TIT FOR TAT in sticklebacks and the evolution of cooperation

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The problems of achieving mutual cooperation can be formalized in a game called the Prisoner's Dilemma in which selfish defection is always more rewarding than cooperation[1]. If the two protagonists have a certain minimum probability of meeting again a strategy called TIT FOR TAT is very successful[2]. In TIT FOR TAT the player cooperates on the first move and thereafter does whatever the opponent did on the previous move. I have studied the behaviour of fish when confronting a potential predator, because conflicts can arise within pairs of fish in these circumstances which I argue resemble a series of games of Prisoner's Dilemma. Using a system of mirrors, single three-spined sticklebacks (*Gasterosteus aculeatus*) approaching a live predator were provided with either a simulated cooperating companion or a simulated defecting one. In both cases the test fish behaved according to TIT FOR TAT supporting the hypothesis that cooperation can evolve among egoists.

Cooperation between individuals which are not closely related has been a difficulty for evolutionary theory until recently. Following Trivers's theory of reciprocal altruism[3], Axelrod and Hamilton[2] used a game theoretical approach including computerized tournaments of iterated games of Prisoner's Dilemma. In this game, two individuals have to choose either to cooperate or to defect. If they cooperate, both do better than if both had defected. But if one player defects while the other cooperates, the defecting one gets more than if both had cooperated, and the cooperating one gets less than if both had defected. Therefore, if the reward for mutual cooperation is R units, for mutual defection is P units, and for cooperation-defection is T units to the defector and S to the cooperator, then $T > R > P > S$ and $R > (S + T)/2$ are the conditions for the dilemma to exist. It pays always to defect if there is only one encounter or a previously known number of encounters between two particular individuals. If there is a certain minimum probability that after the current interaction the two protagonists will meet again, a very simple strategy, called TIT FOR TAT is demonstrably superior[2]: cooperate on the first move, on all subsequent moves do what the other player did on the preceding one. TIT FOR TAT players were successful because they were never the first to defect, they immediately retaliated when provoked, and were forgiving after just one act of retaliation[2].

A variety of situations should give rise to TIT FOR TAT-like strategies for cooperation, but so far the only experimental support is from tree swallows (*Tachycineta bicolor*)[4]. A further requirement must be satisfied before cooperation can evolve[1,5]: the gains expected from future encounters between any two protagonists must not be too heavily discounted. In many biological applications the future is more or less uncertain, so that future gains may be worth less than current ones. This paper investigates a situation in which future gains are worth more than current ones, enhancing the likelihood that TIT FOR TAT will occur.

During the early stages of an attack by a stalking pike (*Esox lucius*), individual minnows (*Phoxinus phoxinus*) leave the shoal and approach to within 4-6 body lengths of the predator, wait there for a few seconds, then slowly turn and go back to the shoal[6-8]. This behaviour, reported first by George[9], has been termed a predator inspection visit[10] and it has been suggested that fish gather knowledge about the predator's identity, precise location and current motivational state[11] from such visits. Of course there is an increasing danger of being attacked with decreasing distance to the predator, although the payoff (the amount of information gathered) may be maximal close to the predator. Similar behaviour has also been described in three-spined sticklebacks[12].

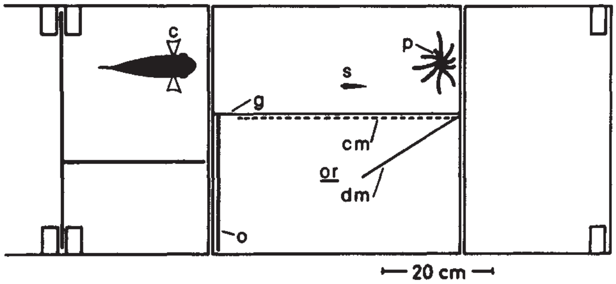

Fig. 1 Plan of the experimental equipment. The glass tanks shown contain the cichlid (c) and the plant (p), respectively. A typical position of a test stickleback (s) is also shown, as are the positions of the cooperating mirror (cm) and the defecting mirror (dm); 0, opaque screen; g, glass partition. Only one of the two mirrors was present in each experiment.

