

PART 3

**Coping with a
Complex World**

Cooperative Behaviour in Fishes

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INTRODUCTION

Nearly half of all vertebrates are fishes (over 25,000 known species in 515 families) (Nelson, 2006). In association with this great phylogenetic diversity is the enormous ecological diversity and unrivaled variation in physiology, life history pathways, and breeding systems (Breder and Rosen, 1966; Pitcher and Hart, 1983; Avise *et al.*, 2002; Sloman *et al.*, 2006). Indeed, studies of fishes have provided some of the greatest contributions to the field of behavioural ecology and have significantly enhanced our understanding of mating systems, parental care and reproductive strategies (Barlow, 1981, 2000; Warner, 1984; Gross and Sargent, 1985; Godin, 1997; Dugatkin, 2004; Alcock, 2006; Munday *et al.*, 2006). Therefore, it

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is all the more surprising that many behavioural ecologists are unaware that some fishes have interesting cooperative strategies. Although documented cooperation in fishes is rare, fishes have the potential to contribute greatly to our understanding of the evolution of cooperation in vertebrates. This is especially so because, in contrast to studies of birds and mammals, it is possible to study hundreds of fish groups of marked individuals in the field and in the laboratory (with small fish), as well as conduct large-scale experimental removals and introductions (Balshine-Earn *et al.*, 1998; Buston, 2004a, b; Stiver *et al.*, 2004, 2005, 2006, 2007; Brouwer *et al.*, 2005; Heg *et al.*, 2005; Heg and Bachar, 2006; Desjardins *et al.*, 2007).

Although only rarely studied in fishes, the topic of cooperation has captured the imagination of evolutionary biologists for nearly 150 years, ever since Darwin (1859) outlined the difficulties that cooperative behaviour posed for his theory of evolution by natural selection. Generally, we expect that natural selection will have favoured those individuals that behave in ways that maximize their own genetic contribution to future generations. If this is true, then selection will have left us with animals that are attempting to efficiently maximize their benefits while minimizing their costs. In light of this theory, cooperative behaviour, where individuals enhance the fitness of others at some cost to themselves, appears as an evolutionary paradox.

Most researchers studying cooperation in fish have concentrated on cooperation in the context of cooperative breeding systems, where some individuals forego their own reproduction and help others to raise young (Emlen, 1991; Solomon and French, 1997; Koenig and Dickinson, 2004). In birds and mammals, this breeding system occurs in around 3% of species in both groups, apparently evolving independently many times (Solomon and French, 1997; Arnold and Owens, 1998, 1999; Koenig and Dickinson, 2004). Cooperative breeding is extremely rare among fishes, with no more than 0.1% of the bony fishes (Teleostei) all from a single family (Cichlidae) documented to have helpers (Taborsky and Limberger, 1981; Taborsky, 1994, 2001; Goodwin *et al.*, 1998; Heg and Bachar, 2006). We consider that there are two good explanations for the scarcity of examples of cooperation among fishes.

Cooperative behaviour could be rare in fishes in relation to birds and mammals because the selective regimes favouring cooperation are absent. One obvious difference relates to the prevalence and value of parental care. All birds and mammals show some level of parental care and this is a pre-requisite for cooperative breeding involving helping. In contrast,

only around 20% of fishes provide any form of parental care (Blumer, 1979; Baylis, 1981; Gross and Shine, 1981; Gross and Sargent, 1985; Gross, 2005); the majority of fishes simply shed gametes into the water column and the larvae fend for themselves. Cooperation may also be rare in fishes because, even when there is parental care, it is commonly performed by a single parent and takes the form of defense and fanning of eggs, which is seemingly less demanding than the parental care seen in birds and mammals (Gross and Sargent, 1985; Clutton-Brock, 1991). If parental care were less demanding in fishes, then the need for help would be reduced. Another obvious difference between fishes and their terrestrial tetrapod counterparts relates to the mode of dispersal. In birds and mammals, dispersal patterns often lead to the formation of kin groups. In contrast, only a very small fraction of fishes ever associate with kin for prolonged periods (Avisé and Shapiro, 1986; Olsen *et al.*, 1998; Griffiths, 2003); the majority of fish larvae disperse very early in life and survival probabilities pre-settlement are low. Since cooperation is particularly favoured among relatives, fishes' large-scale pelagic dispersal strategy reduces the scope for cooperation.


Clearly, there are differences among fishes, birds and mammals, but given the fact that many fishes live in groups (Godin, 1997), the singular most important precondition for the evolution of cooperation, it still seems somewhat surprising that cooperation is so rare. An alternative explanation for the paucity of cooperative behaviour in fishes is simply that it has been overlooked. The number of behavioural ecologists studying birds and mammals is vastly greater than the number studying fishes, and only a tiny fraction of fish species have been studied in detail. The recorded incidence of cooperation in fishes is likely to increase as more long-term studies of marked individuals are conducted. Furthermore, given the difference in the selective regimes that fishes experience, it seems likely that cooperative behaviour might take different forms from those typically observed in birds and mammals, which again could lead to cooperation being overlooked.

In this chapter, we shall describe the various forms of cooperation that have been observed in fishes and review our current understanding of this intriguing social behaviour. Following a brief introduction, we will provide a brief explanation of the terminology and theory used to understand the concept of cooperation. Here we describe the possible selective routes that may have led to the evolution of cooperation. Further, we review four case studies of cooperation among fishes. In each, we demonstrate how the available empirical evidence provides support for

the various evolutionary routes to cooperation. We conclude our chapter with an outline for possible future directions and next steps for the study of fish cooperation.

COOPERATION: DEFINITIONS AND TERMINOLOGY

Like any field of study, research on cooperation has developed a vocabulary to help communicate ideas and concepts, e.g., cooperation, cooperative behaviour, altruism, cooperative breeding, and allocare. The number of terms and their interchangeable use has, however, led to some confusion in the cooperation literature. To avoid further confusion, we use a limited set of terminology consistent with recent reviews of cooperation (Bergmüller *et al.*, 2007; Buston and Balshine, 2007). We use the word 'cooperation' to describe an interaction between individuals that enhances the fitness of all the individuals involved. When two individuals are involved in cooperation, the receiver of the cooperative act clearly benefits but so does the donor (albeit cryptically in some cases) because cooperation is often the best strategy relative to the available alternative actions. We use the term 'Cooperative behaviour', or the verb to 'Cooperate', in order to describe an act performed by one individual (the donor) that enhances the fitness of another (the recipient) within a cooperative interaction. Finally, we use the term 'Cooperative breeding' to describe breeding systems in which certain individuals forego some of their own reproduction and help others to raise young. These definitions are all well and good, but how do we demonstrate that an interaction is cooperative or that an individual is behaving cooperatively?

The first step towards demonstrating cooperation is to show that the apparent recipient benefits from the donor's actions. Cooperative behaviours are not just helpful (Fig. 12.1a); peaceful or affiliative; behaviours can also be considered cooperative because they offset the costs of being together (Fig. 12.1b). To measure the fitness accrued via cooperation, we must first measure a baseline fitness against which to compare the enhancement of fitness caused by cooperation. All too often, the baseline is considered as the fitness of the recipient in the absence of the donor and its cooperative acts, and is determined by the experimental removal of the donors (Fig. 12.1a; e.g., Brown *et al.*, 1982; Leonard *et al.*, 1989; Mumme, 1992; Buston, 2004a; Brouwer *et al.*, 2005). However, for a truly rigorous test, the baseline must be defined as the fitness of the recipient in the presence of the donor but in the absence of its cooperative acts, and measured by experimental removal of the cooperative behaviour (Fig. 12.1b; Wong *et al.*, *in press*)  focus on cooperative behaviour

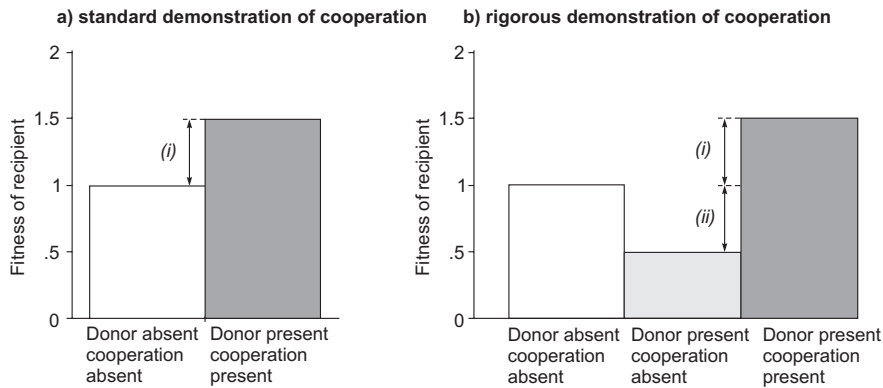


Fig. 12.1 Cooperative interactions. (a) In general, in the cooperative breeding literature, whether or not cooperation occurs and how much cooperation occurs is assessed by the experimental removal of the donors (black arrow, *i*). (b) In rigorous tests, whether or not cooperation occurs and how much cooperation occurs would be assessed by the experimental removal of the cooperative behaviours (black arrows, *i* and *ii*). Rigorous tests would reveal another large group of cooperative behaviours, e.g., those that donors engage in to offset the costs of their presence (*ii*), in addition to the standard well-documented cooperative behaviours (*i*).

that raises the fitness of the recipient above and beyond what it would get in the absence of the donor (Fig. 12.1a), rather than what it would get in the absence of the cooperative behaviour (Fig. 12.1b), means that we are missing a variety of interesting cooperative behaviours. For far too long the term cooperation has been assigned only to overtly helpful acts like feeding the offspring of another individual. Peaceful co-existence, stability among group members or the affiliative interactions necessary to maintain this stability in a social group requires a degree of effort. This benefit of simple peaceful co-existence is often overlooked.

