

Cooperation in fishes

Stéphan G. Reeb
Université de Moncton, Canada
2011-2014

Cooperative foraging

There are few reports of fish cooperating to obtain food. Of course, a good number of species live more or less permanently in shoals, and inasmuch as groups can better spot, flush, herd, or catch prey, then one can say that shoaling fish are hunting cooperatively.¹ But this is not very special. The fish are already living in groups anyway. Their collaboration may simply be an accidental by-product of their individual behaviour.

More interesting is the following. On coral reefs, damselfishes valiantly defend individual territories that contain food – mats of algae – and sometimes their nests filled with eggs. These relatively small fishes are so fearless in their territorial defense that they have been known to attack divers. Not surprisingly then, a single damselfish has no trouble repelling a lone parrotfish, surgeonfish, or wrasse. However, these species may gang up on the damsels. They sometimes form groups of 30-300 individuals that easily overwhelm the defenses of a territorial damselfish and proceed to devour its algae or its eggs. A similar phenomenon is known to take place among the cichlids of Lake Malawi and Lake Tanganyika, where groups of intruders sometimes overpower territory owners in order to eat their eggs. The key observation in all of these cases is that the large groups do not form as readily when the territorial damselfishes or cichlids are less abundant, which suggests that the groups assemble with the specific intent of swamping the territory owners.²

Here is an even better example of collaboration, reported by Russell Schmitt and Steven Strand. While perched on cliff tops along the shoreline of Santa Catalina Island and Danzante Island, in California, these researchers witnessed packs of 7-15 yellowtail amberjacks, *Seriola lalandi*, hunting shoals of jack mackerels and Cortez grunts in the waters below. Maneuvering in U-shaped formations, the amberjacks managed to cut away the tail end of the prey shoals and herd the unfortunate stragglers next to seawalls (when the prey were jack mackerels) or in open waters away from reefs (when the prey were grunts). There the amberjacks were at liberty to lunge at individual prey in the center of the newly-downsized shoal.³

Another example: the bluestreak cleaner wrasse *Labroides dimidiatus* cleans parasites off the skins of other coral reef fishes (clients), though it also cheats sometimes, grabbing a bite of the client's mucus instead. When cheating occurs, clients respond by terminating the cleaning session and taking off. Interestingly, males can associate themselves with the largest females of their harems to offer cleaning as a pair, and clients seem to prefer being cleaned by a pair rather than by a single fish. A

mathematical model developed by Olof Leimar of Stockholm University shows that cleaners working in pairs can remove more parasites from a client, thus offering a better service and eventually building up a bigger clientele. Moreover, field and laboratory observations by Redouan Bshary and Astrid Willener, from the University of Neuchâtel in Switzerland, and Alexandra Grutter of the University of Queensland in Australia, revealed that cleaners – especially the females – cheat less frequently as part of a pair than when they work alone, indicating an apparent willingness to cooperate. Males often chase their female partners away when the females cause the end of a cleaning session by cheating; it remains to be determined whether this behaviour is “punishment” for betraying the collaborative effort, or just frustration at seeing the foraging session suddenly ending. At any rate, the research suggests that paired fish collaborate to provide better service quality to their clients.⁴ (For more interesting thoughts on cleaner fish behaviour, see the page on Social Intelligence.)

The above cases involved cooperation among individuals of the same species. Now here is one of very few known instances in the animal world of two different species cooperating in a hunt. It concerns roving coral groupers, *Plectropomus pessuliferus*, and giant moray eels, *Gymnothorax javanicus*, living in the coral reefs of the Red Sea. Groupers are diurnal and hunt in open waters. Their prey try to escape from them by hiding in corals. Moray eels, in contrast, are nocturnal, and hunt prey within the crevices of the reef. Their prey try to escape from them by swimming into open waters. So imagine the plight of a prey fish if the two predators, whose hunting methods are complementary, were in cahoots: there would be no safe place to go. According to a study by Bshary and collaborators,⁵ the two predators do indeed cooperate – sometimes.

