On Cooperation, Tit-for-tat and Mirrors

Experimental tests of strategies for cooperation during predator inspection behaviour in fish have been the topic of a recent controversy (Milinski 1987; Dugatkin 1988; Lazarus & Metcalfe 1990; Masters & Waite 1990; Milinski 1990). The behaviour consists of breaking away from a shoal to approach predators tentatively. It has been suggested that in such visits the fish can gather knowledge about the identity, precise location, and current motivational state of the predator (Pitcher 1986).

In an influential experimental paper Milinski (1987; see also May 1987) claimed that the problem faced by two fish in this situation resembles a two-player iterated Prisoner's Dilemma. In this game, each player has two options: cooperate or defect. If they cooperate both do better than if both defect. But if one player defects while the other cooperates, the defector gets more than if both had cooperated, and the cooperator gets less than if both had defected. In addition, if both players always cooperate they get more than if they alternate roles with one cooperating and the other defecting.

The Prisoner's Dilemma has been used to analyse the evolutionary stability of cooperative behaviour (Axelrod & Hamilton 1981). Evolutionarily stable strategy (ESS) analysis demonstrated that under many circumstances a strategy called Tit-for-tat (TFT), defined as cooperate in the first game and from then on do whatever the other player did in the preceding game, could spread and persist.

In Milinski's experiment, the distance between sticklebacks, *Gasterosteus aculeatus*, and a predator confined behind glass at one end of the tank was measured in two conditions. In one condition there was a 'cooperative' partner, namely a parallel mirror simulating a companion which followed the subject's moves. In another condition there was a 'defector' partner simulated by a mirror placed at an angle of 32°, giving a reflected self-image that moved off at an angle of 64° as the subject approached the predator. Sticklebacks with the parallel mirror approached the predator more than those with the mirror at an angle. Milinski claimed that in the two conditions the fish behaved according to TFT.

In a replicate experiment using guppies, *Poecilia reticulata*, Dugatkin (1988) obtained similar results. However, his interpretation was that guppies were using a 'conditional approach' rule which does not require the payoff matrix of Prisoner's Dilemma.

Beyond the question of whether the situation really mimics an iterated Prisoner's Dilemma (see Milinski 1987, 1990; Dugatkin 1988; Lazarus & Metcalfe 1990) these experiments present methodological and theoretical problems which are worth clarifying.

One crucial issue which has already been discussed (Lazarus & Metcalfe 1990) is that there was no control for the effect of the predator. Masters & Waite (1990) performed a replicate without the predator and obtained qualitatively similar results to those obtained by Milinski. Thus, at least part of the differences between groups are independent of the presence of the predator and should not be attributed to cooperation in predator inspection behaviour.

Another difficulty with the experimental procedure itself is that while it is true that the mirror produced an image of the prey (the partner), it must also have produced an image of the predator. The virtual image of the predator must have been in a different position in each treatment. Moreover, the mirror per se produced different views of the tank. Thus, the treatments had confounding variables and the group differences could be due to the position of the virtual image of the prey, the position of the virtual image of the predator, or even the different view the fish has of the tank.

The analyses were molar, i.e. based on aggregates of many actions. Lazarus & Metcalfe (1990) pointed out this is not appropriate to test for the dynamics of TFT. Actually, this view could be expanded to say that molar analysis would hardly ever be sufficient to test the use of any strategy specified at the level of individual actions.

In Milinski's and Dugatkin's experiments the 'cooperative' group (parallel mirror) showed a decrease in distance to the predator with time. This effect was weaker in the 'defecting' group (angled mirror). Both authors interpret this as a proof of cooperation during predator inspection, and Milinski claims that this supports TFT. Although this result can be qualitatively consistent with TFT or conditional approach, it can also be consistent with alternative hypotheses, including random behaviour. To prove the latter, we ran Monte Carlo simulations representing these experiments. Our model assumed that each fish moved in a unidimensional space divided into 20 sections, with section 1 representing that closest to the predator compartment. The trial started with the model fish in section 20 and the fish moved one section every 2 s for 5 min (150 movements). In sections 1 and 20, fish attempting to move out of the space stayed in the same position. Following Milinski, the results were

The Editors would like to call attention to the fact that the paper by Lazarus & Metcalfe (1990, *Anim. Behav.*, **39,** 987–988) was received and accepted before that of Masters & Waite (1990, *Anim. Behav.*, **39,** 603–604). We regret the unavoidable delays that have reversed the order of publication.

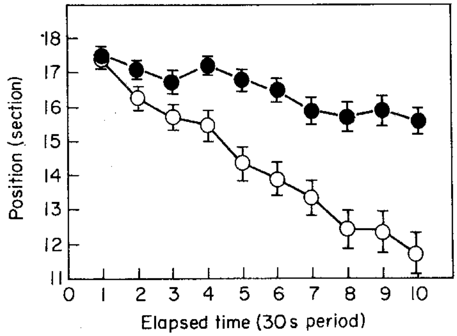

Figure 1. Mean ± SE position of the model fish ($N=100$) each 30 s of the trial. ○: $P=0{\cdot}5$; ●: $P=0{\cdot}45$.

expressed as distance to section 1 each 30 s. In one of the treatments (random) the probability of a movement attempt in each direction was 0·5. In this condition there was a negative correlation between distance to section 1 and elapsed time, exactly as in Milinski's and Dugatkin's 'cooperative' group (Fig. 1). This correlation is a consequence of starting the simulation with the model fish (as in the experiments) in the section furthest from the predator. In another treatment (biased) a directional bias was introduced by setting the probability of a movement attempt towards section 1 as 0·45 and the probability of moving towards section 20 as 0·55. In this case the correlation between distance to the predator and time was weaker than in the random group, as observed in Milinski's and Dugatkin's 'defecting' group. The point of our simulation was to demonstrate that molar outcomes are not satisfactory evidence for dynamic strategies. Random behaviour produced the molar outcome of the 'cooperative' group and any directional bias (as could result from one or more of the confounding variables in the experiments) can lead to the observed difference between groups.

How should strategies be tested? If animals follow a strict TFT rule this produces a deterministic conditional sequence in which the probability of cooperation is unity if the partner had cooperated in the previous game and zero if it had defected. Transition probabilities in actual data can be estimated by means of a first order Markov analysis. These transition probabilities can be compared with the predictions of TFT and of random behavioural sequences. Unfortunately, this molecular analysis cannot be performed in mirror experiments because the reflected images always behave consistently. We believe this is a major obstacle for studies of cooperation with the use of mirrors.

A further point concerns the strength of the predictions. Theoretical studies (Axelrod & Hamilton 1981) have shown that TFT is an ESS against many alternatives (but also see Boyd & Lorberbaum 1987). To our knowledge, it is not clear to what extent probabilistic versions of TFT are ESSs against these alternatives. Given that most empirical evidence of cooperative behaviour has shown reciprocity only in a probabilistic way (i.e. the probability of cooperation is higher if the partner cooperated before) literal TFT has not yet been supported. While TFT remains a useful metaphor, we believe that there is no justification for claiming that reciprocity per se is evidence for TFT.

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