THE EVOLUTION OF COOPERATION

Although cooperative behaviour in nature takes many forms, all cases have been classically understood in the context of 4 evolutionary hypotheses: kin selection; mutualism; reciprocity; and manipulation (Krebs and Davies, 1993). *Kin selection* explains the cooperation between related individuals, where donors of cooperative acts may gain indirect genetic benefits via the reproductive success of close relatives (Hamilton, 1964). *Mutualism* refers to cooperation that leads to direct genetic benefits for all interacting individuals. For example, mutualism is when two individuals work together to defend a breeding territory and, in doing so, both enhance their reproductive success. Alternatively, *reciprocation*

refers to benefits that may be accrued immediately by the recipient while the donor will only eventually accrue benefits in the future (Trivers, 1971). For example, two individuals may work together to defend a breeding territory; one breeds immediately and has enhanced present reproductive success, while the other delays reproduction but stands to inherit breeding status in the future. The final major category of cooperation is *manipulation*, where the individuals behave cooperatively because they are duped, forced, or coerced into doing so or, more generally, because of the costs associated with non-cooperation are too high. For example, one individual might raise the eggs of another together with its own, not because of any benefit accrued from raising the other's eggs but, rather, because in trying to eliminate the other's eggs, it would eliminate some of its own.

While the classical framework has served us well, we consider that the evolution of cooperative behaviour is most simply understood by focusing on when and where the benefits of cooperation are accrued: directly or indirectly, in the present or in the future (Box 12.1). Individuals may cooperate because they increase their own chances of survival and reproductive success, thereby accruing direct genetic benefits either now or in the future. Additionally, individuals may cooperate because they enhance the fitness of relatives who share genes identical by descent, thereby accruing indirect genetic benefits (Hamilton, 1964; Brown, 1980; Griffin and West, 2003). The important point is that, although an individual's phenotype may appear to be behaving altruistically, the individual is ultimately behaving in a manner that serves the best interests of its selfish genes (Box 12.1; Dawkins, 1982). The key to understanding cooperation lies in recognizing that a trait will be favoured by selection if it confers the highest possible fitness on an individual, given its social and ecological context (Box 12.1; Reeve and Sherman, 1993).

Recently, in the existing literature on cooperation, there has been a shift from focusing on indirect genetic benefits to focusing on direct benefits accrued either immediately, in the present, or in the future (Clutton-Brock, 2002; Lehmann and Keller, 2006). However, focus on one set of benefits or the other will not give us a complete understanding of the behaviour. Empirical studies demonstrate that each source of benefits may operate in isolation (e.g., direct, Packer *et al.*, 1991; Balshine-Earn *et al.*, 1998; indirect, Emlen and Wrege, 1989; future, Buston, 2004b) but, more typically, benefits accrue from multiple sources (Clutton-Brock *et al.*, 2001; Stiver *et al.*, 2005; Field *et al.*, 2006). Thus, by studying all sources of potential benefits in concert, we will be able to measure the

Box 12.1 Understanding the evolution of cooperative behaviour relies on identifying the costs and benefits of cooperative and alternative actions, for the donor and its relatives, now and in the future.

Direct benefits

Whether or not cooperation will be favoured by selection can be determined using a simple inequality. In particular, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j > 0 \quad (1)$$

where X_i (or X_j) is the personal reproductive output associated with the i th (or j th) action. Inequality 1 can be used to understand why cooperation evolves as a result of immediate mutualism, immediate reciprocity, or manipulation.

Indirect benefits

Additionally, if $X_i - X_j < 0$, cooperation can still be favoured because of its beneficial effects on kin. The behaviour favoured by selection can be determined by the use of Hamilton's rule (Hamilton, 1964). In particular, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j + r(Y_i - Y_j) > 0 \quad (2)$$

where Y_i (or Y_j) is the other individual's reproductive output, and r is the probability that the two individuals share a copy of a particular gene identical by descent (the coefficient of relatedness). Inequality 2 can be used to understand why cooperation evolves as a result of kin selection.

Future benefits

Alternatively, if $X_i - X_j < 0$, cooperation can still be favoured because of its beneficial effects in the future. The behaviour favoured by selection can be determined using inequalities that consider the future (e.g., Kokko and Johnstone, 1999). Most simply, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j + f(Z_i - Z_j) > 0 \quad (3)$$

Where Z_i (or Z_j) is the personal reproductive output associated with the i th (or j th) action in the future, and f is the probability that those benefits will be realized. Inequality 3 can be used to understand why cooperation evolves as a result of delayed mutualism or delayed reciprocity.

All benefits


Of course, hypotheses for the evolution of cooperation are not mutually exclusive; cooperation can be favoured because of its present direct benefits, present indirect benefits, and future direct benefits. (We consider that the effect of future indirect benefits may be weak because it involves a combination of two probabilities r and f .) Thus, generally, a cooperative action i is favoured over an alternative action j if

$$X_i - X_j + r(Y_i - Y_j) + f(Z_i - Z_j) > 0 \quad (4)$$

We envisage that this general inequality for the evolution of cooperative behaviour will enable us to make sense of all cases of cooperation in nature.

contribution of one source while controlling (statistically or experimentally) for the effect of other sources. With this framework in mind, we now turn our attention to several case studies of cooperation in fishes. These studies have contributed to the greater field of cooperation research, by revealing how and why various forms of behaviour enhance the fitness of recipients and donors involved in cooperative interactions.

COOPERATION IN FISHES

A large number of fish species live in social groups providing a context ripe for the evolution of cooperative behaviour (Krause and Ruxton, 2002). Cases where cooperation has been unambiguously demonstrated and its evolution explained are, however, few and far between. In addition to the reasons outlined above, this may be in part because the necessary experiments simply have not been done. An experimental approach is needed in fishes (as well as other taxa), because positive correlations between group size and fitness, which might be suggestive of cooperation, are confounded. It is common in fishes for group size, territory size, and body size to be correlated with each other and with survival and reproductive success of individuals (Anemone fishes: tt and Mariscal, 2001; Buston, 2003b; Mitchell, 2005; Hawkfishes: Donaldson, 1989; Gobies: Kuwamura *et al.*, 1994; Cichlid fishes: Balshine *et al.*, 2001, Heg, 2006a). These correlations mean that, in order to demonstrate cooperation, it will usually be necessary to conduct long-term observations of marked individuals in conjunction with experiments that remove putative donors of cooperation or, better still, their cooperative behaviours (Fig. 12.1) and multivariate analyses that control for potential confounding variables. Simply taking away the donors of cooperation will not provide the full story. Ideally, researchers need to leave the donor in place but simply stop it from cooperating and then assess the fitness of putative recipients of cooperation following the manipulation (e.g., Brown *et al.*, 1982; Emlen and Wrege, 1989; Leonard *et al.*, 1989; Mumme, 1992; Buston, 2004b; Brouwer *et al.*, 2005).

Here we focus on the small number of well-characterized case studies that have employed the experimental approach so as to demonstrate cooperation. Our intention is that this focus on experiments, in conjunction with previous broader treatments of fish cooperation (Taborsky, 1994, 2001), will give those interested in cooperation plenty of inspiration in the upcoming years. Fortunately, these case studies encompass a wide variety of fish breeding systems, which facilitates a

discussion of cooperation among males, females, and hermaphrodites. We also discuss the various ways that cooperation may lead to individuals accruing fitness benefits (in the present and in the future, as well as directly and indirectly, see Box 12.1). We also examine cases of cooperation among groups with both despotic and more egalitarian breeding (i.e., high and low reproductive skew, Keller and Reeve, 1994; Johnstone, 2000).

COOPERATION AMONG MALES (LOW SKEW WITH DIRECT IMMEDIATE BENEFITS)

Natural History

Throughout the lakes of North America, male bluegill sunfish, *Lepomis macrochirus*, will either nest alone or in colonies with 10 to 300 other individuals (Neff *et al.*, 2004). Each male that builds a nest (termed parental males) can spawn with several females and will care for the eggs and subsequently the fry in his nest for up to 10 days (Gross, 1982; Neff *et al.*, 2004). In addition to parental males, there are two alternative male tactics: female mimics and sneakers (Gross, 1982, 1991; see also Chapter 11 'Alternative Reproductive Tactics in Fishes' by Knapp and Neff, this book). A series of investigations over the last thirty years based on bluegill from Lake Opinicon in Canada have examined the costs and benefits of colonial, synchronous breeding in this species (Gross, 1979, 1980, 1982, 1991; Dominey, 1980, 1981, 1983; Gross and Charnov, 1980; Gross and MacMillan, 1981; Coté and Gross, 1993; Neff, 2001; Neff and Gross, 2001).

Possible Forms of Cooperation

The first form of cooperation exhibited by parental male bluegills is mutual defence of a general breeding area. Gross and MacMillan (1981) investigated the effect of nest density and nest position on factors related to reproductive success in bluegill. They found that males defending an isolated nest were visited by more egg predators (*Ictalurus* spp. and *Lepomis gibbosus*) and experienced more predation attempts on eggs. Within a colony, the density of nests reduced the exposure of bluegill brood to predators, and males in central positions suffered less predation than peripheral males. One of the main reasons for this differential predation is that central colonial nests enjoy extra protection from males having overlapping defence zones, meaning that when a predator intrudes, two or more males chased it simultaneously (Gross and MacMillan, 1981).

The second form of cooperation exhibited by parental male bluegills is that they occasionally care for the eggs of other males. It turns out that within colonies there are two types of cuckolders: sneakers (young males 2-3 years of age that dart into nests during female egg release) and female mimics (young males 4-5 years of age that are about the size of mature females and express female colour and behaviour), that apparently mislead parental males into identifying them as a second female in the nest (Dominey, 1980; Neff *et al.*, 2004). Sneaker males and female mimics effectively manipulate the parental males; they force, dupe, or coerce parental males into caring for their eggs. The parental male often cares for the eggs of others until they hatch (Gross, 1982; Neff, 2001). Cuckolding (sneaking and female mimic strategies) is more common in colonies and at high densities (Neff *et al.*, 2004).

Do Individuals Cooperate?