The initiative seems to lie with the grouper. A grouper will start by visiting the sleeping berth of a moray eel during the day and shake its head directly in front of the moray. The grouper does this only when it is hungry. It appears to be a signal, an invitation to the eel to come out and participate in a joint hunt. In 70 out of 120 instances when the display was given, the moray responded by leaving its crevice and swimming away with the grouper. Sometimes the grouper appeared to lead the moray to a hole into which a small fish had just taken refuge from the grouper. In the probing that ensued, the prey was sometimes captured, either by the moray or by the grouper.

An interesting aspect of these observations is that the grouper actually convinced the moray to “get out of bed”. This is an example of how flexible many fish can be in their capacity to be active at different times of day (see the page “Sleep in fishes”).

(I also get the impression that morays are good listeners in general. Certainly many fishes seem to want to talk to them. Not only do morays receive invitations to hunt in pairs, they also receive invitations from their potential prey to leave the neighbourhood. Various butterflyfishes and surgeonfishes, small enough to succumb to a moray’s attack, have been seen giving lateral displays right in front of morays in their crevices, sometimes even beating their tails at the head of the eel. This has been

interpreted as mobbing behaviour, an attempt to annoy the predator and incite it to leave the area ⁶ – see the page “Mobbing in fishes”.)

Another example of invitation to group hunting involves lionfishes. In an aquarium setting, lionfish *Dendrochirus zebra* were observed flaring up their fins when a potential prey (small fish) was detected. This incited other *D. zebra*, and even another lionfish species, *Pterois antennata*, to join the signaller in cornering the prey. Such group hunting was more successful than solitary hunting. Moreover, the participants took turns striking at the cornered prey and ended up with similar capture rates. The fin flaring seems to be an intentional effort to recruit hunting partners, coupled with a willingness to allow each partner an equal share of the spoils.⁷

There are other examples of coral reef fishes foraging together, but without any particular signal being given to initiate the hunt. Pairs made up of one green birdmouth wrasse, *Gomphosus caeruleus*, and one goldsaddle goatfish, *Parupeneus cyclostomus*, can work the reef together. One fish goes round a coral head one way while the other goes round the other way. Small organisms disturbed by one fish may be captured by the other. Groupers of different species may also hunt in pairs.⁸

Cooperation during parental care

Some species show biparental care: both the male and the female collaborate in defending their eggs – and sometimes their fry too – from the attacks of predators. Biparental species often breed in predator-rich habitats and therefore it is essential that both parents collaborate in the defense of the young. Several studies, mostly done with cichlids, have shown that eggs and fry do not survive well when one of the parents is experimentally removed.⁹

The advantages of cooperative parenting have been invoked in a 2007 study to explain a puzzling observation. As any textbook in biology (or sex education) will tell you, inbreeding – mating among siblings – is a big no-no, mostly because harmful recessive genes stand a better chance of coming together and being expressed. But one species of fish apparently has not read the textbooks. According to a lab study by Timo Thünken and co-workers at the University of Bonn in Germany, females and males of the cichlid *Pelvicachromis taeniatus* prefer to mate with their brothers and sisters. Thünken also reported that during the parental phase, males spend more time near the eggs and quarrel less often with their mate if they are paired with a sister rather than with a non-kin (why this is so is still mysterious). Thus in this case, it seems that the benefit of having two parents who get along with each other can overcome the known disadvantages of inbreeding.¹⁰

In cichlids, there is often some division of labour between male and female parents. The male usually spends more time patrolling the boundaries of the breeding territory, while the female spends more time near the eggs. There is some flexibility

in these roles, however. If one parent is removed, the other often changes its time budget to make up for the missing partner.¹¹

