., & Higham, A. (1988). Information transfer across fish shoals under predator threat. *Ethology*, 78(2), 153–158. <https://doi.org/10.1111/j.1439-0310.1988.tb00226.x>
- Magurran, A. E., & Seghers, B. H. (1990). Population differences in predator recognition and attack cone avoidance in the guppy *Poecilia reticulata*. *Animal Behaviour*, 40(3), 443–452. [https://doi.org/10.1016/S0003-3472\(05\)80524-X](https://doi.org/10.1016/S0003-3472(05)80524-X)
- Masters, W. M., & Waite, T. A. (1990). Tit-for-tat during predator inspection, or shoaling? *Animal Behaviour*, 39(3), 603–604. [https://doi.org/10.1016/S0003-3472\(05\)80431-2](https://doi.org/10.1016/S0003-3472(05)80431-2)
- Milinski, M. (1987). Tit for tat in sticklebacks and the evolution of cooperation. *Nature*, 325(6103), 433–435. <https://doi.org/10.1038/325433a0>
- Milinski, M. (1990a). No alternative to tit-for-tat cooperation in sticklebacks. *Animal Behaviour*, 39(5), 989–991. [https://doi.org/10.1016/S0003-3472\(05\)80966-2](https://doi.org/10.1016/S0003-3472(05)80966-2)
- Milinski, M. (1990b). On cooperation in sticklebacks. *Animal Behaviour*, 40(6), 1190–1191. [https://doi.org/10.1016/S0003-3472\(05\)80189-7](https://doi.org/10.1016/S0003-3472(05)80189-7)
- Milinski, M. (1992). Predator inspection: Cooperation or 'safety in numbers'? *Animal Behaviour*, 43, 679–680. [https://doi.org/10.1016/S0003-3472\(05\)81027-9](https://doi.org/10.1016/S0003-3472(05)81027-9)
- Milinski, M., Külling, D., & Kettler, R. (1990). Tit for tat: Sticklebacks (*Gasterosteus aculeatus*) 'trusting' a cooperating partner. *Behavioral Ecology*, 1(1), 7–11. <https://doi.org/10.1093/beheco/1.1.7>
- Milinski, M., Luthi, J. H., Egger, R., & Parker, G. A. (1997). Cooperation under predation risk: Experiments on costs and benefits. *Proceedings of the Royal Society B: Biological Sciences*, 264(1383), 831–837. <https://doi.org/10.1098/rspb.1997.0116>
- Milinski, M., Pflüger, D., Külling, D., & Kettler, R. (1990). Do sticklebacks cooperate repeatedly in reciprocal pairs? *Behavioral Ecology and Sociobiology*, 27(1), 17–21. <https://doi.org/10.1007/BF00183308>
- Murphy, K. E., & Pitcher, T. J. (1991). Individual behavioural strategies associated with predator inspection in minnow shoals. *Ethology*, 88(4), 307–319. <https://doi.org/10.1111/j.1439-0310.1991.tb00285.x>
- Nocera, J. J., Taylor, P. D., & Ratcliffe, L. M. (2008). Inspection of mob-calls as sources of predator information: Response of migrant and resident birds in the neotropics. *Behavioral Ecology and Sociobiology*, 62(11), 1769–1777. <https://doi.org/10.1007/s00265-008-0605-5>
- Noë, R. (2006). Cooperation experiments: Coordination through communication versus acting apart together. *Animal Behaviour*, 71(1), 1–18. <https://doi.org/10.1016/j.anbehav.2005.03.037>
- Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution*, 10(8), 336–339. [https://doi.org/10.1016/S0169-5347\(00\)89123-5](https://doi.org/10.1016/S0169-5347(00)89123-5)
- Ostlund-Nilsson, S., Mayer, I., & Huntingford, F. A. (Eds.). (2007). *Biology of the three-spined stickleback*. CRC Press. <https://doi.org/10.1201/9781420004830>
- Phylopic. (2023). Retrieved from <https://www.phylopic.org/>
- Pimentel, A. F. N., Lima-Maximino, M. G., Soares, M. C., & Maximino, C. (2021). Zebrafish cooperate while inspecting predators: Experimental evidence for conditional approach. *Animal Behaviour*, 177, 59–68. <https://doi.org/10.1016/j.anbehav.2021.04.014>
- Raihani, N. J., & Bshary, R. (2011). Resolving the iterated prisoner's dilemma: Theory and reality. *Journal of Evolutionary Biology*, 24(8), 1628–1639. <https://doi.org/10.1111/j.1420-9101.2011.02307.x>
- Reboreda, J. C., & Kacelnik, A. (1990). On cooperation, tit-for-tat and mirrors. *Animal Behaviour*, 40(6), 1188–1189. [https://doi.org/10.1016/S0003-3472\(05\)80188-5](https://doi.org/10.1016/S0003-3472(05)80188-5)
- Schweinfurth, M. K., & Call, J. (2019). Reciprocity: Different behavioural strategies, cognitive mechanisms and psychological processes. *Learning & Behavior*, 47(4), 284–301. <https://doi.org/10.3758/s13420-019-00394-5>
- Stevens, J., Volstorf, J., Schooler, L., & Rieskamp, J. (2011). Forgetting constrains the emergence of cooperative decision strategies. *Frontiers in Psychology*, 1, 1–12. <https://doi.org/10.3389/fpsyg.2010.00235>
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46(1), 35–57. <https://doi.org/10.1086/406755>
- Turner, G. F., & Robinson, R. L. (1992). Milinski's tit-for-tat hypothesis: Do fish preferentially inspect in pairs? *Animal Behaviour*, 43(4), 677–678. [https://doi.org/10.1016/S0003-3472\(05\)81026-7](https://doi.org/10.1016/S0003-3472(05)81026-7)
- van der Bijl, W., Thyselius, M., Kotrschal, A., & Kolm, N. (2015). Brain size affects the behavioural response to predators in female guppies (*Poecilia reticulata*). *Proceedings of the Royal Society B: Biological Sciences*, 282(1812), 20151132. <https://doi.org/10.1098/rspb.2015.1132>
- Walling, C. A., Dawney, N., Kazem, A. J. N., & Wright, J. (2004). Predator inspection behaviour in three-spined sticklebacks (*Gasterosteus aculeatus*): Body size, local predation pressure and cooperation. *Behavioral Ecology and Sociobiology*, 56(2), 164–170. <https://doi.org/10.1007/s00265-004-0763-z>
- Ward, A., & Webster, M. (2016). *Sociality: The behaviour of group-living animals*. Springer.
- Ward, A. J. W., Botham, M. S., Hoare, D. J., James, R., Broom, M., Godin, J.-G. J., & Krause, J. (2002). Association patterns and shoal fidelity in the three-spined stickleback. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1508), 2451–2455. <https://doi.org/10.1098/rspb.2002.2169>
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20(2), 415–432. <https://doi.org/10.1111/j.1420-9101.2006.01258.x>
- Zaguri, M., & Hawlena, D. (2019). Bearding the scorpion in his den: Desert isopods take risks to validate their 'landscape of fear' assessment. *Oikos*, 128(10), 1458–1466. <https://doi.org/10.1111/oik.06477>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Veiros, A. L., Schweinfurth, M. K., & Webster, M. M. (2023). On closer inspection: Reviewing the debate on whether fish cooperate to inspect predators. *Ethology*, 00, 1–10. <https://doi.org/10.1111/eth.13427>