Gross and MacMillan (1981) showed that males in colonies had more young survival (higher reproductive success) than solitary males, and that males nesting in areas of high density had higher young survival than males in areas of low density. These results suggest that mutual or joint defense was a successful strategy. Alternatively, it could imply that colonial males are higher quality males; however, solitary males were of the same size and age as colonial males and were in fact in better condition with fewer parasites (Neff *et al.*, 2004). To determine whether colonial males gain direct benefits by breeding together, it is necessary to conduct an experiment in which some co-defending breeding males are removed. While Gross and MacMillan (1981) removed co-defending males, they subsequently measured the survival of eggs belonging to the removed individual (which decreased) and, in doing so, they effectively demonstrated the benefits of male parental care but not the benefits of cooperation. The key to demonstrate cooperation is to measure the effects of such a male removal on the egg survival/fitness of neighbouring males in the colony—this remains to be done. Still, it seems likely that parental males do provide direct benefits to each other.

Sneaks and female mimics that can get territorial males to care for their eggs will do better than those that cannot. Parental males are sensitive to the level of sneaking (Neff and Gross, 2001; Neff, 2003), and do seem to reduce their level of care when their paternity is low (Neff and Sherman, 2003). However, parental males still raise the eggs of other males and thus provide direct benefits to sneaker males and female mimics.

Such manipulation by sneakers and female mimics is clearly manipulative and the territorial males would undoubtedly enjoy higher fitness without these parasitic males. However, we argue that such a manipulation still ought to be considered cooperation, because relative to the alternative available options, the territorial male will increase its fitness by caring for these parasitic eggs. Thus, such manipulation too fits our definition of cooperation.

Why do Individuals Cooperate?

In bluegill, the mutual defense of nests appears to be an effective cooperative strategy by which individuals accrue immediate direct benefits, reducing egg predation and increasing spawning success. One might wonder why some parental males breed solitarily when isolated nests appear not to confer all of the same egg survival benefits as colonial nests (see also Coté and Gross, 1993). It turns out that female mimics and sneaker males are attracted to colonies and significantly reduce the reproductive success of colonial parental males (Gross, 1991; Jennings and Phillips, 1992; Neff, 2001). Indeed, colonial parental males may fertilize as few as 25% of the eggs in their nest (Neff, 2001), making the success of central colony males equivalent to that of solitary males (Neff *et al.*, 2004).

The perplexing question of why these colonial parental males agree and essentially cooperate to raise the young of sneaks and mimics still remains. The key to understanding why such males cooperate is to realize that exiting the cooperative interaction would be prohibitively expensive (Box 12.1). These costs come about because of limitations in the parental males' recognition systems (Reeve, 1989; Sherman *et al.*, 1997; Buston and Balshine, 2007) and their ability to distinguish: (1) female mimics from females (Neff and Sherman, 2003) and (2) own offspring from the offspring of others (Neff, 2003). Parental males do reduce their level of care when they are heavily cuckolded, but will do so only once the eggs have hatched, possibly because only after eggs have hatched can males detect their own young based on their MHC complex (Neff, 2003; Neff and Sherman, 2003; Hain and Neff, 2006).

Questions for Future Study

The cooperative strategies exhibited by bluegills are likely to be common in fishes. First, males in many fish species have clustered breeding territories. In a number of fish species, cooperation by co-defence of a

nest or breeding area has been demonstrated for two or more males: e.g., Moamaos *Abudefduf abdominalis* Tyler, 1995; *Pelvicachromis pulcher* Martin and Taborsky, 1997; Azorean Rockpool Blenny, *Parablennius sanguinolentus parvicornis* Santos, 1985; Oliveira *et al.*, 2001, 2002. In each of the above cases, the two co-defending males both reproduce, or attempt to, and will collectively enjoy higher reproductive success than solitary males. An interesting question to examine in these systems is whether males trade-off the benefits of cooperation against the costs of competition among males.

Second, because male parental care and alternative reproductive tactics (e.g., sneakers and female mimics) often co-occur, manipulation as a form of cooperation is also likely to be common in fishes. Some might question whether manipulation should be classified as a form of cooperation. We argue (as have other authors, see Krebs and Davies, 1997; Dugatkin, 2004) that manipulation is a form of cooperation because, relative to alternative possible actions (e.g., abandoning the eggs), the manipulated individual will still benefit by providing care. So while in mutualism both parties enjoy an overall increase in fitness benefits due to the cooperative behaviour, in manipulation, the manipulated party loses some fitness to parasites but, once engaged in the interaction, it will do best to stay as it experiences a net benefit by continuing to care.



Alternative reproductive tactics (ARTS) have been found in at least 140 species in 28 different fish families (Taborsky, 1998; Oliveira, 2006, see also Chapter 11 Alternative Reproductive Tactics in Fishes by Knapp and Neff, this book). The extent of forced cooperation, where males will care for young of other individuals, will strongly depend on the evolved recognition systems and the cognitive abilities of individuals to detect manipulators and kin (Reeve, 1989; Sherman *et al.*, 1997; Neff and Sherman, 2003, Buston and Balshine, 2007) and the relative costs of detection as opposed to manipulation. Although some notable studies have begun to address the issue of cheater detection and kin recognition in fishes (Olsen, 1998; Griffiths and Magurran, 1999; Arnold, 2000; Braithwaite, 2006), this research area is still in its infancy.

COOPERATION AMONG FEMALES (LOW SKEW AND DIRECT IMMEDIATE BENEFITS)

Natural History

The striped parrotfish, *Scarus iserti*, is a common Caribbean coral reef fish (Buckman and Ogden, 1973; Ogden and Buckman, 1973). Solitary males

defend territories that encompass several female territories (Clifton, 1989). Within each female territory, there are 2 to 8 females that exhibit a size-based dominance hierarchy, and larger individuals displace smaller individuals during feeding bouts. The fish are protogynous hermaphrodites; if the local male dies, he will be replaced by a large female from the population (Clifton, 1989). All territorial females spawn daily despite the strong size-based dominance hierarchy, although large females have much greater fecundity than smaller females (Kenneth Clifton, pers. comm.).

Possible Forms of Cooperation

As with bluegill, there also are two forms of cooperation in striped parrotfish. First, large females (> 65 mm SL) engage in joint defence, in this case defence of the territory and the algal resources within the territory against conspecific intruders (Clifton, 1989). Per capita rate of defence does not seem to depend on group size, indicating that larger groups are better defended (Clifton, 1989). In addition, large and small females within a group will act as co-food-finders. Time to food patch discovery was inversely related to group size, indicating that larger groups more rapidly find food (Clifton, 1989). Moreover, time to food discovery by the largest dominants was negatively related to group size, indicating that the dominants are using subordinates as food finders.

Do Individuals Really Cooperate?

Kenneth Clifton (1989) used a series of removal experiments to investigate whether females that share territories might be benefiting from cooperation in defence and food finding. Following the removal of large subordinates, Clifton found that dominant individuals spent more time defending the territory against conspecifics, suggesting that co-defence was beneficial. Furthermore, following the removal of either large or small subordinates, he found that the dominant individuals spent more time swimming, less time feeding, and took longer to discover high quality food patches. Although measures of survival and reproductive success are still lacking, it seems very likely that these benefits of having subordinates around would be translated into fitness benefits.

Why do Individuals Cooperate?

Female subordinate striped parrotfish, at least the large subordinate ones, obtain significant fitness benefits from having a share of the reproduction

within the territory. Large subordinates also benefit immediately from the presence of a dominant as they reduce the time spent defending the territory and increase overall food intake in the presence of a dominant. The situation of small subordinates is harder to understand, because larger individuals displace these smaller fish from food (Clifton, 1989). However, both large and small subordinates benefit from simply being in the territory because they stand a chance to inherit the territory following the disappearance or sex change of the dominant. Hence, female subordinate *S. iserti* appear to benefit both by immediate direct benefits (increased survival and reproduction) and future direct benefits (inheritance) and these are likely to induce the cooperation observed (Clifton, 1989).

Questions for Future Study

It would be interesting to determine whether striped parrotfish form kin groups and, hence, might also be gaining indirect genetic benefits. Historically, the formation of kin groups in the marine environment has been considered unlikely because of the planktonic larval phase (see review in Leis, 1991), but recent studies are revealing that many marine larvae return to their natal reefs (Jones *et al.*, 2005; Gerlach *et al.*, 2007) and may settle in kin clusters (Selkoe *et al.*, 2006).

This mating system with multiple females in a single territory is common in many marine fishes (Warner, 1984). The focus on sex change and mating systems in marine fishes may have obscured interesting observations on cooperative interactions among females and among group members in general. These systems will provide an interesting test bed to examine reproductive skew among females and the relationship between reproductive partitioning and the degree, form and intensity of cooperative behaviour.

COOPERATION AMONG HERMAPHRODITES (HIGH SKEW, FUTURE DIRECT BENEFITS)

Natural History

The 28 species of **anemone fishes** (Pomacentridae) found on coral reefs throughout the Indo-Pacific (Allen, 1972; Fautin and Allen, 1992) present excellent opportunities for investigating cooperation in fishes. Groups of anemone fish inhabit sea anemones that afford an oviposition site and protection from predators (Mariscal, 1970; Fautin, 1992; Elliott

et al., 1995; Elliott and Mariscal, 2001; Buston, 2003b). Generally, all anemones on the reef are occupied, i.e., the habitat is completely saturated at the scale of the population, because recruitment rates consistently outweigh mortality rates (Fricke, 1979; Fautin, 1992; Elliott and Mariscal, 2001; Buston, 2003b). Indeed, these fish can live for 20, 30 or even 40 years (Fautin and Allen, 1992; Buston and García, 2007; Srinivasan *et al.*, in review). Anemones are separated by large expanses of inhospitable terrain, and post-settlement dispersal among groups is rare or non-existent (Elliott and Mariscal, 2001; Buston, 2003b). Although post-settlement dispersal is rare, individuals within groups are not related because of the larval dispersal phase common to reef fishes (Wellington and Victor, 1989; Jones *et al.*, 2005; Buston *et al.*, in review). Within each anemone, there is a single group minimally composed of a breeding pair and most commonly including a number of non-breeders (Fricke and Fricke, 1977; Fricke, 1979; Fautin, 1992; Fig. 12.2). Within each group there is also a size-based dominance hierarchy; the female is largest, the male is second largest, and the non-breeders get progressively smaller as the hierarchy descends (Fricke, 1979; Buston, 2003a). Anemone fishes protandrous hermaphrodites (Fricke and Fricke, 1977; Moyer and Nakazano, 1978); if the female of a group dies, then the male changes sex and assumes the position vacated by the female, and a large non-breeder from the reef inherits the position vacated by the sex-changing male (Fricke, 1979; Ochi, 1989; Hattori, 1994; Buston, 2004a; Mitchell, 2005). The questions of whether or not anemone fish non-breeders cooperate with breeders, why anemone fish non-breeders might cooperate with breeders, and why breeders tolerate non-breeders have been repeatedly raised (Fricke, 1979; Taborsky, 1984; Krebs and Davies, 1993). Only recently have the questions begun to be resolved with clarity (Buston, 2003a, b, 2004a, b; Mitchell, 2005; Mitchell and Dill, 2005; Buston and Cant, 2006; Buston *et al.*, in review).