Three-spined sticklebacks approach a live cichlid more closely when in a group of two than when alone[13], like minnows approaching a pike model[10] and paired birds attacking or mobbing a predator[14,15]. The two sticklebacks remain close to each other and move in a jerky way: short moves of a few centimetres towards the predator alternate with hesitations. Either the two fish alternated positions or, more frequently, one followed the other. Although both fish may benefit from selfish herd effects[16] or predator confusion[11], one or other fish has to be first to make a move forward running a higher risk of being preyed upon. Both fish finally rush back when the predator moves towards them. If each forward jerk of swimming is one episode of cooperation, then the entire inspection visit of the two fish is equivalent to a sequence of encounters. The payoff (information gathered) from each episode should increase with decreasing distance to the predator. For the fish which follows, staying behind (defecting) may decrease its risk but increases its payoff by watching the fate of the other fish. This investigation tests whether the leading fish adopts TIT FOR TAT when a simulated companion either follows immediately behind it (cooperates) or stays behind and ultimately disappears (defects).

The experimental tank (43 × 43 cm, water level 18 cm) was divided by a glass partition into two compartments: the experimental compartment containing a plant (*Vallisneria* sp.) at one end and another compartment containing a mirror (Fig. 1). In one experiment there was a long mirror (38 cm) just behind the glass partition and parallel to it. This 'cooperating mirror' simulated a companion which followed immediately a proceeding stickleback. In another experiment there was a short mirror (19 cm) at an angle of 32° to the glass partition, called the 'defecting mirror' because it simulated a companion which stayed increasingly behind a proceeding stickleback. The experimental tank was positioned between two other tanks one of which contained a tame cichlid (*Tilapia mariae*, ~18 cm long) which resembles a perch (*Perca fluviatilis*), a common predator of three-spined sticklebacks[17]. Light was provided by four fluorescent tubes mounted 3 m above the tanks. The outside walls were covered with grey paper to avoid visual distraction.

Before a trial, a stickleback (the first to swim voluntarily into the net in the storage tank) was released above the plant in the experimental compartment. Trials of the two types of experiment were alternated and the length distribution of the fish was similar in both experiments (4.0 ± 0.6 cm, mean ± s.d., $n = 25$). The experiments were made outside the breeding season and each stickleback was used once only. Both the cichlid and the stickleback were observed with a video camera suspended 1.5 m above the tanks. On the video screen, the length of the experimental compartment was subdivided into 20 sections of 2.15 cm each

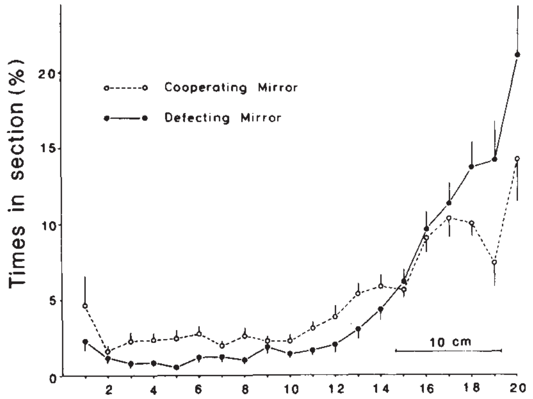

Fig. 2 Mean percentage of occasions on which fish with (○, broken line) the cooperating mirror ($n = 25$) and fish with (●, solid line) the defecting mirror ($n = 25$) were found in each of the 20 sections representing different distances to the predator; bars, 1 s.e.m.