Again in cichlids, it is possible to find a few examples of what is called “cooperative breeding”. The phenomenon also goes by the name of “helpers at the nest”. Essentially, offspring from former broods stay with their parents to help raise new broods. These helpers share all parental duties, repelling territory intruders, removing debris, cleaning and fanning the eggs. As they grow older and bigger, helpers have the option of moving out to initiate their own breeding venture – often a dicey proposition because safe spots are limited in their habitat. Many, on the other hand, prefer to stay a while longer in the hope of inheriting their parents’ territory, should one of them disappear. Such a system has been particularly well studied in the cichlid *Neolamprologus pulcher*. For more details on cooperative breeding, see the page “Are fishes good parents?”.

Cooperation between males during mating

Sharks practice internal fertilization. During copulatory attempts, the male often bites the female, usually on her pectoral fins. The bite may prompt the female to mate, and it may also stimulate her to ovulate. The proper male position, involving as it does the simultaneous acts of intromission and biting, is hard to maintain when the pair is moving. In the nurse shark *Ginglymostoma cirratum*, a second male sometimes places his body in front of the heads of the mating pair, acting as a block to their forward movement and therefore assisting their attempt at copulation. It is unclear whether this second male gains anything from this altruistic behaviour.¹²

On the page about the sex lives of fishes, you will see a mention that spawning often occurs in trios in many species of suckers (family Catostomidae).¹³ Two males adjoin a female on either side and seem to press their body against hers. Both males release their sperm when the female let go of her eggs. It has been suggested that the pressure exerted in concert by the two males squeezes more eggs out of the female than would normally be released, but this cooperation hypothesis has not been tested yet.

Cooperation during building

Lampreys spawn in pits that they excavate in shallow freshwater streams. Both sexes contribute to the digging. In some species, up to 20 adults can dig a single communal nest together. Each individual lamprey attaches its suckorial oral disc to single stones and moves them away. But sometimes, two individual lampreys fasten their disc to a single large stone and move it together.¹⁴ It is hard to say if this is conscious teamwork or just two fish that happen to latch onto the same rock at the same time.

Cooperation during intraspecific cleaning

Sometimes, fish can be seen eating ectoparasites off the body of other fish of their own species. Among the species where this has been observed are the Californian salema *Xenestius californiensis*, the Panama sergeant major *Abudefduf troschelli*, the common carp *Cyprinus carpio*, the bluegill sunfish *Lepomis macrochirus*, the Sumatran barb *Puntius tetrazona*, and the guppy *Poecilia reticulata*.¹⁵

Because both fish in the interaction are willing participants and seem to derive benefits from it, intraspecific cleaning can be viewed as cooperation. However, if ectoparasites really provide significant meals (something that is still not clear), then the benefit to the cleaned fish is only an accidental by-product of the foraging activities of the cleaner. This would not constitute a strong example of cooperation as we normally understand it. It would be more impressive if the ectoparasites did not provide substantial nourishment, and the cleaner would only perform its service in the hope of receiving the same treatment from the cleaned fish later on (a case of “If you scratch my back, I’ll scratch yours”). Such reciprocity has not been clearly established yet.

Cooperation for more peace in the world

Several fish species – salmonids especially – are known to be able to discriminate between kin and non-kin. In a series of studies conducted at Memorial University in Newfoundland, juvenile Atlantic salmon that had been allowed to establish adjacent feeding territories in artificial stream channels exhibited less aggression towards one another when they were brothers and sisters as opposed to when they were unrelated. In a way, this is a form of cooperation based on kin recognition.¹⁶

Cooperation during predator inspection

Take a shoal of guppies, sticklebacks, or minnows in a fish tank, and next to it place a bottle containing a predatory fish (a blue acara cichlid for example). A funny thing may very well happen. At first the shoaling fish will gather at the end furthest away from the predator. But then some of the fish will, on their own or as a small group, approach the predator in a hesitant manner, a quick lunge forward followed by a pause, then another lunge forward followed by a pause, and so on until the fish stops for the last time fairly close to the predator (less than 30 cm or so) before turning away and swimming back to the rest of the shoal.