Possible Forms of Cooperation

Groups of anemone fish potentially, rife with cooperation, and a number of investigators have put forward potential ways in which subordinates might cooperate. Following the work of Gerry Allen (1972), Hans Fricke conducted the first detailed field studies of the *Amphiprion* breeding system and proposed that non-breeders might assist in territory defence (as seems to be common in fishes, see above) and non-breeders might serve as rapid mate replacements for breeders (Fricke and Fricke, 1977; Fricke, 1979). The logic behind the mate-replacement idea is that



Fig. 12.2 A group of *Amphiprion percula*, in Madang Lagoon, Papua New Guinea. Photo credit: Shane Paterson.

if one of the breeders dies and non-breeders are present then the widowed breeder might recommence reproduction relatively rapidly. Others have raised the possibility that the non-breeders might be engaged in helpful cooperation, assisting the breeders to raise eggs as observed in cichlid fishes (see below) and in birds and mammals (Taborsky and Limberger, 1981; Krebs and Davies, 1993). More recently, it has been proposed that in the short-term, non-breeders might regulate their growth to avoid inflicting costs (i.e., provide benefits) on the breeders and, in the long-term, non-breeders might enhance the fitness of breeders by enhancing the fitness of the anemone (Buston, 2004b, see below).

Do Individuals Really Cooperate?

A one-year observational and experimental study of *A. percula*, in Madang Lagoon, Papua New Guinea, tested multiple alternative hypotheses for the benefits that breeders might accrue from the presence of non-breeders (Buston, 2004b). This study revealed that non-breeders had no effect on the survival, growth, or reproductive success of breeders (see also Mitchell, 2005). Furthermore, non-breeders had little effect on the time taken for a widowed breeder to recommence breeding (Fricke, 1979; Buston, 2004a). Finally, although non-breeders stood to inherit the territory in the future (Buston, 2004b), they provided no benefit to the breeders since non-breeders were uninjured to breeders (Buston *et al.*, in review). Combined, these studies demonstrate that non-breeders are not providing help in the classical sense.

An intriguing result of Buston (2004b) was that *A. percula* non-breeders had no negative effects on the fitness of breeders, despite their obvious potential to act as competitors for food or reproduction. Further, it seemed more likely that non-breeders were actively maintaining their neutrality. Since breeding spots are severely limited, the mere presence of non-breeders makes them potential competitors for reproduction, suggesting that they must do something to mitigate this effect and prevent their eviction by the much larger breeders (Buston, 2003b). It was hypothesized that non-breeders avoid becoming actual competitors for reproduction by regulating their growth and remaining small (Buston, 2003a; Buston and Cant, 2006). Such growth regulation would be best viewed as a form of peaceful cooperation—the avoidance of inflicting a cost—as payment to stay (Fig. 12.1; Gaston, 1978; Balshine-Earn *et al.*, 1998; Kokko *et al.*, 2001; Buston, 2003a, 2004a; Mitchell, 2003). The final piece in this puzzle, required to demonstrate that subordinates in size hierarchies are indeed cooperating to stay, comes from the work of Marian Wong on the coral dwelling goby *Paragobiodon xanthosomus* (Wong *et al.*, in press; Fig. 12.2, Fig. 12.3).

In addition to their peaceful cooperation in the short-term, evidence is accumulating that non-breeders provide measurable benefits to the breeders in the long-term (or multi-year effects) because of effects mediated by the anemone—and that breeders live long enough (20–40 years) to reap these rewards, (Fautin and Allen, 1992; Buston and García, 2007; Srinivasan *et al.*, in review). Fish defend the anemone against predators, influence the photosynthetic behavior of the anemone, and provide ammonia to the anemone, all of which can enhance tissue

Box 12.2 Threat of punishment enforces peaceful cooperation in *Paragobiodon xanthosomus*.

The coral goby *Paragobiodon xanthosomus* has a very similar breeding system to the clown anemonefish *Amphiprion percula*. Groups of these tiny fish live in coral heads that provide protection from predators and oviposition sites. Each group is composed of a breeding pair and up to 15 non-breeders. Within each group there is a size-based dominance hierarchy; the largest individuals are the breeders, and non-breeders get progressively smaller as the hierarchy is descended. In a twist to *Amphiprion*, the fish are protogynous hermaphrodites; if the male dies, the female changes sex, and the largest non-breeder occupies the vacant female breeding spot. The size hierarchy reflects a queue for breeding status, within which there will be conflict between individuals adjacent in rank.

A quantitative investigation of the *P. xanthosomus* size hierarchy revealed that, just as in *A. percula*, the distribution of size ratios of individuals adjacent in rank was not random (Fig. 12.1). This non-random pattern was caused by subordinates regulating their growth to converge on a size ratio of 0.93 with respect to their immediate dominants (Fig. 12.2). Such growth regulation was proposed to be a form of peaceful cooperation by which subordinates would avoid inflicting costs on their immediate dominant to avoid punishment in the form of forcible eviction. This was confirmed by an elegant experiment in which Wong and her colleagues (2007) demonstrated that: (1) above the ratio of 0.93 the subordinate becomes a threat to its immediate dominant, and as a result, and (2) above the ratio of 0.93 dominants are much more likely to evict their immediate subordinates (Fig. 12.3).

growth, regeneration, and indeed reproduction (Schmitt and Holbrook, 2003; Porat and Chadwick-Furman, 2004, 2005; Holbrook and Schmitt, 2005). In turn, there is the potential for enhanced anemone fitness to enhance the fitness of the breeders. The anemone fish is utterly dependent on anemone survival for their own survival (Mariscal, 1970; Elliott *et al.*, 1995; Buston, 2003a, b). Furthermore, anemone size can influence the growth of the dominant (Buston, unpubl. data), and the size of the dominant might influence its egg production (Fricke, 1979; Buston, unpubl. data). Documentation of such effects would be a remarkable case of group augmentation mediated through interspecific mutualism (Brown, 1987; Emlen, 1997; Kokko *et al.*, 2001).

Why do Individuals Cooperate?

Having addressed the question of whether anemone fish breeder cooperation enhances the fitness of recipients, we now turn to the question of why anemone fish non-breeders cooperate: why is it in their best interests to remain small and avoid becoming reproductive competitors with their dominants? Using the framework for understanding

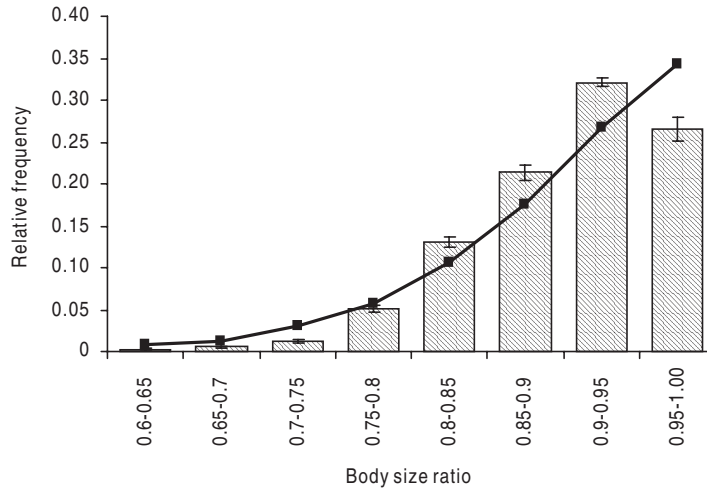


Fig. 12.3a Frequency distribution of size ratios of group members adjacent in rank. Size ratios are expressed as SL rank N+1 / SL rank N. Bars are observed distribution of ratios, while line is expected distribution of ratios generated by a Monte Carlo simulation. There is an overabundance of observed ratios between 0.90 and 0.95.

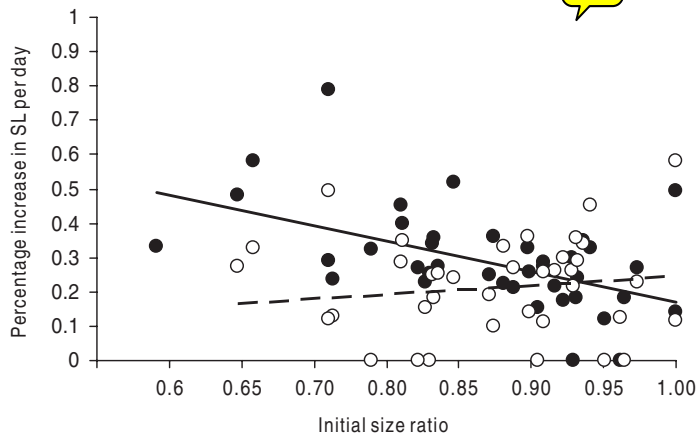


Fig. 12.3b Percentage change in SL of group members adjacent in rank. Growth rates of subordinates (filled circles solid line) and dominants (open circles dotted line) are shown in relation to the initial size ratio existing between them. Size ratio remains constant when growth rates are the same, i.e., when ratio is 0.93.

cooperation (Box 12.1), it is clear that there are two questions to be answered if we are to fully understand subordinate cooperation. First, what present direct, present indirect, and future direct benefits do subordinates accrue by cooperating? Second, what are the benefits associated with plausible alternative actions?

