

Tit-For-Tat in guppies (*Poecilia reticulata*): the relative nature of cooperation and defection during predator inspection

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Summary

The introduction of game-theoretical thinking into evolutionary biology has laid the groundwork for a heuristic view of animal behaviour in which individuals employ 'strategies' – rules that instruct them how to behave in a given circumstance to maximize relative fitness. Axelrod and Hamilton (1981) found that a strategy called Tit-For-Tat (TFT) is one robust cooperative solution to the iterated Prisoner's Dilemma game. There exists, however, little empirical evidence that animals employ TFT. Predator inspection in fish provides one ecological context in which to examine the use of the TFT strategy.

Here we describe a study in which guppies were tested in multiple predator inspection trials. An individual was tested with its mirror images as well as a series of live conspecifics. Results indicate that guppies are capable of recognizing and remembering their partner's behaviour and seem to employ TFT-like strategies over the course of many inspection visits. In addition, significant differences exist between individuals in the degree to which they will inspect a predator, suggesting that 'cooperator' and 'defector' may be relative terms rather than discrete categories of behaviour.

Keywords: Game theory; Tit-For-Tat; predator inspection; guppy.

Introduction

Axelrod and Hamilton's (1981) employment of the Prisoner's Dilemma game (Fig. 1) to model the evolution of cooperation between unrelated individuals has provided evolutionary biologists with a theoretical framework for examining this fascinating question. The Prisoner's Dilemma models a situation in which each individual ('player') receives a higher payoff for not cooperating (defecting) than for cooperating, while mutual cooperation provides each player with a higher payoff than mutual defection.

Using both analytical models and computer simulations Axelrod and Hamilton (1981) found that provided the probability of meeting one's 'partner' in the future exceeds some critical threshold value, a conditionally cooperative strategy called Tit-For-Tat (TFT; a strategy created by A. Rapoport) emerged as one robust solution to the iterated Prisoner's Dilemma (but see Boyd and Lorberbaum (1987)). TFT instructs a player to cooperate on the first move of a game and subsequently to copy its partner's last move. Thus, TFT is said to possess the following characteristics: (1) TFT is a 'nice' strategy, i.e. it cooperates on the first move of a game; (2) TFT is 'retaliatory', i.e. it follows a move of defection by its partner with its own move of defection; (3) TFT is 'forgiving', i.e. if its partner defects, but then subsequently cooperates, TFT 'forgives' the prior move of defection (by cooperating with its partner). Nice behaviour allows strings of

		PLAYER 2	
		COOPERATE	DEFECT
PLAYER 1	COOPERATE	<p>R</p> <p>Reward for mutual cooperation</p>	<p>S</p> <p>The 'Sucker's' payoff</p>
	DEFECT	<p>T</p> <p>Temptation payoff</p>	<p>P</p> <p>Punishment for mutual defection</p>

Figure 1. The payoff matrix for the Prisoner's Dilemma. The game qualifies as a Prisoner's Dilemma if $T > R > P > S$ and $2R > T + S$. Player 1's payoffs are shown.

mutual cooperation to begin, retaliation prevents strings of sucker's payoffs from occurring, and forgiving allows reestablishment of strings of mutual cooperation with individuals that occasionally defect or defect by mistake (Boyd, 1989).

Theoretical population biologists have considerably extended Axelrod and Hamilton's results (Brown *et al.*, 1982; Michod and Sanderson, 1985; Peck and Feldman, 1986; Feldman and Thomas, 1987; Boyd and Richerson, 1988; Boyd, 1989; Dugatkin, 1990; Dugatkin and Wilson, 1991), but empirical research on the use of such conditionally cooperative strategies as TFT has lagged behind theory. Predator inspection in fish (Pitcher *et al.*, 1986) provides one ecological context to examine the use of the TFT strategy. Predator inspection occurs in numerous schooling species of fish in which one to a few individuals (the 'inspectors') break away from the school and approach a potential predator in a slow saltatory manner. Inspection has been noted in *Gambusia patreulis* (George, 1960), *Poecilia reticulata* (Seghers, 1973; Dugatkin, 1988), *Phoxinus phoxinus* (Pitcher *et al.*, 1986; Magurran, 1986), *Gasterosteus aculeatus* (Milinski, 1987) and *Stegastes planifrons* (Helfman, 1989).