Looking attentively at the approaching fish, we can see that they are very alert, keeping an eye on the predator, beating their fins nervously, moving jerkily. For all the world it looks as if they are cautiously “checking things out”, assessing the danger. Indeed fish ethologists believe that approaching a new fish is a way for prey

to take a closer look at a stranger, to determine if it is a predator, and to see if the predator looks hungry and about to attack. In fact, in many quarters the behaviour is called “predator inspection” rather than predator approach, so certain are ethologists about the function of this action. Both freshwater and marine fishes are known to inspect predators.¹⁷

Sticklebacks and guppies seem to feel safer when they approach a predator as part of a group, or at least as part of a duo rather than all by themselves. Therefore they have a tendency to inspect a predator fairly closely when they are accompanied by a partner, but to chicken out and turn around further away from the predator if they are alone or if their partner quits on them. A pair of inspectors can therefore be viewed as cooperators: being together makes each of them bolder and allows them to get a closer view of the potential predator.

The lab of Manfred Milinski at the University of Bern has been very active in this field of enquiry. Milinski has used sticklebacks as inspectors and trout as predators. In a long raceway he confined a trout at one end and placed a stickleback at the other end. On one of the long sides of the transparent raceway wall was a mirror. In one treatment the mirror was parallel to the long axis of the tank all the way to the trout. Therefore a stickleback that advanced towards the trout had the impression of being “accompanied” by a cooperating partner – its own image. In the other treatment, the mirror was angled away. The inspecting fish was therefore accompanied by a “partner” who tended to fall back and away. Milinski observed that his sticklebacks came close to the trout when faithfully accompanied by their mirror image but stayed further away from the trout when the “partner defected”. Subsequent experiments with guppies and mosquitofish in other labs have yielded comparable results.¹⁸

Working in Milinski’s lab, David Külling modified this set-up slightly and showed that sticklebacks came closer to predators when they were escorted by large partners rather than by small ones. The raceway was flanked by two long outer compartments, one on each side. One-way mirrors between the central raceway and the outer compartments allowed the central fish to see outside, but not the outer fish to see inside. These outer fish could be made to go forward in their compartment by lighting a green light at the end – they had been trained to swim toward the light in order to get food. The outer fish could be a large one (5 cm long) or a small one (3-4 cm long) depending on the condition. During each test, a stickleback was dropped into the central raceway and given 15 min to get used to the place. Then a partition was lifted to reveal the trout at the other end. At that point, one of the outer fish was sent forward by lighting the green light in its compartment. The central fish thought this was an inspection and usually participated by tagging along. Eventually of course the central fish turned away from the predator, but the interesting thing was that it did so some 2 cm closer to the trout when the outer fish was a big guy. Külling and Milinski already knew that trout preferred to attack larger sticklebacks, and they postulated that the central stickleback knew this fact too and felt bolder when it was accompanied by a partner who, because of its larger size, was more likely to deflect attack upon itself.¹⁹

Fishes seem to be more willing to join another inspector when they are familiar with that companion. When four minnows captured from the same shoal were placed in the presence of a pike model, they inspected in pairs fairly often. But when the same experiment was tried with four minnows that came from different shoals, the fish tended to inspect alone. It may be that individual fish can recognise partners that are familiar to them, can remember how bold these shoalmates are, and feel more confident in following proven heroes rather than complete strangers. It may also be that subtle cooperation, for example by taking turns in occupying the leading (and more risky) position during inspection, is facilitated by acquaintance.²⁰

