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Cooperative Behaviour in Fish: Coalitions, Kin Groups and Reciprocity

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Cooperative behaviour, especially beyond sexual partnerships, has always puzzled people and is often viewed as a 'test case' for certain evolutionary theories, as it sometimes seems to be altruistic. How can these complex behavioural interactions be understood within the framework of natural selection? Part of the problem is the stability of cooperation against cheating and defection. These and related questions have been investigated with social insects (see Hamilton's influential papers, 1964, which brought a fruitful reconsideration of this issue), birds and mammals (*e.g.* Emlen 1982, Brown 1985), but not many examples of highly cooperative behaviour have been reported from other taxonomic groups. Recently, however, some elaborate social systems with high degrees of cooperation have been found in a few species of fish. This paper aims to (1) review the occurrence of cooperative behaviour in fish, *other than the collaboration between pair members*, (2) discuss the evolutionary framework of these examples, *e.g.* the fitness costs and benefits to cooperating parties and the occurrence and prevention of defection, (3) investigate the reasons for the confinement of the examples found to date to related taxonomic groups, and the common features of these observed examples,

and (4) point to the practical suitability of fish systems for studies concerning the evolution and stability of cooperative and seemingly atruistic behaviour, as viewed in the light of natural selection.

Firstly, I shall describe and classify the forms of cooperative behaviour found in fish and discuss the explanations considered to date.

16. 1 COOPERATIVE BROOD DEFENCE OF JOINING PARENTS

There are at least 4 examples of communal broodcare among cichlids, in which 2 or 3 parental pairs have been occasionally observed to defend jointly a school of their merged young (*Etroplus surratensis* in Ward and Wyman, 1975; *Cichlasoma citrinellum* in McKaye and McKaye, 1977; *Leptotilapia inuine* by Loiselle, personal observation cited in McKaye and McKaye, 1977; *Tilapia rendalli* in Ribbink *et al.*, 1981). These species are spread over the whole geographic range of cichlids with two African examples and one each from America and Asia. McKaye (1985) twice observed interspecific cooperative defence of merged schools of young of the cichlid *Crytocara pleurostigmoides* and the bagrid catfish *Bagrus meridionalis*. In many additional instances adult cichlids at least remained near a catfish pair which defended a mixed school of their own and cichlid young.

The suggestion put forward to date is that cooperative defence of young is an anti-predator response: the combination of many conspecific parents is perhaps more effective than solitary pairs in defending broods from predators (McKaye and McKaye, 1977). A second possibility is that neighbouring schools of young, merging simply because of proximity, cannot be separated. An adaptive explanation would not then be required for the observed phenomenon. To my knowledge, no analysis of the costs and benefits of singly *versus* cooperatively defending parental pairs has yet been made in any case. In the interspecific example, the survivorship of catfish young was greater when cichlid young were present and a similar advantage is also suggested for the cichlids.

Is the cooperative defence of young stable against cheating, *i.e.* one participant abandoning the mixed brood? No conclusive data are available as yet, but defection is probably widespread (see also McKaye, 1985). Some evidence comes from mixed species broods which are frequently found to be guarded by parents of one species only (*e.g.* Ribbink *et al.*, 1979; Goff, 1984; Yanagisawa, 1985), while on the other hand only one

case is known of joint defence by heterospecific parents (see above). The situation is probably similar within species; however in that case it is much harder to observe an exchange between young of different parents and therefore evidence is scarce.

16. 2 COOPERATIVE RESOURCE DEFENCE

Anemones are jointly defended by subordinates and a breeding pair of the pomacentrid *Amphiprion akallopisos* (Fricke, 1979). This may be explained by an overlap of 'interests.' Young fish are not yet capable of defending an anemone of their own, nevertheless need one for their protection and for future reproduction. For pair members, subordinate recruits are valuable potential reproductives in the case of partner loss. The factors controlling the amount of defence displayed by each participant are yet to be evaluated.

16. 3 'HELPERS-AT-THE-NEST'

Six Lake Tanganyika cichlids of two closely related genera have been found to have non-breeding helpers (*Lamprologus brichardi, L. pulcher, L. savoryi, Julidochromis marlieri, J. ornatus, J. regani*). In these species conspecifics other than the reproducing pair participate in various duties of defence, broodcare and territory maintenance (Taborsky and Limberger, 1981). The tasks may be shared unequally between family members, according to size and status (Taborsky, 1982).