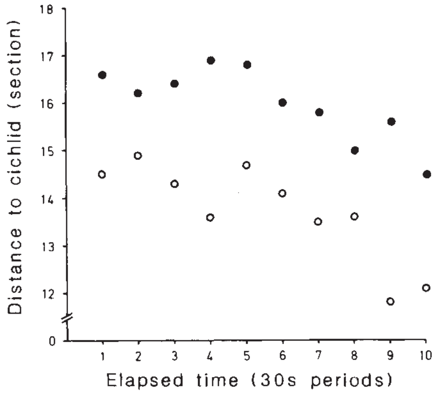

Fig. 3 Mean distance to cichlid (section number) of fish with cooperating mirror and of fish with defecting mirror in each half min of the trial; for the defecting mirror, $r_s = -0.79$, $P < 0.01$; for cooperating mirror, $r_s = -0.83$, $P < 0.005$ (two-tailed test with 23 d.f.).

with section 1 nearest the cichlid. The section containing the tip of the stickleback's snout was recorded at a clock signal every 5 s during 5 min after the fish had been transferred to the experimental compartment. The results therefore showed on how many occasions out of a total of 60 the fish had been found in each section.

The cichlid spent most of its time close to the wall where it watched the stickleback, and often pushed the wall as it tried to attack. The stickleback usually stayed close to the plant after being transferred, but after some hesitation approached the cichlid in its typical jerky manner along the glass partition. Normally it stopped after a distance of a few centimetres and retreated abruptly, especially when the cichlid attacked it. Some fish approached no more closely than to section 15, whereas others reached section 1 and stayed there for >5 s, rushing back as soon as they were attacked.

Although in both experiments the sticklebacks preferred to stay in the back half of their tank, there were differences between experiments. With the cooperating mirror the sticklebacks were twice as often in the front half (mean 25.1%) as with the defecting mirror (mean 12.1%, $P < 0.003$, two-tailed Mann-Whitney U-test). Figure 2 shows how often fish in each experiment were found in each of the 20 sections. With the cooperating mirror the fish were found significantly more frequently in each of the 3 front quarters than in the experiment with the defecting mirror (section 1-5, $P < 0.05$; section 6-10, $P < 0.004$; section 11-15, $P = 0.04$; two-tailed Mann-Whitney U-tests). With the defecting mirror, fish were found more often in the back quarter of the tank than in the experiment with the cooperating mirror ($P < 0.005$, two-tailed Mann-Whitney U-test).

In both experiments the sticklebacks decreased their mean distance to the cichlid significantly during the 5 min of the trial (Fig. 3). The fish with the cooperating mirror had not only a shorter mean distance to the predator in each half minute of the trial but also decreased their distance more than proportionally from the first to the fifth minute as compared to the fish with the defecting mirror (the ratio of mean section during the first minute to the mean section during fifth minute was 1.54 with the cooperating mirror and 1.17 with the defecting mirror, $P < 0.05$, one-tailed Mann-Whitney U-test). There are consistent differences between individual fish. In the experiment with the cooperating mirror there is a significant positive correlation between distance in the first minute and in the fifth minute ($r = 0.43$ with 23 d.f., $P < 0.04$, two-tailed test). Thus, there were bold fish and more cautious ones. This correlation is not significant for fish with the defecting mirror ($r = 0.34$ with 23 d.f., $P > 0.07$, two-tailed). The 13 fish which had a shorter mean distance during the first minute are called 'bold' and the remaining 12 fish 'cautious' in either experiment. With the cooperating mirror both bold and cautious fish significantly decreased their mean distance from the first to the fifth minute (Fig. 4), although bold fish were still closer to the cichlid than cautious ones by the fifth minute ($P < 0.04$, one-tailed Mann-Whitney U-test). In the experiment with the defecting mirror, however, only the cautious fish significantly decreased their mean distance to the predator (Fig. 4): bold fish were not significantly closer to the cichlid than the cautious ones by the fifth minute ($P > 0.1$, one-tailed Mann-Whitney U-test).