In fact, something akin to “trust” may develop between inspectors. Again with a system of parallel raceways separated by one-way mirrors (so that a central fish could see inside the two flanking raceways, but not vice-versa), Milinski could give an inspecting stickleback (in the central raceway) the impression that it was accompanied by either an apparent collaborator (a fish that was made to advance far in the next raceway because it could not see the predator there) or a non-collaborator (a fish that was made to stop short in the third raceway). The inspector soon learned to distinguish between the two individuals. Then, when the former collaborator was forced by the experimenters to stop short in its raceway, the inspector continued to move forward towards the predatory trout. Milinski interpreted this result as a sign that the inspector had built up trust towards the former cooperater and was confident it would soon follow.²¹

¹ For example: Mittelbach, G., 1984, Group size and feeding rate in bluegills, *Copeia* 1984, 998-1000; Eklöv, P., 1992, Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns, *Animal Behaviour* 44, 313-326; Arnegrad, M.E., and Carlson, B.A., 2005, Electric organ discharge patterns during group hunting by a mormyrid fish, *Proceedings of the Royal Society of London B* 272, 1305-1314.

² Barlow, G.W., 1974, Extraspecific imposition of social groupings among surgeonfishes (Pisces: Acanthuridae), *Journal of Zoology (London)* 174, 333-340; Robertson, D.R., Sweatman, H.P.A., Fletcher, E.A., and Cleland, M.G., 1976, Schooling as a mechanism for circumventing the territoriality of competitors, *Ecology* 57, 1208-1220; Foster, S.A., 1985, Group foraging by a coral reef fish: a mechanism for gaining access to defended resources, *Animal Behaviour* 33, 782-792; Foster, S.A., 1987, Acquisition of a defended resource: a benefit of group foraging for the neotropical wrasse, *Thalassoma lucasanum*, *Environmental Biology of Fishes* 19, 215-222; Marsh, A.C., and Ribbink, A.J., 1986, Feeding schools among Lake Malawi cichlid fishes, *Environmental Biology of Fishes* 15, 75-79; Kohda, M., and Takemon, Y., 1996, Group foraging by the herbivorous cichlid fish, *Petrochromis fasciolatus*, in Lake Tanganyika, *Ichthyological Research* 43, 55-63.

³ Schmitt, R.J., and Strand, S.W., 1982, Cooperative foraging by yellowtail, *Seriola lalandei* (Carangidae), on two species of fish prey, *Copeia* 1982, 714-717.

⁴ Bshary, R., Grutter, A.S., Willener, A.S.T., and Leimar, O., 2008, Pairs of cooperating cleaner fish provide better service quality than singletons, *Nature* 455: 964-966 (see also page xv in the same issue); Bshary, R., and Schäffer, D., 2002, Choosy reef fish select cleaner fish that provide high quality service, *Animal Behaviour* 63, 557-564.

⁵ Bshary, R., Hohner, A., Ait-el-Djoudi, K., and Fricke, H., 2006, Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea, *PloS Biology* 4, 2393-2398. See also: Vail, A.L., Manica, A., and Bshary, R., 2014, Fish choose appropriately when and with whom to collaborate, *Current Biology* 24: R791-R793; Diamant, A., and Shpigel, M., 1985, Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba), *Environmental Biology of Fishes* 13, 153-

159; Dubin, R.E., 1982, Behavioral interactions between Caribbean reef fish and eels (Muraenidae and Ophichthidae), *Copeia* 1982, 229-232; and pages 64-67 in: DeLoach, N., and Humann, P., 1999, Reef Fish Behavior: Florida, Caribbean, Bahamas, New World Publications Inc., Jacksonville (FL).

⁶ Motta, P.J., 1983, Response by potential prey to coral reef fish predators, *Animal Behaviour* 31, 1257-1259, and references therein.

⁷ Lönnstedt, O.M., Ferrari, M.C.O., and Chivers, D., 2014, Lionfish predators use flared fin displays to initiate cooperative hunting, *Biology Letters* 10 (6), doi 10.1098/rsbl.2014.0281.

⁸ Ormond, R.F.G., 1980, Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators, *Journal of Zoology (London)* 191, 247-262.