Inspectors gain information about the risk posed by a potential predator, a benefit that is shared by all of the fish in the vicinity (Magurran and Higgam, 1988). The risk of approaching the predator is spread among all of the inspectors, but is not shared by those that remain at a distance. In game theory terminology, consider a two person game in which inspection is equated with cooperation and non-inspection with defection. Three types of groups can be formed: cooperate/cooperate, cooperate/defect, and defect/defect. Let B = the benefit and C = the cost of inspection. If both fish cooperate and approach the predator they both obtain the benefit (B) and share the cost (C) (i.e. the payoff to each inspector equals $(B - C/2)$). If one fish approaches the predator and the other remains distant, both obtain the benefit while only one obtains the cost ($(B - C)$ for the cooperator, B for the defector). If neither approaches the predator then let costs and benefits equal zero. If $C > B$, but $B > C/2$ these payoffs satisfy the inequalities of the Prisoner's Dilemma (Fig. 1).

Using two 'mirror' treatments, Milinski (1987) and Dugatkin (1988) examined whether sticklebacks and guppies, respectively, use TFT during their predator inspection visits. In one treatment a mirror placed parallel to a tank created a second image that swam beside the subject during predator inspections (the 'cooperating' image), while in the other, an angled mirror created an image that swam behind and away from the subject during inspections visits (the 'defecting' image). Differences between mirror treatments were interpreted as evidence that both sticklebacks and guppies use a TFT-like strategy during inspection behaviour (Milinski, 1987; Dugatkin, 1988). Individuals were tested only once, however, and were never tested with live conspecifics.

The above 'mirror' experiments (Milinski, 1987; Dugatkin, 1988) have been the subject of two recent critiques (Lazarus and Metcalfe, 1990; Masters and Waite, 1990; but see Milinski, 1990; Dugatkin, 1991a, for responses). Lazarus and Metcalfe (1990) and Milinski (1990) debate the question of whether the payoffs for predator inspection qualify as a Prisoner's Dilemma and also discuss alternative hypotheses to TFT, while Masters and Waite (1990) and Dugatkin (1991a) discuss what constitutes predator inspection as well as what constitutes evidence of TFT. Regardless of the outcome of this exchange, many critical questions on the use of TFT-like strategies during predator inspection remain unanswered.

Milinski *et al.*, (1990a, b), Dugatkin (1991b) and Dugatkin and Alfieri (1991) have followed up the original mirror experiments by examining the behavioural dynamics of two and three live fish during predator inspection. Milinski *et al.* (1990a, b) have demonstrated that sticklebacks build up 'trust' with cooperating co-inspectors and that in larger groups individuals pair up with a particular co-inspector more often than expected by chance alone. Dugatkin and Alfieri (1991) found that given a choice, guppies will choose to associate with the more cooperative of two co-inspectors. In addition Dugatkin (1991b) found that guppies display nice, retaliatory and forgiving behaviour *during the course* of an inspection visit. Thus the 'micromoves' of inspecting guppies appear to satisfy the criteria of the TFT strategy.

The current study was undertaken to address the following four questions: (1) do guppies use TFT-like strategies during predator inspection when paired with a second fish (i.e. a live co-inspector rather than its mirror image)? (2) do guppies treat each inspection visit as a move in a larger game and do they play TFT over considerable periods of time? (3) are individuals relatively consistent in the degree of inspection behaviour they display and if so, do individuals differ in this characteristic? (4) is the behaviour displayed during mirror trials a good predictor of behaviour displayed when a fish is paired with a live conspecific? To examine these questions it is necessary to test individuals numerous times with numerous partners.