Three-spined sticklebacks are able to adjust their behaviour according to the risk of predation[18]. In both experiments the safest place for the stickleback was close to the back wall of the experimental compartment. This was also the place where the companion fish, simulated by the mirror, was very close. Nevertheless, in both experiments the test sticklebacks left this place to make inspection visits towards the cichlid. In the experiment with the long parallel mirror, a cooperating companion was simulated which followed the proceeding stickleback immediately, that is, it adopted TIT FOR TAT. In the experiment with the short oblique mirror, a companion was simulated which stayed increasingly behind the stickleback the further the fish advanced, and it disappeared half-way to the cichlid, so that it

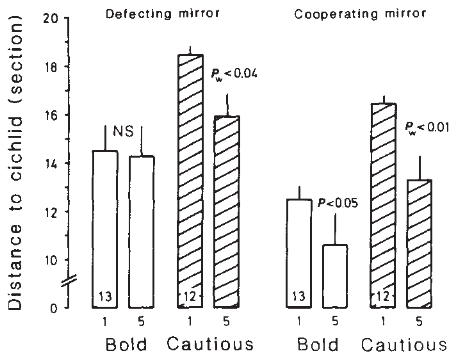

Fig. 4 Mean distance to cichlid (section number) of (open bars) bold and of (hatched bars) cautious fish in the first and fifth minute of the trial in the experiment with the defecting mirror and in the experiment with the cooperating mirror; bars above columns give 1 s.e.m. Wilcoxon matched pairs signed-ranks test (two-tailed) gives for cautious fish, $P_w < 0.04$ with defecting mirror; $P_w < 0.01$ with cooperating mirror. Dixon and Mood sign-test (two-tailed) gives for bold fish, no significant difference between minutes 1 and 5 with the defecting mirror; $P < 0.05$ with the cooperating mirror.

mostly defected. If the sticklebacks adopt TIT FOR TAT in this situation, with each jerky approach of some centimetres towards the cichlid representing one opportunity for cooperation, then fish with the cooperating mirror should approach the predator more closely than those with the defecting mirror. This was the case. The sticklebacks acted as if they perceived that a companion was either following them or staying increasingly behind.

Individual sticklebacks differ consistently in their levels of boldness[12,19] which seems generally typical for fish behaviour[20,21]. With the cooperating mirror, the sticklebacks that were bolder in the first minute were also bolder in the fifth minute of the trial, although the cautious fish also approached the predator more and more closely during the trial. Hence, despite individual differences in boldness, all the fish seemed to adopt the same strategy when the simulated companion cooperated. This was different when a defecting companion was simulated. Here only the cautious fish approached the cichlid a bit more closely in the fifth than in the first minute. Over this distance the simulated companion did not stay much behind. The bolder fish, however, reacted to the disappearance of their companion in that they neither decreased nor increased their mean distance from the cichlid during the trial. Thus, they seem to 'forgive' after once having rushed back themselves. They went forward time and again, but on the average exactly as far in the fifth minute as they had done in the first minute. So a further requirement for TIT FOR TAT seems to be fulfilled, the equivalent of cooperation on the first move.

Whether the condition $T>R>P>S$ is fulfilled was not determined quantitatively; there is, however, qualitative support for it. The bold fish with the cooperating mirror seemed to rush back mainly when the cichlid actually launched an attack. Therefore, the ultimate information the fish try to gather seems to be the predator's attack distance. The rearmost fish achieves this by watching from a safe distance what happens to the leading fish, so $T>R$ seems to be fulfilled. $R>P$ seems to hold because if both fish stay away, they do not learn about the predator's attack distance. $P>S$ holds because if the leading fish relies on confusion or the selfish herd effect it may approach close enough to learn the predator's attack distance but runs a high risk of being eaten. $R>(S+T)/2$ should also be fulfilled. A group of two fish may detect an impending attack earlier[6] which may be less frequently successful anyway because of the confusion effect of two prey compared to one[22]. Either cooperating fish may gather maximum information while running less than half of the predation risk of a single fish. Thus, the sticklebacks support Axelrod and Hamilton's assumptions and predictions[2] concerning the evolution of cooperation based on reciprocity.

