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# Tit for Tat, by-product mutualism and predator inspection: a reply to Connor

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In his critique, Connor (1996) raised a number of questions surrounding predator inspection behaviour in fish and the evolution of cooperation. Here I will address three claims made by Connor and make a few general comments on the questions he raised. First, however, I wish to touch briefly on another issue. Following West-Eberhard (1975) and Brown (1983), I have argued that by-product mutualism is one means of achieving cooperation among individuals, and I have gone as far as to say that

> Although the evidence from empirical studies is inconclusive, it strongly suggests that reciprocal altruism is only one of three categories of cooperative behavior among unrelated individuals in nature: it fails to justify the bias toward reciprocity in the recent theoretical literature. . . . In particular the potential importance of by-product mutualism appears to have been overlooked [Mesterton-Gibbons & Dugatkin 1992, page 278]

So, my argument with Connor (1996) is not that by-product mutualism is a weak force, nor that it does not allow for partner choice, but rather that, in the case of predator inspection in fish, by-product mutualism does not explain the available data as well as Tit for Tat.

The following comments address Connor's specific claims.

(1) Connor (1996) remarked, 'Unable to provide unequivocal evidence for a Prisoner's Dilemma or to reject shoaling hypotheses conclusively in favour of Tit for Tat, various authors have argued that consistent patterns of partner preference support the hypothesis that the dynamics of joint inspection are governed by Tit for Tat (page 452). The first part of this statement is only partly true, and the second part is completely false. With respect to the claim that evidence for a Prisoner's Dilemma is weak, Milinski has argued numerous times (starting with Milinski 1987) that the biology of predator inspection probably satisfies the Prisoner's Dilemma (temptation to cheat, $T$, >reward for mutual inspection, $R$, >punishment when no one inspects, $P$, >sucker's payoff when a lone fish inspects, $S$). Empirical evidence, gathered outside the context of predator inspection and cooperation (e.g. from work on the selfish herd, spatial 'oddity' and predation threat; Milinski 1977a, b), suggests that $S$ (inspecting alone) is indeed the worst payoff for inspection. Furthermore, Dugatkin (1992) explicitly tested one inequality of the Prisoner's Dilemma, namely that within groups containing both inspectors and non-inspectors, inspectors suffer greater predation threat; i.e. $T>R$. The data, although correlational, suggest that this inequality is indeed met when inspecting predators (cf. Godin & Davis 1995). Thus, some of the inequalities of the Prisoner's Dilemma can be gleaned from the available literature, and the others can be inferred from an understanding of predator–prey interactions and predator inspection; as such, Connor's statement that evidence for the Prisoner's Dilemma is unavailable is only partly true.

The second part of Connor's (1996) quote, that researchers have not been able to distinguish Tit for Tat from 'shoaling hypotheses' (an amorphous term in this context) is incorrect. Although the 'Tit-for-Tat controversy' has burned long and hard (particularly in this journal), the sum of the experimental evidence now available strongly supports the notion that fish are indeed playing Tit for Tat (Milinski 1987; Dugatkin 1988, 1991; Milinski et al. 1990a, b; Dugatkin & Alfieri 1991a, 1992; Huntingford et al. 1994). Perhaps the most direct test of this is Dugatkin's (1991) study, which showed experimental evidence that guppies from areas of high-predation threat display all

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the characteristics associated with Tit for Tat when inspecting a predator. Furthermore, inter-population evidence shows that guppies from areas of low predation pressure do not display Tit for Tat, just as predicted (Dugatkin & Alfieri 1992; see also Huntingford et al. 1994, for evidence of inter-population differences in sticklebacks).

Given the above evidence, it should be clear that the partner choice experiments cited by Connor (1996) (Milinski et al. 1990a; Dugatkin & Alfieri 1991b) were meant to examine corollary predictions made by the Prisoner's Dilemma model (e.g. do cooperators prefer to associate with other cooperators?) and were not intended as a replacement for evidence of Tit for Tat. In summary, Connor's quote has misrepresented the history and intent of prior work on cooperation and predator inspection.

(2) Connor (1996) wrote 'It is not clear, however, how much benefit the trailing fish obtains (Murphy & Pitcher 1991)' (page 452). Whether the trailing fish receives information is critical to the Tit for Tat argument, because it affects the 'temptation to cheat' payoff of the Prisoner's Dilemma (*S*). Despite Connor's claim, such evidence does exist. In an elegant experiment using one-way mirrors, Magurran & Higham (1988) found that inspecting fish transferred information to their non-inspecting shoal mates, who could see them inspect, but could not see the predator. Surely information transfer must be even greater to a trailing co-inspector, who can see the predator! Under the logic of by-product mutualism, no such information transfer is predicted or necessary. As such, Tit for Tat better explains the empirical evidence for information transfer than does by-product mutualism.

(3) In discussing when fish stop an inspection, Connor (1996) wrote 'The stopping point may reflect a compromise between the inspecting motive, which favours moving forward, and the shoaling response which favours retreat' (page 452). Although it certainly can be argued that the three traits associated with Tit for Tat (niceness, retaliation and forgiving; Axelrod 1980a, b) appear rather anthropocentric terms, they are each explicitly defined in theory and in empirical work (e.g. Dugatkin 1991). It is, however, very difficult to know what Connor (1996) referred to when he spoke of an inspecting 'motive' or, for that matter to what precisely a shoaling 'response' refers. Until such terms are clearly defined, this statement is untestable.

I wish to make one last general point. The critical question surrounding whether by-product mutualism or Tit for Tat better explains predator inspection behaviour ultimately rests on which theory better explains the data. In addition to the cases delineated above, by-product mutualism models make different predictions from reciprocity models, and so it is in theory possible to see which model more closely fits the data. Two cases can illustrate this point. First, Dugatkin (1991) found that a fish leading an inspection stopped and turned back away from the predator if its partner trailed behind. This former lead fish would then wait for the former trailing fish to begin an inspection before it would again start inspecting; in the language of theory, the lead fish 'forgave' its partner (where 'forgiving' is explicitly defined by measurable parameters). This outcome is precisely what one would predict if fish were using Tit for Tat. No clear prediction emerges from by-product mutualism theory with respect to this issue. If anything, by-product mutualism theory predicts that sometimes the lead fish should wait for its partner to move ahead, and sometimes the converse. Second, under by-product mutualism, individuals receive a higher payoff for cooperating than for not. In game theory terms, the mutual cooperation payoff (*R*) is higher than the temptation to cheat (*T*). As Milinski (1990) noted, however, if this were the case, one would predict that once any fish began inspecting, everyone (or at least the great majority) in a school would do likewise. The Prisoner's Dilemma framework, however, predicts that pairs of inspecting fish or fish inspecting alone should often occur. The data support the latter interpretation. Dugatkin & Godin (1992) provided evidence that when guppies inspect in their native stream of Trinidad, singletons and pairs of inspectors were by far the most commonly occurring group size (see also; Milinski 1992; Turner & Robinson 1992).

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