Materials and methods

Subjects

Two groups (numbered 1 and 2) were established, each comprised of ten individually recognizable male guppies. Each group of males was housed in a 40 litre aquarium containing 10 females and tested one week after group formation. Within a group, all individuals were approximately of equal size (< 5% difference in standard length; $\bar{x}_{\text{group 1}} = 23 \pm 0.67$ cm; $\bar{x}_{\text{group 2}} = 23 \pm 0.98$ cm). All fish were drawn from two stock tanks containing over two hundred guppies each. Guppies were descendants of wild-caught fish from the Turure River, Trinidad. Group 1 was tested in late November 1989, while group 2 was tested in late March 1990.

A pumpkinseed sunfish (*Lepomis gibbosus*) was used as a predator (standard length 15.2 cm) for both groups. Pumpkinseed body shape is very similar to that of *Aquedens pulcher*, a native predator of guppies in the streams of Trinidad.

Experimental apparatus

The experimental apparatus was similar to that used by Milinski (1987) and Dugatkin (1988) (Fig. 2). Adjacent to a 20 l aquarium containing a predator was a 40 l aquarium. A 40 cm × 12.2 cm deep plexiglas tank was placed into the 40 l aquarium adjacent to the predator's tank. The plexiglass tank was divided into two 'lanes' by another sheet of clear plexiglas. On the bottom was a grid dividing the tank into 20 sections of equal length (2.03 cm), section 1 being furthest from the predator.

Each lane had an small artificial plant in section 1 to act as a potential refuge for guppies.

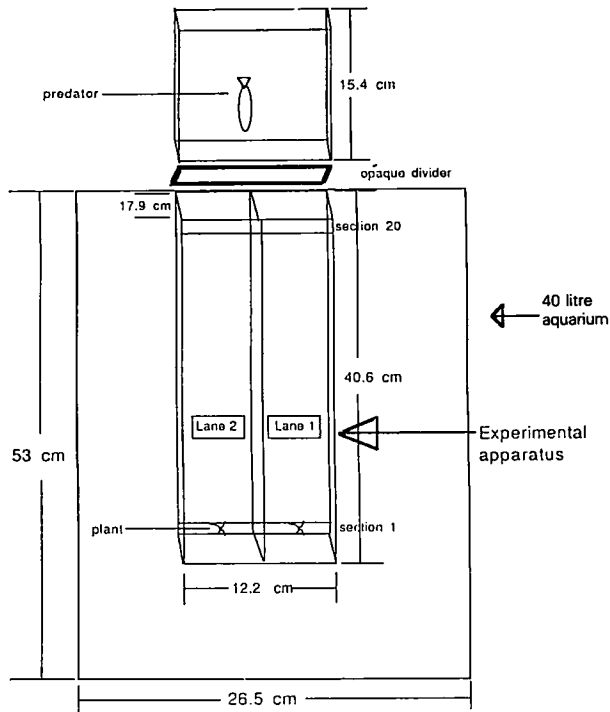


Figure 2. The experimental apparatus placed in a 40 l aquarium (viewed from above). All sides of the 40 l tank except the side near the predator's tank are covered with opaque paper.

Experimental protocol

The experimental protocol for group 1 was as follows: on days 1–3 each fish was tested once a day in a parallel mirror trial. Prior to the introduction of the fish into lane 1 of the experimental apparatus (Fig. 2), a 40.6 cm mirror was placed against this lane (see Introduction). After the mirror was in place, a single fish was placed into lane 1 and given 5 minutes to swim freely before the start of a trial. During this period an opaque partition obstructed the view between the experimental tank and the predator's tank. After this, the fish was placed behind a clear partition in the section furthest from the predator's tank and the opaque partition keeping the predator out of view was lifted. Thus, the predator and prey were in visual contact. One minute later the divider (which kept the guppy in section furthest from the predator) was raised and the 'trial' period began. The five minute period at the start of a trial when the guppy and predator were not in visual contact was not filmed.