Several fitness gains may be involved in the evolution and preservation of this type of cooperation. Breeders may benefit from sharing costs and from an increased production of young. Helpers might benefit either by increasing the production of relatives, by gaining broodcare experience, by inheriting the pair's territory, by enjoying increased protection within the defended territory and by the possibility of parasitizing the pair's reproduction. In *L. brichardi* a cost/benefit analysis testing for all these possibilities (Taborsky, 1984) showed that parents do have some risk of reproductive parasitism exerted by their helpers, but due to the help they receive they save energy and lay more eggs, thus producing higher numbers of young. Helpers grow more slowly than non-helping individuals, but they gain by enhancing the production of close relatives and by increased protection from the pair's territory defence and their access to

shelters. Occasionally, they may benefit from reproductive parasitism (Taborsky, 1984, 1985).

Because *L. brichardi* helpers stay when a parent is replaced, which happens occasionally in nature, their expected degree of relatedness to the young they care for declines with their age (Taborsky and Limberger, 1981). Cheating should therefore increase as helpers grow older, thus causing an increased level of conflict between helpers and breeders. This indeed happens as large male helpers may sometimes try to fertilize eggs deposited in their home territory; large helpers of both sexes may pair with the territory owner of the other sex, thereby outcompeting the same sex dominant (Taborsky, 1985); and with increasing size, hence age, the helpers increase their tendency to feed on eggs rather than clean them (Siemens, 1984). Reproductive parasitism is a rare event, but its potential threat may be the major ultimate cause for parents to expel large helpers. Above the size at which most helpers attain sexual maturity, which coincides with a great reduction in their predation risk, helpers are often tolerated only when they are needed, *e.g.* when there is competition for space. It has been shown experimentally that after expulsion they are re-accepted when competition is increased (Taborsky, 1985). The 'interests' of breeders and large helpers diverge and the latter may be viewed as paying for staying. The relation between these family members, which are on average close kin, is thus characterised by conflict and reciprocity. Two important preconditions for reciprocity (Axelrod and Hamilton, 1981) are met. Breeders recognize their helpers individually (Hert, 1985) and prob-ably *vice versa* (personal observation), and they recognize and punish defection of helpers (the latter are severely attacked when found to eat eggs; Taborsky, 1985).

As for the proximate mechanism of helping behaviour, an experi-mental analysis revealed that the control of direct broodcare changes with helpers' ages (Siemens, 1984). Small subordinate fish invariably clean the eggs they find in their territories, whereas dominants eat them. With large helpers dominance is not the sole factor deciding whether eggs are cared for or consumed, as other variables, such as past experience and how others treat the eggs, have an additional influence. In breeders still dif-ferent variables regulate the egg care.

16.4 COOPERATION BETWEEN REPRODUCTIVE COMPETITORS

In three congeneric Mediterranean wrasses (*Symphodus ocellatus, S. roisalli* and *S. tinca*) males cooperate in nest defence and interactions with females (Taborsky *et al.*, 1987). Brightly coloured, large territorial males build nests of algae and care for the eggs successively deposited by several visiting females (Soljan, 1930, 1931; Fiedler, 1964), much like in sticklebacks. They are often joined by medium-sized males which par-ticipate in nest defence against conspecifics, mainly against smaller klepto-gamic males. These 'satellites' behave submissively towards nest-builders and are tolerated to a variable extent. In one of three populations of *S. ocellatus* investigated so far, more than 80% of nest-builders were joined by a satellite male for some time during the nest's spawning phase. The exact percentage is unknown in the other two populations.

It is of special interest that reproductive competitors cooperate in these systems. The cooperators are not related to each other above average, as the larval stage is planktonic and cooperating males frequently belong to different age classes. The evolution and stability of this cooperative behaviour may be based on various cost and benefit functions. Satellites may be social parasites gaining at the expense of nest-builders, who may not be able to evict satellites in an economical way. On the contrary, both parties may have a net gain, either directly by the effect of cooperation (*e.g.*, any female brought to the nest as a result of cooperation would be better than none, even if the fertilizations are shared) or by a reciprocal action (*e.g.*, a male could benefit its collaborator in one way while gaining from it in another). The third possibility where territorials gain and satellites lose is improbable, as satellites work hard for their position de-spite other alternatives (*e.g.* pure kleptogamy; Taborsky *et al.*, 1987).

In *S. ocellatus* there is a high correlation between the presence of satellites and the nest-builders' success. Builders spawned more than twice as often when satellites were present ($N=75$ configurations), and 92% of nests with satellites were successful (*i.e.* they received eggs and were tended long enough for the larvae to hatch), whereas only 23% of nests without satellites may have hatched larvae ($N=86$ nests). However, these data do not reveal whether the presence of satellites is the cause or the effect of the nest-builders' success. A removal experiment showed that satellites decrease the rate of fertilization attempts exerted by smaller kleptogamic males, but this positive effect for the nest owners is com-

pletely compensated by the satellites' own fertilization attempts. The immediate influence of a satellite's behaviour directed towards an approaching female in spawning mood decreases the probability of the female entering the nest and spawning. This is in contrast to the stimulating effect that a nest owner's behaviour has on a female that is ready to spawn (Taborsky, in preparation). Thus, no direct mutual benefit could be demonstrated for nest-builders and satellites.