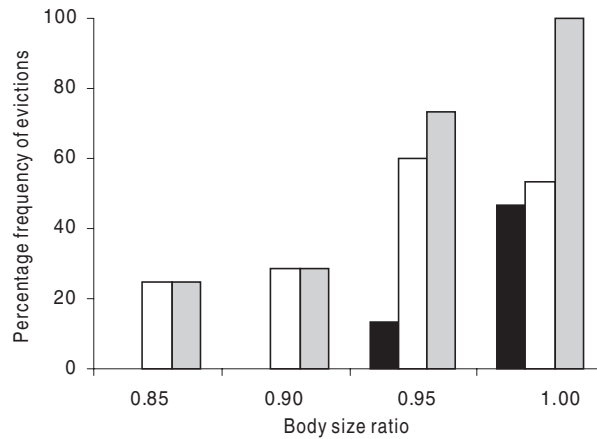



Fig. 12.3c Eviction from social groups. Percentage of dominant, subordinate, and any eviction in relation to size ratio of contestants. White = subordinate evicted, black = dominant evicted, grey = someone evicted. At ratios of 0.93 subordinates are able to evict their dominants, but are much more likely to be evicted themselves.

Anemone fish breeders do not enhance breeder fitness in the short-term and are not related so they do not accrue indirect benefits from being in a group (Buston, 2004b; Buston *et al.*, in review). Non-breeders do not have functional gonads and will not breed until they take over a breeding position (Fricke and Fricke, 1977; Moyer and Nakazano, 1978; Fricke, 1979). Instead, anemone fish breeders cooperate because, by doing so, they increase their chances of survival and future reproduction: if the female of the group dies, the male changes sex to become the breeding female, and the largest non-breeder from the anemone inherits the position vacated by the sex-changing male. The size hierarchy represents a queue to attain breeding positions; individuals only ascend in rank as those ahead of them disappear, and newcomers always join the bottom of the hierarchy—the bottom of the queue (Fricke, 1979; Buston, 2004a; Mitchell, 2005).

Subordinates enjoy both immediate benefits via enhanced survival and future direct benefit from queuing, but we still do not know why individuals adopt their peaceful cooperative strategy of remaining small and queuing, rather than growing and challenging. To fully understand why the peaceful action is favoured by selection, the payoff to the cooperative action must be compared to the payoffs associated with plausible alternatives such as: (1) dispersing to breed elsewhere and (2) contesting to breed in their anemone (Box 12.1). Queuing can be favoured by selection if it confers a greater probability of attaining breeding status

than the alternatives (Kokko and Johnstone, 1999; Ragsdale, 1999). This probability can be maximized by pursuing the strategy that conveys the highest probability of ascending in rank at each step in the hierarchy. In anemone fish, the probability of ascending in rank by queuing is greater than 0.5, while the probability of ascending in rank by dispersing is much lower, because *A. percula* are poor swimmers and are rapidly preyed upon outside of the anemones (Mariscal, 1970; Elliott *et al.*, 1995; Buston, 2003b, 2004). Furthermore, the probability of ascending in rank by contesting is likely even lower, because subordinates are at most about 80% of the body size of the dominant and thus have an almost 0% chance of winning a fight with the larger dominant. If subordinates attempt to grow more, they might have a greater chance of winning a fight, but they will also have a stronger chance of being evicted and the associated extremely low probability of successful dispersal (Buston and Cant, 2006; Wong *et al.*, *in press*, Box 12.2). 

Questions for Future Study

We expect that peaceful cooperation by the regulation of growth will be widespread in fishes. Some likely candidates include other members of the genus *Amphiprion* (Allen, 1972; Fricke, 1979; Ochi, 1986; Hattori, 1991; Mitchell, 2005), and members of the goby genera *Gobiodon* and *Paragobiodon* (Lassig, 1976, 1977; Hobbs and Munday, 2004), which are sex changers that form groups composed of a dominant breeding pair and a number of subordinate non-breeders. Also, members of the damselfish genus *Dascyllus* (Coates, 1980; Sweatman, 1983; Forrester, 1990, 1991; Booth, 1995; Schmitt and Holbrook, 1999), which are sex changers but form groups composed of a dominant male and a number of subordinate females, are possible candidates. Additionally, members of the cichlid genus *Neolamprologus* (Taborsky, 1984; Balshine-Earn *et al.*, 1998; Heg *et al.*, 2004a, see below), form groups composed of a dominant breeding pair and a number of subordinate non-breeders. Common to all these species are potential benefits for subordinates that remain in a territory, in terms of gaining access to better breeding positions and access to a limited essential habitat. There are also potential costs to a dominant of tolerating a subordinate, in terms of having their rank challenged, which together generate evolutionary conflict. We suggest that subordinate cooperation, by the regulation of growth, may help to resolve this conflict in all of these species.

**COOPERATION AMONG MALES AND FEMALES
(INDIRECT BENEFITS, DIRECT PRESENT AND
FUTURE BENEFITS, BOTH HIGH AND LOW SKEW)**

Natural History



Cooperation and cooperative breeding, in particular, have been studied in cichlids for over  years. By far the best-studied species is a small cichlid called *Neolamprologus pulcher* from the south of Lake Tanganyika (Fig. 12.4). *N. pulcher* is a sister species or subspecies of *Neolamprologus brichardi* found in the northern lake basin, and the two have a similar breeding system. *N. pulcher* lives in small groups on rocky substrates from 3 to 45 meters depth (Taborsky and Limberger, 1981; Balshine-Earn *et al.*, 1998). Social groups are clustered into colonies or sub-populations of 2 to >100 groups (Stiver *et al.*, 2007). The average distance between two social groups within a colony is 1.6 m and the average distance between two colonies is 22.3 m (Stiver *et al.*, 2007). Groups are reasonably stable but dispersal between groups and colonies, mainly by large males, has been documented (Stiver *et al.*, 2004, 2007; Bergmüller *et al.*, 2005a; Stiver *et al.*, *in review*). 



Fig. 12.4 Three *N. pulcher*, a dominant breeder and two smaller helpers from a territory in Kasakalawe Bay, Lake Tanganyika (Zambia). Photo Credit: Julie Desjardins.

Each *N. pulcher* group is composed of a single breeding pair and 0–20 smaller subordinates called helpers (Balshine *et al.*, 2001, Heg *et al.*, 2005). The group co-defends a small territory (mean area = 3,150 cm²) made up of a system of interconnected rocks and crevices that are used both for breeding and as shelter from predators (Balshine *et al.*, 2001). All individuals participate in territory defense and care and maintenance of the brood, but female breeders or subordinate helpers tend to expend more effort on these tasks than male breeders (Taborsky and Limberger, 1981; Taborsky and Granter, 1998; Balshine *et al.*, 2001; Desjardins *et al.*, 2007; Desjardins *et al.*, in review a, b).

Large males may hold the dominant breeding position in more than one group; many males in the population hold a harem of groups with each group containing its own breeding female and subordinates (Limberger, 1983; Stiver *et al.*, 2006; Desjardins *et al.*, 2007). The breeding male is always the largest individual in each group and rarely exceeds 70 mm in standard length (SL); the breeding female rarely exceeds 60 mm in SL, and subordinates generally range in size from 15–64 mm in SL. All members of the social group conform to a strict dominance hierarchy, mainly determined by body size. The fish compete for a spot in this dominance hierarchy, which reflects a queue for breeding status (Balshine-Earn *et al.*, 1998; Werner *et al.*, 2003; Heg *et al.*, 2004b).

Most of the individuals in a group are not related to each other (mean coefficient of relatedness = 0.16, Stiver *et al.*, 2005); 84% of 114 typed subordinates could be excluded as offspring of the breeding pair. However, there are some interesting patterns in the pairwise relatedness. Smaller/younger and more submissive subordinates tended to be more related to the breeding pair than are larger, older, less submissive subordinates (Dierkes *et al.*, 2005; Stiver *et al.*, 2005). Further, subordinates are typically more closely related to the breeding female ($r = 0.17 \pm 0.06$) than they are to the breeding male ($r = 0.02 \pm 0.05$, Stiver *et al.*, 2005, see reasons for this sex difference below).

Possible Forms of Cooperation

As mentioned above, *N. pulcher* subordinates help in all aspects of brood care, and such help might enhance the fitness of the breeder. Help consists of: (1) cleaning and fanning eggs and larvae, (2) defending eggs, hatched larvae and free-swimming young from predators, (3) maintaining the territory (removing snails, digging and carrying away sand and debris from the breeding shelter) and (4) defending the territory (chasing away

predators and both heterospecific and conspecific space competitors) (Taborsky and Limberger, 1981; Taborsky, 1984; Balshine *et al.*, 2001; Werner *et al.*, 2003; Stiver *et al.*, 2005). Among subordinates, the amount and type of help displayed varies with: (1) sex, (2) pairwise relatedness; and (3) social rank (Stiver *et al.*, 2005). For example: (1) female subordinates helped more than male subordinates, (2) subordinates more related to the breeding female helped more than less related subordinates; and (3) lower-ranked subordinates helped more than higher-ranked subordinates (Stiver *et al.*, 2005). But note that a stepwise regression analysis showed that sex contributes most to observed variance in helping effort (Stiver *et al.*, 2005). Finally, as first described for **anemone fishes** (see above), subordinate ***N. pulcher*** also regulate their growth potentially minimizing the costs they inflict on their immediate dominants (Heg *et al.*, 2004b).

Do Subordinates Help?