On days 4–12 each fish was tested in a series of ‘pair’ trials, identical to the mirror trials, except that instead of a mirror placed against lane 1, a second fish from the same group was introduced into lane 2. Each guppy was randomly assigned three other fish to act as partners for its pair trials. A pair of fish was tested once a day for three consecutive days (days 4–6) at which point all five pairs were dissolved and new pairs were formed (using the randomly assigned partners mentioned above). The new pairs were tested for three days (days 7–9), broken up, and then a third set of pairs was formed (days 10–12). Each three day period with a given partner will be referred to as a ‘bout’. Lane assignment (lane 1 or 2) for each fish in a pair was determined in a random fashion each day of a bout. All trials (mirror and pair) lasted 2.5 minutes and were videotaped using a camera mounted 75 cm above the test apparatus. While examining the video tape, the position of the guppy(ies) was recorded every 5 seconds. The mean position during a 2.5 minute trial was used as a measure of inspection behaviour. (Dugatkin (1991b) has examined in detail the cooperative behaviour displayed by guppies *during* a predator inspection visit).

The protocol for group 2 was similar to that used for group 1 with two exceptions. First, fish in group 2 were placed into the apparatus 20 minutes prior to visual contact with the predator. This period was videotaped and served as a ‘no-predator’ control. Second, two additional mirror trials were run (on days 13 and 14) after the pair trials were completed to test for habituation to the predator (these will be referred to as ‘late’ mirror trials). Due to experimenter handling error, one fish in group 2 died after its trial on day 10.

Results

Habituation

A paired *t*-test on mean position in early and late mirror trials (in group 2) indicates no habituation to the predator. That is, no difference in average position was found between early and late mirror trails ($df = 8$, $t = 0.77$, $p > 0.4$).

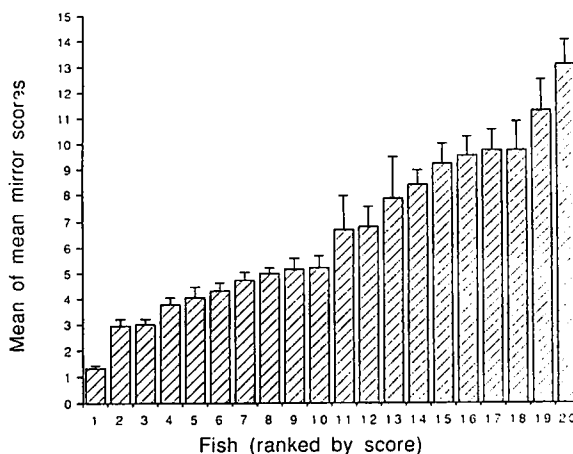


Figure 3. The Y axis represents the mean (1 SE) of the mean positions of all 20 fish during the mirror trials. Fish are ranked from lowest to highest value on the X axis. Note that high scores denote position closer to the predator.

Within and between subject differences in inspection

A split plot ANOVA on mean position during early mirror trials indicates that individuals are consistent in the level of inspection they display, but significant differences exist in the level of inspection displayed by different individuals (Fig. 3, between subjects; $F_{19,59} = 8.07$, $p < 0.001$, within subjects; $F_{2,59} = 2.01$, $p > 0.15$). Consistent individual differences are further corroborated by a significant rank order correlation of mean position of individuals in mirror and pair trials (Spearman rank test; $N = 20$, $Z = 3.135$, $p < 0.05$). This finding also indicates that mirror trials provide reliable measures of how fish will behave in trials with live partners.

Figure 4 shows the mean of the mean positions ($+ 1$ SE) of all fish in all pair trials. A split plot ANOVA on pair trial data (using the nine days of pair trials as a repeated measure) yields a significant difference in average position both between subjects ($F_{19,156} = 68.6$, $p < 0.001$) and within subjects ($F_{8,152} = 27.58$, $p < 0.005$). Thus, the behaviour of a fish is more variable when paired with other fish than when paired with its own image.