I thank R. Axelrod, W. D. Hamilton, A. E. Magurran and T. J. Pitcher for comments on the manuscript, and C. Wynne for improving my English.

Received 15 September; accepted 21 November 1986.

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Efficiency characteristics of crescent-shaped wings and caudal fins

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Caudal (tail) fins of fish and aquatic mammals that cruise long distances, and wings of certain birds, often have the shape of a crescent moon. This study investigates how the crescent shape contributes to the travelling performance of these animals. A steady-flow theory[1] that correctly models the trailing wake was used to analyse lifting surface efficiency, which is dependent on the level of induced (or vortex) drag for a given lift and span of the lifting surface. This analysis shows that backward curvature of a wing improves induced efficiency to a value greater than that of the flat untwisted wing of elliptical shape considered optimal in classical wing theory[2,3]. This increase of induced efficiency results from the nonplanar trailing vortex sheet produced by the crescent-shaped wing at a given angle of attack.

Many aquatic animals that swim fast for long distances have adopted the mode of propulsion Lighthill[4] terms carangiform with lunate (crescent) tail. Forward thrust is generated exclusively by the caudal fin mounted on the slender tail section of the heavy body. Scombroid fishes (Fig. 1*a*) have the caudal fin strengthened by ossified fin rays allowing this fin to have a high aspect ratio[5]. Fast-swimming sharks (Fig. 1*b*) and cetaceans (Fig. 1*c*) have lunate tails of a lower aspect ratio because of lower structural strength and stiffness in their caudal fins.

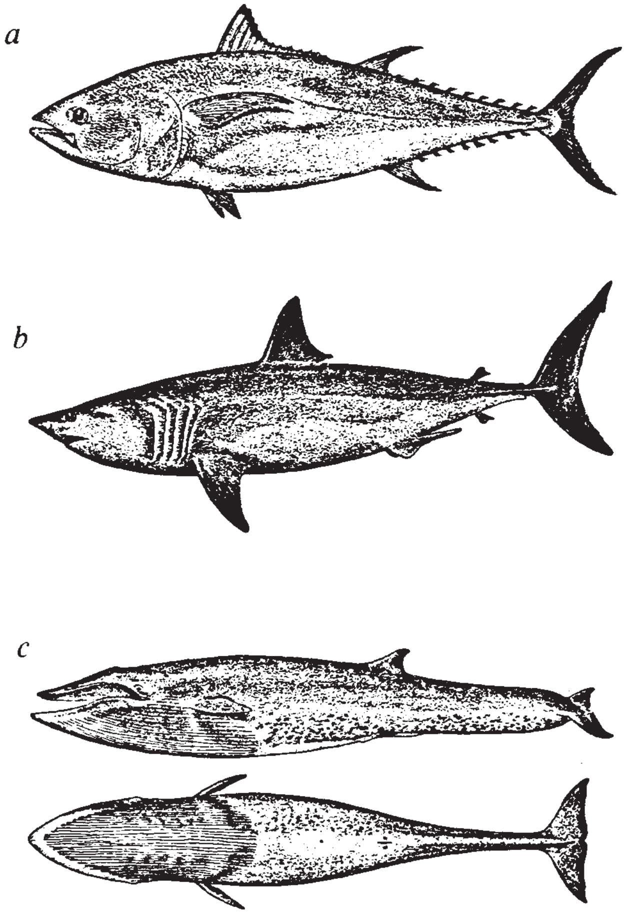

Fig. 1 Typical aquatic animals with crescent-shaped caudal fins[19]: *a, Thunnus thynnus*; *b, Isurus oxyrinchus*; *c, Balaenoptera borealis.*