There is little doubt that ***N. pulcher*** subordinates help dominant breeders, but does such help enhance the fitness of the breeders? Laboratory experiments have shown that breeders with subordinates produced more eggs and did so more quickly than breeders without helpers (Taborsky, 1984). More recent field studies have indicated that breeders with more helpers (larger groups) had reduced workloads, fed more and had greater reproductive success (Balshine *et al.*, 2001). However, the critical experiment on this species was only recently conducted (Brouwer *et al.*, 2005), **more than** years since the non-breeders were first called helpers. Brouwer and her colleagues experimentally removed ***N. pulcher*** helpers in the field and demonstrated that, in the short-term at least (i.e., one week following removal), the survival of fry was lower in groups in which subordinates were removed compared to control groups (Fig. 12.5). This is the type of field experiment necessary to demonstrate beyond any doubt that subordinates enhance the fitness of breeders and are cooperating.

Why do Subordinates Help?

There are at least three different reasons why subordinates cooperate in ***N. pulcher***. First, as originally suggested by Taborsky and Limberger (1981), subordinates help because they are related to breeders and can gain indirect fitness benefits by enhancing the fitness of their relatives. However, the average coefficient of relatedness between breeders and helpers is much lower than originally anticipated (Taborsky and

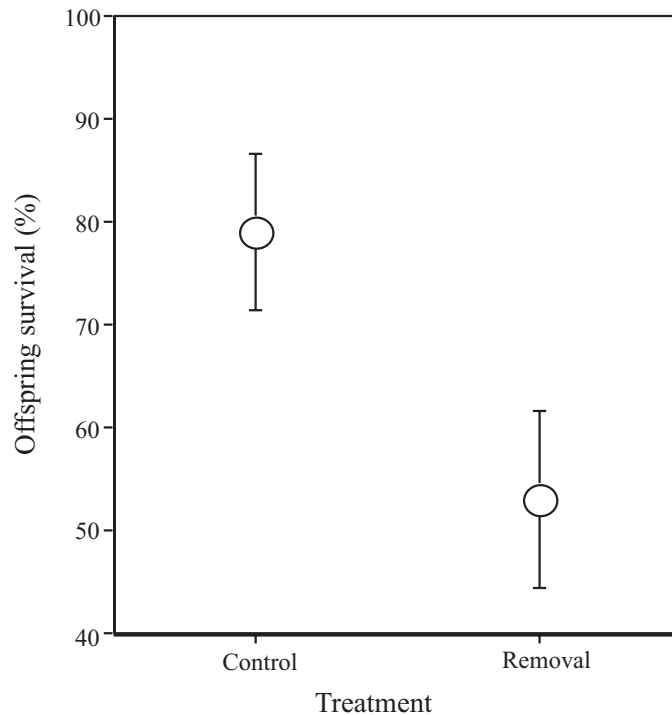


Fig. 12.5 The mean percentage survival of offspring was higher in non-manipulated control groups than in manipulated groups from which subordinates were removed (measured after 7 days from the start of the experiment, paired t test, $t=-2.66$, $p=0.026$.) Means and SE are shown. Removal and control groups were matched (8 pairs and 1 trio) in terms of number and sizes of helpers prior to the manipulation. In removal groups two helpers (one large >37 mm and one small 25-37 mm) were removed. Redrawn with permission from Lyanne Brouwer.

Limberger, 1981); while some helpers are relatives of the breeding pair, most are not (Dierkes *et al.*, 2005; Stiver *et al.*, 2005). But some support of the indirect benefits hypothesis has been found; subordinates more related to the breeding female helped by defending the territory more frequently than subordinates unrelated to the breeding female (Stiver *et al.*, 2005). In contrast, however, subordinates that were less related to the breeding male defended more (Stiver *et al.*, 2005). Given the patterns of pairwise relatedness and help described above, one might be tempted to infer that smaller/younger subordinates are accruing indirect genetic benefits from helping the breeding female. However, these small subordinates might also be the most ineffectual of helpers (having little effect on the reproductive success of breeders), calling into question the magnitude

of the indirect benefits they accrue. They take home the message is that, despite the emphasis on indirect benefits, such benefits cannot be the whole story behind helping because unrelated subordinates also help (Stiver *et al.*, 2005).

Why do unrelated individuals help? Another benefit often put forward for *N. pulcher* subordinates (especially male subordinates) is that by helping, these individuals may gain access to a spawning reproductive female and that they will attempt to sneak fertilizations from the breeding male (Taborsky, 1984; Dierkes *et al.*, 1999; Heg *et al.*, 2006b). In support of this, artificial laboratory experimental setups have suggested that subordinates might obtain a small share of reproduction (0–7%, Dierkes *et al.*, 1999; Heg *et al.*, 2006b) and helpers and breeders in one laboratory study showed no difference in excreted androgen levels (Oliveira *et al.*, 2003; Bender *et al.*, 2006, but see also Aubin-Horth *et al.*, 2007). However, in the field, breeder males have *much* higher levels of androgens circulating in the blood than subordinate males, indicating that subordinates may not be reproductively active (Aubin-Horth *et al.*, 2007; Desjardins *et al.*, a, *in review*). Furthermore, reproductive characteristics of subordinate males from the field (gamete size, sperm number, speed and swimming duration) strongly argue against the idea that male subordinates are sneaking fertilizations (Fitzpatrick *et al.*, 2006; Desjardins *et al.*, 2007; Fitzpatrick *et al.*, *in review*). Although these direct benefits, along with the indirect benefits outlined above, were proposed as an important ultimate cause of helping behaviour in the early study of cichlids (Taborsky, 1985, 1994), the evidence for these hypotheses now seems debateable.

So, why do subordinate cichlids help? An additional hypothesis, proposed by a number of researchers, is that help functions as payment or rent to breeders, for subordinates to be permitted to remain within the social group (Gaston, 1978; Balshine-Earn *et al.*, 1998; Kokko *et al.*, 2002; Bergmuller and Taborsky, 2005; Bergmuller *et al.*, 2005b; Stiver *et al.*, 2005). The critical prediction of this pay-to-stay hypothesis is that helpers who do not participate in help should be punished or evicted by breeders (Gaston, 1978; Kokko *et al.*, 2002). Despite an apparently widespread belief to the contrary, this prediction has not found support in *N. pulcher*. In both laboratory (Bergmuller and Taborsky, 2005) and the field experiments (Balshine-Earn *et al.*, 1998), helpers prevented from helping were punished (attacked) by other subordinate helpers but not by the dominant breeders. Furthermore, formalization of Gaston's (1978) ideas

by Kokko and her colleagues (2002) predict that the only thing subordinates need to do to ‘pay-to-stay’ is to avoid inflicting any costs—a prediction which has now received support in several fishes (Buston, 2004b; Buston and Cant, 2006; Wong *et al.*, in press). In support of this idea in cichlids, it seems that subordinate *N. pulcher* do regulate their growth and gonads. This constrained growth and reproductive capacity would help them to avoid conflict with their immediate same sex dominant (Heg *et al.*, 2004b; Balshine, unpubl. data, Fitzpatrick *et al.*, in review). Furthermore, field and lab experiments have shown that conflict is most intense when individuals are of similar size and of the same sex (Balshine-Earn *et al.*, 1998; Werner *et al.*, 2003; Hamilton *et al.*, 2005; Table 12.1).

If subordinate growth regulation is sufficient payment to stay and accrue the benefits of being in the territory, and helping subordinates do not gain significant indirect genetic benefits or direct genetic benefits (as a result of shared reproduction), then why on earth do subordinates help? The final hypothesis on the table is that helping in cichlids has a signalling component (Lotem *et al.*, 1998). Subordinates immigrating into new groups are observed to help intensely (Bergmuller *et al.*, 2005a; S. Balshine, pers. obs.), and a temporary removal elicited intense helping by returning subordinates (Balshine-Earn *et al.*, 1998; Bergmuller and Taborsky, 2005). Both of these results support the notion that help may have a signalling component in *N. pulcher*. Even more intriguing, are



Table 12.1 The frequency of fight outbreaks between two size-matched *N. pulcher* helpers (<5 mm size differences) was much higher when the two helpers were also sex-matched. Fights only occurred when the two helpers are matched both in size and sex. Data comes from 19 social groups in Lake Tanganyika. See Werner *et al.*, 2003, and Balshine-Earn *et al.*, 1998, for experimental details. Subordinates were either passively accepted back into the group without aggression (9/19 trials), or the returning subordinate was aggressively attacked (bitten, rammed and chased) by the other size matched control subordinate. The results strongly support the notion that there is a strong size and sex based hierarchy in *N. pulcher*. While individuals usually queue with low levels of aggression, when the hierarchy is perturbed they will fight to move up the dominance hierarchy (see also Box 12.2). These data have not been published elsewhere.

Removal type	Fighting	No fighting
Opposite sex (n=7)	0	7
Same sex (n=12)	10	2

data emerging from studies of territory inheritance. Despite earlier reports to the contrary (see Taborsky and Limberger, 1981; Taborsky, 1984), subordinates have been shown to inherit the territory in which they were helping (Balshine-Earn *et al.*, 1998; Stiver *et al.*, 2006; Fitzpatrick *et al.*, in review), paralleling the patterns of territory inheritance observed in other cooperative fishes (Fricke, 1979; Buston 2004a; Mitchell, 2005; Mitchell and Dill, 2005; Wong *et al.*, in press). See breeder removal experiments have been conducted on *N. pulcher* and these reveal not only that both sexes stand to inherit but also that females are much more likely to inherit than are males (Stiver *et al.*, 2006). When the results of the three experiments are analysed together, an interesting result emerges: it appears that the probability of inheritance by females is influenced both by her rank (the largest subordinate female commonly inherits) and by how much help she was performing prior to the creation of a breeding vacancy. If the largest subordinate female wasn't particularly helpful she doesn't inherit (Fig. 12.6, Balshine-Earn *et al.*, 1998; Stiver *et al.*, 2006; Fitzpatrick *et al.*, in review). This pattern is not observed among the male inheritors (Fig. 12.6). These observations suggest that help has a signalling component and subordinates—at least female subordinates—may obtain future direct genetic benefits as a product of their help because it enhances their probability of territory inheritance. It is now a serious and tantalizing possibility that helping serves multiple signalling functions, and this will be something for future research to unravel.