⁹ Keenleyside, M.H.A., 1978, Parental care behavior in fishes and birds, Pp. 3-29 In: *Contrasts in Behavior* (Reese, E.S., and Lighter, F.J., eds.), John Wiley & Sons, New York; Keenleyside, M.H.A., Bailey, R.C., and Young, V.H., 1990, Variation in the mating system and associated parental behaviour of captive and free-living *Cichlasoma nigrofasciatum* (Pisces, Cichlidae), *Behaviour* 112, 202-221.

¹⁰ Thünken, T., Bakker, T.C.M., Baldauf, S.A., and Kullmann, H., 2007, Active inbreeding in a cichlid fish and its adaptive significance, *Current Biology* 17, 225-229.

¹¹ Mrowka, W., 1982, Effect of removal of mate on parental care behaviour of the biparental cichlid *Aequidens paraguayensis*, *Animal Behaviour* 30, 295-297; Lavery, R.J., and Reeb, S.G., 1994, Effect of mate removal on current and subsequent parental care in the convict cichlid (Pisces: Cichlidae), *Ethology* 97, 265-277; Itzkowitz, M., Santangelo, N., and Richter, M., 2001, Parental division of labour and the shift from minimal to maximal role specializations: an examination using a biparental fish, *Animal Behaviour* 61, 1237-1245; Itzkowitz, M., Santangelo, N., Cleveland, A., Bockelman, A., and Richter, M., 2005, Is the selection of sex-typical parental roles based on an assessment process? A test in the monogamous convict cichlid fish, *Animal Behaviour* 69, 95-105.

¹² Carrier, J.C., Pratt, H.L. Jr., and Martin, L.K., 1994, Group reproductive behaviors in free-living nurse sharks, *Ginglymostoma cirratum*, *Copeia* 1994, 646-656.

¹³ Page, L.M., and Johnston, C.E., 1990, Spawning in the creek chubsucker, *Erimyzon oblongus*, with a review of spawning behavior in suckers (Catostomidae), *Environmental Biology of Fishes* 27, 265-272; Cooke, S.J., and Bunt, C.M., 1999, Spawning and reproductive biology of the greater redhorse, *Moxostoma valenciennesi*, in the Grand River, Ontario, *Canadian Field-Naturalist* 113, 497-502;

¹⁴ Keenleyside, M.H.A., 1979, *Diversity and Adaptation in Fish Behaviour*, Springer-Verlag, Berlin.

¹⁵ Dugatkin, L.A., 1997, *Cooperation among Animals : an Evolutionary Approach*, Oxford University Press, New York.

¹⁶ Brown, G.E., and Brown, J.A., 1993, Social dynamics in salmonid fishes: do kin make better neighbours? *Animal Behaviour* 45, 863-871; Brown, G.E., and Brown, J.A., 1993, Do kin always make better neighbours?: the effects of territory quality, *Behavioral Ecology and Sociobiology* 33, 225-231; Brown, G.E., and Brown, J.A., 1996, Does kin-biased territorial behavior increase kin-biased foraging in juvenile salmonids? *Behavioral Ecology* 7, 24-29; Brown, G.E., Brown, J.A., and Wilson, W.R., 1996, The effects of kinship on the growth of juvenile Arctic charr, *Journal of Fish Biology* 48, 313-320. See also: Olsén, K.H., Järvi, T., and Löf, A.-C., 1996, Aggressiveness and kinship in brown trout (*Salmo trutta*) parr, *Behavioral Ecology* 4, 445-450; Griffiths, S.W., and Armstrong, J.D., 2002, Kin-biased territory overlap and food sharing among Atlantic salmon juveniles, *Journal of Animal Ecology* 71, 480-486. By the way, recently it has been shown that even some plants can recognize their kin and minimize the level of competition with them, more precisely at the level of their roots: Dudley, S.A., and File, A.L., 2007, Kin recognition in an annual plant, *Biology Letters* 3, 435-438.