Nevertheless coalition partners benefit from each other. Satellites obtain higher spawning rates than other kleptogamic males, and nest-builders attract more females when a satellite is present, even though the behaviour of the latter obstructs the females' approach. Several lines of evidence suggest that satellites serve a poster function for females ready to lay eggs. By spawning in nests with a satellite, females may greatly enhance the probability of their larvae hatching (Taborsky, in preparation; see also Ross, 1983 for a somewhat similar case of satellite presence and toleration by territorial males in the fallfish minnow. Ross also suggested an attraction of females by satellites).

These reproductive coalitions of wrasses are characterised by reciprocity, similar to the relation between breeders and *large* helpers in the cichlids. Defection may not be a great problem for wrasses because the presence of satellites and their tolerance by territorials, rather than the satellites' behaviour, are the crucial features. Nevertheless, one could speculate that the possibilities of defection prevent even higher levels of cooperation occurring, despite the high potential for it. For example, cooperative care for jointly fertilized eggs is a possibility not encountered to date.

16. 5   THE SIGNIFICANCE OF COOPERATIVE BEHAVIOUR IN FISH

Let us recall the aims introduced at the beginning of this paper. I set out to show that fish behaviour includes a wide scope of cooperative phenomena, even though the number of examples is still small (which is presumably due to practical reasons). They include such different examples as: parents jointly defending merged schools of young; family groups in which young participate in all the duties of breeders, who are most often the helpers' parents; and the coalitions of competing reproductive males with divergent reproductive tactics. In the examples analysed for costs and benefits of the participants, seemingly altruistic and

purely selfish tendencies go together. We must not view cooperation and social parasitism as mutually exclusive, opposing phenomena. I would expect that each cooperative system also bears features of social parasitism. The characteristic responsible for our classification of a system as either 'cooperative' or 'parasitic' should be the net ratio of costs and benefits of both (all) parties. If benefits outweigh costs for all participants we may speak of cooperation in a functional sense. If this is only true for one party then we may view it as social parasitism. In practice, however, the term 'cooperation' is mostly used operationally, as in this paper. It simply describes the superficial observation that participants 'co-operate,' long before anything is known about costs and benefits.

As for the examples of cooperative behaviour in fish found to date, it is intriguing that they belong to cichlids mainly, or to closely related perciform families. This may have many explanations. One is certainly the disproportionate amount of attention these fish have so far attracted from behavioural ecologists. Another important feature is probably the genetic predisposition of members of these groups, which includes the potential for complex behavioural interactions between social partners, the high potential for evolutionary change as exemplified by the considerable degree of adaptive radiation, and the already advanced forms of reproductive patterns and parental care. It may be viewed as evidence for the genetic predisposition hypothesis that similar forms of helping behaviour occur in closely related Tanganyika cichlids, despite some great differences in other aspects of their social behaviour, and that there are similar relations between territorials and satellites in some closely related Mediterranean wrasses. The ecology of species may also have some importance (*e.g.*, all given examples only include substrate breeders).

I believe that within the vertebrates fish are well suited, for practical reasons, to studying the variables of theoretically predictable influence on the fitness components of competing and/or cooperating individuals. Fish often have a fast brood succession, relatively short generation time, small home ranges, and they are often easily observed and experimentally manipulated under natural and seminatural conditions (see Taborsky, 1984). Thus, fish may be viewed as magnificent 'models' for investigation of the functional mechanisms regulating complex social systems.

SUMMARY

This paper describes four types of cooperative behaviour which have been observed in fish (the collaboration of pair members is not considered): (1) in four cichlid species two or three parental pairs may cooperatively defend a school of their merged young. This was also reported to occur interspecifically between a cichlid and a catfish. (2) Subordinate anemonefish defend an anemone jointly with a breeding pair. (3) The young of six Lake Tanganyika cichlids stay for a prolonged time in their natal territories and share in all duties of the breeders. (4) In three Mediterranean wrasses satellite males associate with territorial males and help to defend the nest against intraspecific reproductive parasites (sneakers). They also take part in interactions with females.

These examples of cooperative fish behaviour are examined for fitness costs and benefits of the parties involved and the occurrence and prevention of defection. The confinement of examples to a few taxonomic families and the suitability of fish social systems for studies on the evolution and stability of cooperative and seemingly altruistic behaviour are discussed.

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