Questions for Future Study

The history of studies of cooperation in cichlids is an interesting one (from Taborsky and Limberger, 1981), which runs in parallel to the history of studies of cooperation in anemone fishes (Fricke, 1979). At first, it seemed that the potential for kin selection would be the big difference between the systems and that this would explain why subordinate cichlids helped but subordinate anemone fishes not (Fricke, 1979; Taborsky and Limberger, 1981). However, while kin selection has been shown to be non-existent in the anemone fishes expected (Buston *et al.*, in review), its role does not explain all cooperation observed in cichlids (Stiver *et al.*, 2005). Now it seems that help—rather than the potential for kin selection—is the big difference between these breeding systems, and we have yet to arrive at a clear understanding of why subordinate cichlids help. Currently, the most compelling hypotheses for why subordinate cichlids help are related to signalling.

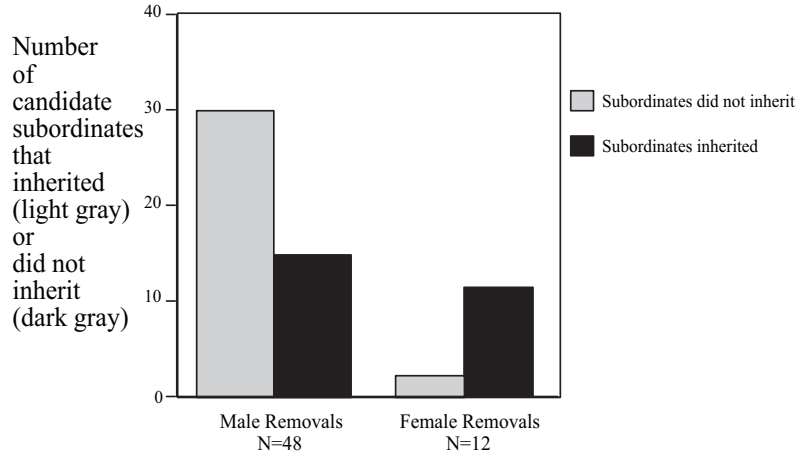


Fig. 12.6a Subordinate female group members are much more likely to inherit a breeding vacancy (10/12 cases, $X^2=9.5$, $p<0.01$) than are subordinate male group members (15/45 cases), i.e. subordinate male group members are more likely to have their inheritance usurped by a male from outside of the group. Results are based on combining data from three separate studies where breeding vacancies were experimentally created by removing one breeder and observing the behaviour of sex-matched candidate helpers. Candidate inheritors are large breeder-sized subordinate group members (see Balshine-Earn *et al.*, 1998; Stiver *et al.*, 2006 and Fitzpatrick *et al.*, in review tails).

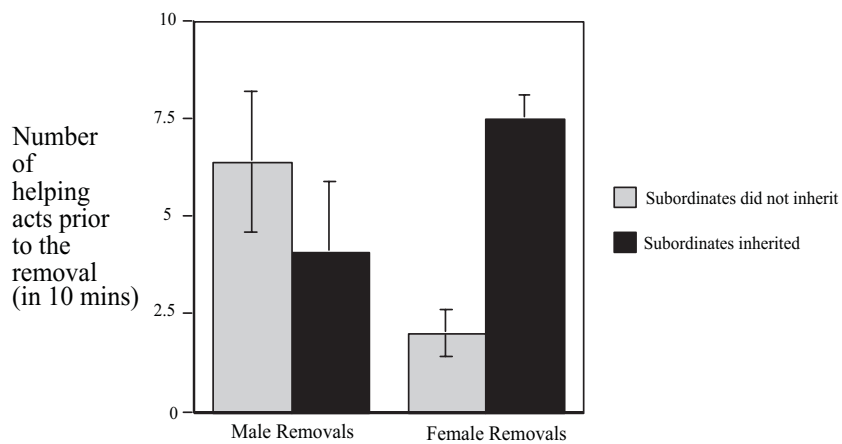


Fig. 12.6b Female subordinates that inherited performed more help before the breeder removal than female subordinates that did not inherit. No such pattern was found among male subordinates. These results are based on combining data collected in three different breeder removal experiments, see Balshine-Earn *et al.*, 1998; Stiver *et al.*, 2006 and Fitzpatrick *et al.*, in review).

Cooperative breeding, where individuals assist other individuals in breeding and territory defence is being discovered in a growing number of cichlid fish species from Lake Tanganyika (Taborsky, 1994; Heg and Bachar, 2006). In addition to *Neolamprologus pulcher/brichardi*, cooperation has been suggested to occur in a total of 18 other cichlid species (Heg and Bachar, 2006), all from Lake Tanganyika's subfamily/tribe Lamprologini. There are a wide variety of cooperative systems within this tribe. There are systems where the breeding is pluralistic (low skew) and many individuals within the group are co-breeding, as well as systems with despotic breeding (high skew), in which only a breeding pair reproduces and non-breeders assist in the raising of young.

N. pulcher and its close relatives present wonderful opportunities for the study of helpful cooperation in fishes (Yamagashi and Kohda, 1996; Heg *et al.*, 2006b). Below we outline the first reported findings of other cooperating cichlids. In those species and others in the tribe, the critical experiments evaluating whether subordinates are providing assistance that increases the fitness of dominant breeders remain to be done.

The smallest cichlid in the world, *Neolamprologus multifasciatus* lives in permanent social groups made up of close relatives (Kohler, 1997; siblings or offspring of the breeders, Schradin and Lamprecht, 2000, 2002). In this species, several co-breeding males and females plus their subordinates will vigorously co-defend the territory (a gastropod shell bed at depths of 9–11 m) against conspecifics (Schradin and Lamprecht, 2000). In contrast to *N. pulcher*, female-biased dispersal has been observed; 9/15 females immigrated but only 2/15 males immigrated, and often individuals move to territories with more empty shells (Schradin and Lamprecht, 2000, 2002). The ecological and evolutionary causes for the difference in the degree of kinship between *N. pulcher* and *N. multifasciatus* require investigation.

Another reasonably studied cooperating cichlid species is *Julidochromis ornatus* in which 39% of breeders are accompanied by smaller male and female subordinates (mean number of subordinates = 1.5, range 1–6, Awata *et al.*, 2005; Heg and Bachar, 2006). Male subordinates are more common than females (Awata *et al.*, 2005). These groups of *J. ornatus* appear to be more transient in terms of group composition than *N. pulcher*. Researchers report that subordinates remained closer to the breeding shelter (a large flat rock), than breeders, but perform few defence or territory maintenance activities (Awata *et al.*, 2005; Heg and Bachar, 2006). Awata *et al.* (2005) used 4 polymorphic loci to show that helpers were unrelated and that they frequently sire young (44%, low skew).

Group size was positively related to male size but not female size and, in contrast to *N. pulcher*, group size had no influence on reproductive success (Heg and Bachar, 2006).

FISH COOPERATION: THE NEXT FRONTIER

People often forget that about 71% of the Earth is covered by water (salt 97% and freshwater 3%); the diverse aquatic ecosystems on our planet contain thousands of fish species, many of which have evolved an incredible variety of social behaviours, including cooperative behaviours. We began this chapter by arguing that, despite the 40 plus years focus on cooperation in behavioural ecology, cooperation among fish has only rarely been experimentally documented and the prevalence of cooperation behaviour in fishes is likely to have been vastly underestimated. The dearth of examples of fish cooperation undoubtedly stems from the difficulties of aquatic research compared to terrestrial research and because cooperation in fishes often takes a different form from that typically studied (allocare in the form of provisioning of young) in other vertebrates. In birds and mammals, the defining characteristics of a cooperative breeding system are delayed dispersal and allocare. Here we highlight what fish might contribute to the study and development of our understanding of cooperation. We also suggest a number of useful next steps for the study of fish cooperation and elaborate on why a multidisciplinary approach is likely to be especially fruitful.

Lessons from Fish

Despite the dearth of well-studied examples of fish cooperation, the few available fish studies turn up some interesting insights that could be more broadly applied including:

1. Cooperation can have many forms.
2. Delayed dispersal from the natal territory and kinship are not required for cooperation.
3. Restricted dispersal from the current territory is associated with cooperation.

Cooperation can have Many Forms

In fishes, cooperation can take many forms: mutual defence of a breeding area or food resources (Gross and MacMillan, 1981; Clifton, 1989), joint predator inspection (Milinski, 1987), joint food finding (Clifton, 1989),

strategic growth/peaceful cooperation (Buston, 2003a) and allocare (Taborsky and Limberger, 1981; Neff and Gross, 2001). Clearly, allocare is not the only form of cooperation that deserves study in fishes. The focus on allocare—imported from mammal and bird studies—may have meant that other interesting forms of cooperation may have been overlooked in fishes. Considering fish cooperative systems alongside other vertebrates will result in the recognition of a more diverse array of cooperative behaviours across taxa and lead to a broader and fuller understanding of cooperation.

Delayed Dispersal from Natal Territory and Kinship are not Necessary Prerequisites for Cooperation

In the past, cooperation, especially cooperative breeding, has been linked to delayed dispersal and the formation of kin groups (Griffin and West, 2003). From the few studies in which cooperation has been demonstrated in fishes (see above), we conclude that neither of these factors is associated with the evolution of cooperation in fishes. Cooperation occurs among unrelated individuals (Neff and Gross, 2001; Awata *et al.*, 2005; Dierkes *et al.*, 2005; Stiver *et al.*, 2005; Buston *et al.*, *in review*) among individuals that disperse in the first few days of their lives (Clifton, 1989; Buston, 2003b; Wong *et al.*, *in review*) when that most fish disperse very early in life, and likely do not form kin aggregations, it seems unlikely that this conclusion will change. The lack of kin groups removes one key incentive for individuals to cooperate, but clearly does not obviate selection favoring the evolution of cooperation.

Restricted Dispersal from Current Territory is Associated with Cooperation

Delayed dispersal from the natal territory does not seem to play a major role in the evolution of cooperation in fishes. However, restricted dispersal does seem to play a major role in all of the case studies in this chapter. By restricted dispersal we mean that movement is costly once an individual has settled, because of either the high likelihood of being eaten when moving among territories or the lack of suitable breeding territories available (Buston, 2003b; Heg *et al.*, 2004b). Restricted dispersal is a more general concept than delayed dispersal, and this concept may be exportable to the general literature on cooperative breeding.