¹⁷ For example: Csányi, V., 1985, Ethological analysis of predator avoidance by the paradise fish (*Macropodus opercularis* L.) I. Recognition and learning of predators, *Behaviour* 92, 227-240; Pitcher, T.J., Green, D.A., and Magurran, A.E., 1986, Dicing with death: predator inspection behaviour in minnow shoals, *Journal of Fish Biology* 28, 439-448; Magurran, A.E., 1986, Predator inspection behaviour in minnow shoals: differences between populations and individuals, *Behavioural Ecology and Sociobiology* 19, 267-273; Dugatkin, L.A., and Alfieri, M., 1991, Tit for Tat in guppies: the relative nature of cooperation and defection during predator inspection, *Evolutionary Ecology* 5, 300-309; Huntingford, F.A., Lazarus, J., Barrie, B.D., and Webb, S., 1994, A

dynamic analysis of cooperative predator inspection in sticklebacks, *Animal Behaviour* 47, 413-423; Milinski, M., Lüthi, J.H., Eggler, R., and Parker, G.A., 1997, Cooperation under predation risk: experiments on costs and benefits, *Proceedings of the Royal Society of London B* 264, 831-837; Brown, G.E., and Cowan, J., 2000, Foraging trade-offs and predator inspection in an ostariophysan fish: switching from chemical to visual cues, *Behaviour* 137, 181-195;

¹⁸ Milinski, M., 1987, Tit for Tat in sticklebacks and the evolution of cooperation, *Nature* 325, 433-435. For guppies: Dugatkin, L.A., 1988, Do guppies play Tit for Tat during predator inspection visits? *Behavioral Ecology and Sociobiology* 23, 395-399. For mosquitofish: Stephens, D.W., Anderson, J.P., and Benson, K.E., 1997, On the spurious occurrence of Tit for Tat in pairs of predator-approaching fish, *Animal Behaviour* 53, 113-131. For a bit of controversy, see also: Masters, W.M., and Waite, T.A., 1990, Tit-for-tat during predator inspection, or shoaling?, *Animal Behaviour* 39, 603-604; Lazarus, J., and Metcalfe, N.B., 1990, Tit-for-tat cooperation in sticklebacks: a critique of Milinski, *Animal Behaviour* 39, 987-988; Milinski, M., 1992, Predator inspection: cooperation or “safety in numbers”? *Animal Behaviour* 43, 679-680. For a wrap-up of the whole story, see pp. 59-70 in: Dugatkin, L.A., 1997, *Cooperation among Animals: an Evolutionary Approach*, Oxford University Press, New York.

¹⁹ Külling, D., and Milinski, M., 1992, Size-dependent predation risk and partner quality in predator inspection of sticklebacks, *Animal Behaviour* 44, 949-955.

²⁰ Chivers, D.P., Brown, G.E., and Smith, R.J.F., 1995, Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour, *Canadian Journal of Zoology* 73, 955-960. See also: Milinski, M., Pflüger, D., Külling, D., and Kettler, R., 1990, Do sticklebacks cooperate repeatedly in reciprocal pairs? *Behavioral Ecology and Sociobiology* 27, 17-21; Croft, D.P., James, R., Thomas, P.O.R., Hathaway, C., Mawdsley, D., Laland, K.N., and Krause, J., 2006, Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*), *Behavioral Ecology and Sociobiology* 59, 644-650.

²¹ Milinski, M., Külling, D., and Kettler, R., 1990, Tit for Tat: Sticklebacks (*Gasterosteus aculeatus*) “trusting” a cooperating partner, *Behavioral Ecology* 1, 7-11. See also: Dugatkin, L.A., and Alfieri, M., 1991, Guppies and the Tit for Tat strategy: preference based on past interactions, *Behavioral Ecology and Sociobiology* 28, 243-246.