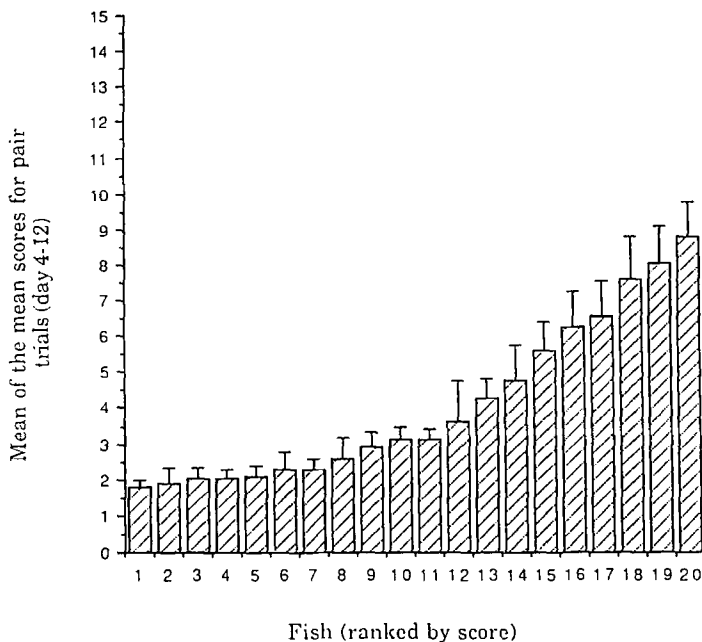


Figure 4. The mean positions ($+ 1$ SE) of all 20 fish during the nine pair trial days (days 4–12). Fish are ranked from lowest to highest value on the X axis. Note that high scores denote position closer to the predator.

Response to co-inspectors

Do fish temper their levels of inspection based on the behaviour of co-inspectors, i.e., does the lead fish respond to its trailing co-inspector? Examining behaviour in a three day bout with a particular partner may provide an answer to this question. Due to the between individual differences, we expect to see one fish (call it fish *A*) inspect more closely (have a higher mean position in the tank) on the first day than its partner (fish *B*). If a pair is divided into *A* and *B* fish based on their behaviour on the *first* day, then for a given bout, six categories can be formed: A_1 (all '*A*' fish on the first day of a bout), B_1 (all '*B*' fish on the first day of a bout), A_2 , A_3 , B_2 , B_3 (Fig. 5). An ANOVA indicates a significant difference in average position between the six

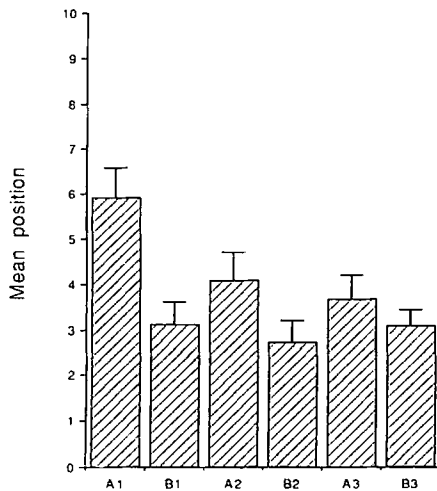


Figure 5. The mean position of fish grouped by their behaviour during a three day bout with a partner (see text).

categories ($F_{5,170} = 4.92$, $p < 0.005$). Follow up analysis, however, indicates no difference in average position between A_2 , A_3 , B_1 , B_2 , B_3 ($F_{4,141} = 1.21$, $p > 0.3$), but a significant difference in average position between A_1 and the other five categories combined ($F_{1,174} = 20.53$, $p < 0.001$). Thus fish with the higher average position on the first day of a bout seem to copy their partner's lower average position (on the first day of the bout) when meeting these fish for a second and third trial. This holds true regardless of the absolute value of the average position measure. For example, let us divide Fig. 5 into two groups; those with the ten highest average positions (high) and those with the ten lowest (low). For high/high and low/low pairs, results similar to the above are found (High/high: 6 categories; $F_{5,48} = 9.18$, $p < 0.001$; 5 categories (no A_1); $F_{4,40} = 0.521$, $p > 0.7$; A_1 vs other categories; $F_{1,52} = 46.8$, $p < 0.005$; Low/low: 6 categories; $F_{5,44} = 4.89$, $p < 0.005$; 5 categories (no A_1); $F_{4,37} = 0.199$, $p > 0.9$; A_1 vs other categories; $F_{1,48} = 25.7$, $p < 0.005$).