FUTURE RESEARCH ON FISH COOPERATION

To date, the majority of the research on cooperation among vertebrates has focussed on its functional consequences rather than on the physiological or genetic mechanisms underlying this behaviour. We argue that significant future progress will be made by combining classical behavioural and ecological studies (with a strong experimental emphasis on the critical experiments) with studies of the neurobiology and genetic architecture modulating cooperative behaviour. Nobel prize-winner Niko Tinbergen, a pioneer in the study of animal behaviour, argued that to understand behaviour one must marry research on the causation of behaviour, with work on its development, its survival value and its evolution (1963). The proximate and ultimate approaches complement each other and investigation of both in tandem will enhance our abilities to understand cooperative behaviour. In general, these are exciting times for researchers interested in fish cooperative behaviour as there are many state-of-the-art techniques and results from other disciplines to glean. In particular, we wish to highlight two major research areas, currently making use of fish models on a large scale, that we believe will make valuable contributions to the study of fish cooperation namely genetics and neuroscience.

Cooperation in the Era of Sociogenomics

The advent of molecular genetic techniques allowing for identification of offspring and relatives has revolutionized our understanding of cooperative breeding and social organization in other taxa. To date, there have been only five species for which microsatellite data has been used to quantify the degree of relatedness among fish cooperators (*N. multifasciatus* Kohler 1997; Dierkes *et al.*, 2005; *N. pulcher* Stiver *et al.*, 2005; *J. ornatus* Awata *et al.*, 2005; *A. percula* Buston *et al.*, *in review*; *Lepomis macrochirus* Neff and Gross, 2001). Clearly, it will be necessary to conduct more studies before robust patterns of relatedness within social groups or dyads can be uncovered, and thoroughly compared to birds and mammals. However, the limited available sample suggests that cooperative groups of fish are much less likely to be kin based. Importantly, the use of microsatellite data to assign parentage will also make it possible to quantify the degree of reproductive partitioning or skew among individuals, across social groups, populations and species. We envision that, in the coming years, microsatellite analyses will be commonly



employed with cooperative fish species to study the degree of relatedness and its relation to helping effort (see Stiver *et al.*, 2005), dispersal (Knight and Turner, 1999; Taylor *et al.*, 2003; Stiver *et al.*, 2004; in press) and reproductive skew (Neff, 2001; Heg *et al.*, 2006b; Fitzpatrick *et al.*, in review).

In the last few years, large-scale projects to sequence entire genomes have moved away from the traditional model organisms such as *Drosophila melanogaster* and *Mus musculus* to include several fish species such as the puffer fishes (*Takifugu rubripes* and *Tetraodon nigroviridis*) (Aparicio *et al.*, 2002). Other fish species such as the stickleback, *Gasterosteus aculeatus*, the zebrafish *Danio rerio*, salmon and some cichlids are scheduled to have their sequences completed in the near future. In particular, the zebrafish has become the model of choice for many development and neurobiology studies, with literally hundreds of researchers now working with this model fish organism. All of this bodes well for fish researchers interested in cooperation. These fish genome projects are already providing information and comparative data on gene function and this type of analysis could lead to key insights of social behaviour and cooperation. For example, using a brain microarray with 8000 candidate genes, Aubin-Horth and colleagues have shown that particular genes related to social behaviour appear to be upregulated in the brains of dominant *N. pulcher* breeders compared to subordinate helpers (Aubin-Horth *et al.*, 2007). The first needed step is clearly to describe the patterns in genes that are likely to be involved in cooperative behaviours, such as help and strategic growth. Eventually, techniques like genetic knockouts or gene knockins, specific to one or several genes important in social behaviour, will be developed for cooperative breeders so that particular targeted individuals do not express social and cooperative behaviours to the same extent as normal controls. We will then be able to examine experimentally the effect of the absence of cooperation on donors and recipients. By combining classical behavioural studies with new molecular studies, we will gain a much more solid scientific foundation for understanding the molecular and genetic mechanisms underlying cooperative behaviours such as allocare and strategic growth.

Cooperation in the Era of Neuroscience

Along with the genetic revolution, another scientific revolution has occurred in the area of brain or neurosciences. Just as with the genetic architecture, the underlying neural-physiological mechanisms impacting

variation in cooperation and social conflict also remain largely unexplored. Astrid Grantner performed some of the first physiological studies with a cooperatively breeding fish. Using a Perspex flow-through respirometer chamber, Grantner and Taborsky showed that in *N. pulcher* helping increased an individual's metabolic energy expenditure by four times when an individual performed defensive aggression and by six times when the individual performed territory maintenance activities (Grantner and Taborsky, 1998; Taborsky and Grantner, 1998). These studies not only suggest that help is costly, but also that these costs are substantial, supporting the idea that help may indeed be an honest signal. Further, Buchner *et al.* (2004) has shown that dominant *N. pulcher* grow faster and have higher levels of liver protein and plasma cortisol than subordinates. Dominant breeders show higher levels of gene expression for the neuropeptide, arginine vasotocin, a homologue to arginine vasopressin, a peptide known to influence social behaviour (Santagelo and Bass, 2006, Aubin-Horth *et al.*, 2007). Variation in hormone and neuropeptide profile, energy stores and energetic expenditure, now need to be linked to long-term fitness consequences.


The growth in neuroscience has generated a watershed of techniques including immunocytochemistry, *In situ* hybridization, electroencephalography, electrocardiogram, intra- and extracellular electrophysiological recordings, electromyogram, biotelemetry, and neuro-imaging of the neurochemical circuits of the brain (Sloman *et al.*, 2006). All of these state-of-the-art techniques can be borrowed from neuroscience and may shed light on how the brain changes during complex social behaviour such as allocare and strategic growth or to perturbations to the social context. Findings based on zebrafish may lead to important information crossover and exchange for fish behavioural ecologists interested in examining cooperation. Genetic and brain imaging techniques have the potential of providing a more comprehensive understanding of the evolution of cooperation as well as likely shedding light on the role that cooperative actions play in sculpting group dynamics and social behaviour in general.

Until recently, fish cognitive abilities were rarely studied but recent studies on fish learning and memory are revealing that fish are capable of complex cognitive capacities (reviewed in Odling-Smee and Braithwaite, 2003; Laland *et al.*, 2003; Braithwaite, 2006; Grosenick *et al.*, 2007; see also Chapter 2 'Cognition: Learning and Memory' by Braithwaite and Salvanes, this book). For example, many fish species are capable of recognizing and remembering individual conspecifics and can assign and infer competitive abilities of these individuals (Metcalf and Thomson,

1995; Balshine-Earn and Lotem, 1998; Oliveria *et al.*, 1998; Griffiths and Ward, 2006; Grosenick *et al.*, 2007). Indeed, if cooperation evolves as a result of reciprocation, fish require the ability to assess cues of reciprocation probability or the chances of receiving help in the future. They would also require the ability to track such cues or information in a large number of conspecifics. Similarly, for an individual to accrue indirect genetic benefits, it must be able to distinguish kin from non-kin. It would seem that cognitive machinery required for kin selection may be less complicated than that required for reciprocity, as a learning rule, to distinguishing kin from non-kin is likely to be simple and to apply to large numbers of individuals. Clearly, some species of fish have evolved the ability to recognize kin and cheaters (in the context of parental investment in bluegills: Neff, 2001, 2003; Neff and Sherman, 2003, 2005, in the context of predator inspection in sticklebacks and guppies: Milinski, 1987; Dugatkin, 1988; in the context of egg trading in black hamletfish, Fischer and Pattersen, 1987). In cleaner fishes (wrasses and blennies), it has been argued that a system of punishment and reputation stabilizes cooperation between cleaners and their clients (Bshary and Grutter, 2002a, b; Freckleton and Côté, 2003; Grutter, 2004; Bshary and Grutter, 2005; see also Chapter 16 'New Perspectives on Marine Cleaning Mutualism' by Bshary and Côté, this book). The growing interest in fish cognitive abilities is likely to provide useful insights and tools for further study of the evolution of cooperative behaviour. In summary, the functional and proximate approaches to the study of cooperation complement each other as natural selection operates at the level of the individual and the level of the cellular machinery; investigation of both in tandem will enhance our abilities to understand the cooperative behaviour.

Conclusions

Fishes are known to display some of the most complex reproductive and social strategies and tactics known among the vertebrates (Warner, 1984; Godin, 1997; Barlow, 2000; Munday *et al.*, 2006). In this chapter we have focused on cooperative strategies, which vary from simple mutual defence to helpful cooperation with the rearing of others' offspring. We have examined the three ways in which individuals can accrue benefits leading to the evolution of cooperation, and provided a review of the empirical support for each source of benefits in fishes. Based on the small number of available studies, it appears that cooperative behaviour founded on indirect genetic benefits is relatively rare in fishes but that cooperative

behaviour founded on direct benefits accrued in the present or in the future is relatively common. Cooperation can be found in both low skew and high skew groups, with high skew tending to occur when there is restricted dispersal and individuals stand to gain direct benefits in the future. Barring a few well-studied examples in cichlids and anemone fishes, few of the critical experiments needed to clearly demonstrate cooperation have been conducted. A mere association between two or more individuals is not sufficient to warrant the cooperation label and the term cooperation needs to be used more consistently and rigorously in fish studies: cooperation is an interaction between individuals that enhances the fitness of all individuals involved while cooperative behaviour is an act performed by one individual that enhances the fitness of another. Along with the critical experiments, long-term studies on marked individuals needs to be done to examine the long-term benefits of cooperative interactions. Finally, we emphasize the need for further multidisciplinary research that links ultimate causation and the underlying proximate mechanisms. We hope our review will encourage researchers to embark on a rigorous course and conduct the essential experiments that address the critical question(s)  demonstrate that individuals indeed cooperate.

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