Does a lead fish on the first day of a bout (fish A) that stays even with its partner (B) on days 2 and 3 revert to its former average position when it is paired with a new fish (i.e. increase its average position at the start of a new bout)? Do B fish increase their average position at the start of a new bout? If we compare the average position of A fish on the last day of a given bout with the average position on the first day of the next bout, a significantly higher average position is found at the start of the next bout (Fig. 6, paired t -test; $df = 19$, $t = 2.25$, $p < 0.05$). This does not hold true for B fish (Fig. 6, paired t -test; $df = 19$, $t = 0.16$, $p > 0.15$). In addition, both A and B fish show no difference between average position on the first day of a given bout and average position on the first day of the next bout (paired t -test: A fish; $df = 19$, $t = 0.10$, $p > 0.90$, B fish; $df = 19$, $t = 1.27$, $p > 0.2$).

No predator control

It is possible that between subject differences in inspection behaviour are: (1) an artifact on some fish being more active in general than others, whether a predator is present or not or (2) that regardless of the predator, some fish prefer the half of the apparatus near the predator's tank while others prefer the half of the apparatus furthest from the predator. In order to address the first possibility, the coefficient of variation (CV) was used as a measure of activity. No significant

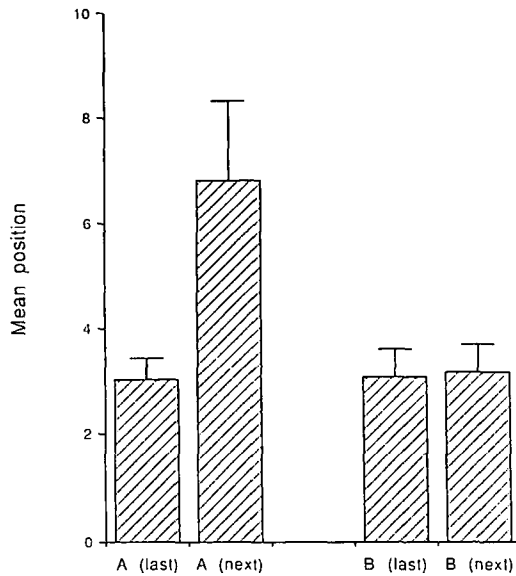


Figure 6. The mean position of fish across bouts. 'A' represents the position of fish who had the higher score on day 1 of a given bout. A (last) is A's average position on the last day of a given bout and A (next) is the average position on the first day of the subsequent bout. 'B' represents the position of fish who had the lower score on day 1 of a given bout.

correlation was found between CV in the no-predator control period and the trial period for a given fish ($N = 86$, $r^2 = 0.007$, $p > 0.5$). To address the second possibility, a correlation between mean position in control vs trial periods was run. Again, no significant correlation was found (Pearson correlation: $N = 86$, $r^2 = 0.01$, $p > 0.2$). In addition, no correlation was found between CV in the control period and mean position in the trial period ($N = 86$, $r^2 = 0.02$, $p > 0.7$). It thus appears that the behaviour displayed during the trial period is, in fact, a specific response to a potential predator.

Discussion

Our study provides further evidence that guppies use the Tit-For-Tat strategy for considerable periods of time when engaged in a series of predator inspection visits. Two lines of evidence point to the use of TFT. First, individuals respond to a trailing co-inspector on the first day of a trial by 'retaliating' (Axelrod and Hamilton, 1981) against such individuals in future encounters. This retaliation takes the form of only going out towards the predator as far as the co-inspector did on the prior day, in other words, 'subsequently copying your partner's last move'. The fish that trailed behind on the first day of the bout does not increase (or decrease) its average position over the course of a bout. This is exactly what should occur if the guppies are using TFT. A null 'shoaling' model which predicts that fish should decrease the distance between themselves over the course of a bout, with the lead fish lowering its position half the time and the trailing fish increasing its position half the time, is not in accord with the results found here. Two possible mechanisms for retaliation are proposed: (A) Guppies remember the approximate average position of their co-inspector and only go that distance in the next encounter with that co-inspector, or more likely (B) Guppies simply remember that a co-inspector trailed behind during a predator inspection visit and respond in figure encounters with such an individual by only going

as far as it does. This differs from the first mechanism in that a guppy must only remember the general behaviour of its co-inspector (i.e. 'it trailed behind') rather than the approximate position of the co-inspector during the last predator inspection visit. Implicit in either mechanism is the memory abilities necessary to employ TFT.

Secondly, individuals start new bouts of inspection by being 'nice'. Again, consider two fish 1 and 2 at the start of a three day bout. Because of individual differences in the tendency to inspect, on average, one fish (say fish 1) will have a position closer to the predator on the first day of the bout. Fish 1 then retaliates against its partner on days 2 and 3. When fish 1 meets a new partner (i.e. starts a new bout) it then increases its average position back to that of the first day of the prior bout, i.e. it treats the initiation of a new bout as the start of a new game and is 'nice' to its new partner. It thus appears to obey the rule 'cooperate at the start of the new game' as TFT instructs. Fish 2 has nothing to retaliate against (as it trailed on the first day of the original bout) and thus has the same average position on all days of the first bout and the first day of the second bout.

The between individual differences in the tendency to inspect are interesting in the context of game theory and the evolution of cooperation, as well as in their own right. Consider three fish that show consistent scores in the parallel mirror trials. Suppose fish 1 on average moves x units toward the predator, fish 2, y units and fish 3, z units, such that $x > y > z$. Now if inspection is equated with cooperation when 1 and 2 meet, 1 is cooperating while 2, in a relative sense, is defecting. In such a case we expect fish 1 to retaliate against 2 in future. If, however, fish 2 is paired with fish 3, 2 is now viewed as cooperating while 3, again in a relative sense, is not cooperating and we expect to see 2 retaliate against 3. If this is so, cooperator and defector become relative terms rather than labels permanently assigned to individuals.

The results obtained in this study can not simply be attributed to the 'dilution effect'. Rather than try and keep a certain distance from *any* co-inspector (to dilute the threat of predation), guppies are remembering the behaviour of *particular individuals* and responding in a manner predicted by TFT. Likewise, the 'selfish herd' hypothesis (Hamilton, 1971) does not explain the behaviour displayed by guppies during predator inspection. In fact, breaking away from a shoal of fish (or in the case of these experiments one other fish) and inspecting a potential predator is the antithesis of the 'selfish herd' idea.

Lastly, this study adds a layer of complexity to the question of TFT during predator inspection. While prior work (Milinski, 1987, 1990; Dugatkin, 1988, 1991b) has argued that guppies play TFT with a co-inspector *during* a predator inspection visit (here jerky motions toward the predator are viewed as moves in a game), the present study provides evidence that guppies use the TFT rule *across* predator inspection visits as well.

Acknowledgements

We are deeply indebted to D. S. Wilson for comments on all versions of this paper. J. L. Brown also provided his usual invaluable advice. We also wish to thank A. Clark, J. G. Godin, J. Lazarus, M. Milinski, S. Ohlsen, B. Robinson, D. Rubinstein and S. Trumbo for helpful suggestions. Lastly we thank C. Rosenzweig for her patience. This work was funded by NSF grant BSR-8914333 to LAD and DOE Grant DE-FG02-89ER60884, Ecological Research Division, Office Of Health and Environmental Research, US Department of Energy to Dr David Sloan Wilson.

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