



Alloparental care in fishes

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Abstract

Alloparental care, care directed at non-descendant young, presents a potential challenge to evolutionary ecologists because investment in non-descendant eggs and young gives the appearance of maladaptive behaviour. Yet wherever there is parental care in fishes, there is usually alloparental care. As such, alloparental care is an integral part of care in fishes. Alloparental care appears to have arisen independently many times in disparate taxa. The chief reason for this is the low cost of care, relative to homeotherms, both in terms of low post-zygotic investment to nourish young, and low risk of predation to the parent during brood defence. In some cases, alloparenting is misdirected parental care and maladaptive. A celebrated example of brood parasitism in fish is that of the catfish *Synodontis multipunctatus*, which parasitizes broods of mouthbrooding cichlids. Previously

unpublished data on the reproductive biology of *S. multipunctatus* are reported here. However, in the majority of cases, particularly for the widespread phenomena of zygote dumping (nest associates) in the Cyprinidae and adoption of non-descendant free-swimming young in brood-guarding Cichlidae, alloparental care is a mutualistic relationship maintained by natural selection. This review describes broad patterns of known examples of alloparental care, the pathways to adoption, and highlights the ways in which alloparents derive fitness benefits. By caring for non-descendant young, an alloparent may benefit by one or more of the following phenomena: acquisition of mates, confusion effect, dilution effect, selfish herd effect, selfish shepherd effect, kin selection, and reciprocal altruism. Although the breadth and diversity of examples of alloparental care in fishes is growing, to date, these accounts have been largely descriptive. Future research should be directed at careful documentation of the fitness consequences for both donor and alloparent. These are the data that are needed to fully understand the evolutionary underpinnings of alloparental care, and by extension, parental care.

Key words: adoption, alloparental care, brood parasitism, fish, mutualism

Introduction

Parental care has been defined a number of ways in the literature, each reflecting the particular biases of the author or aspect of care being considered (review: Crawford and Balon, 1996). In his seminal paper, Trivers (1972) considered parental care in his definition of parental investment, defined as "...any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". Two things are implied by this definition: first, that there is a fitness cost of parental care to the individual providing the care (review: Smith and Wootton, 1995), and second, that there is a concomitant fitness benefit to the care giver by increasing the probability that its offspring survive to reproduce. The widespread occurrence of parental care, in various forms, throughout the animal kingdom is testimony to the fact that in many situations, the fitness benefits accrued to individuals that perform parental care outweigh the fitness costs (Clutton-Brock, 1991).

Alloparental care is care directed at non-descendant young and as such would appear to be potentially maladaptive. Alloparental care incurs the costs of conventional care without necessarily providing a fitness benefit. In some cases, alloparental care is indeed the outcome of a parasitic act by conspecifics or heterospecifics. Often, however, alloparents reap fitness benefits from providing care to unrelated offspring so that the alloparental relationship is mutualistic rather than parasitic.

In this review, I first survey known examples of the types of alloparental care in fishes observed in nature. This review is organized according to successive stages of brood development at which alloparental care is directed: first care of eggs, then care of free-swimming young. Next, I consider evolutionary conditions that favour the origin and maintenance of alloparental care in fishes. I will conclude with a description of gaps in current knowledge and directions for future research. But first, I will clarify my usage of terms that may appear in other publications with slightly different emphases and interpretations.

Terminology

For the purposes of this review, I define alloparental care as *any parental care directed at non-descendant young*. My use of the phrase *non-descendant young* allows for the inclusion of conspecific and heterospecific young, and helping behaviour of older siblings at the parents' nest. The degree of relatedness (r) between the alloparent and non-descendant young is often assumed to be ≈ 0 , but may not be. Thus, the term *non-descendant* is preferable to *non-related*. I include in this definition three of the four classes of energy expenditure from a parent to offspring considered in Crawford and Balon (1996, p. 78). Investment in gametes (type I) is not included in this definition. Crawford and Balon (1996) take a broad view of parental *investment* but I wish to restrict parental *care*, and hence alloparental *care*, to behavioural considerations. The trade-off of the number

of eggs versus the size of individual eggs is interdependent with the nature and degree of parental care, which in turn influences the capacity and propensity for alloparental care (Sargent et al., 1987; Nussbaum and Shultz, 1989; Wootton, 1992) but is beyond the scope of this review. My definition of alloparental care includes the remaining three types of parental investment described in Crawford and Balon (1996): pre-zygotic investment in nest construction and territory defence (type II), post-zygotic investment in the form of direct food provisioning (type III), and tending, feeding and defending the young (type IV). This definition of parental care is consistent with those of Blumer (1979) and Sargent et al. (1987) but broader than that of Baylis (1981), who excluded pre-zygotic investment. This definition is also broader than the one used by Taborsky (1994), who excludes strictly parasitic relationships (fertilization stealing and egg dumping – his terms for zygote dumping) and joint brood care as alloparental care.

Scientific nomenclature in fishes, particularly in the Cichlidae, has been in a state of flux in recent years. In an attempt both to adopt recent advances in the knowledge of phylogenetic relationships, and to retain some connection to familiar names of the (recent) past, in the text I use the outdated but familiar names used in the source papers, but give the currently accepted names in the Appendix. I followed Eschmeyer et al. (1998) as the authority for scientific names.

Alloparental care of eggs

There are five main mechanisms by which care-giving fish come to provide care for non-descendant eggs: sperm dumping (kleptogamy or stolen fertilizations), egg dumping, zygote dumping, nest take-overs, and zygote stealing. I will cover these mechanisms in order of the degree of active participation on the part of the caregiver.

Sperm dumping

A number of fish species exhibit alternative tactics for achieving the ultimate goal of maximizing the number of fertilized zygotes. The most common form is through sneak fertilizations, whereby a male waits until a female is engaged in a spawning act with another male and at the moment of gamete release, rushes within close proximity of the spawning pair and

releases sperm. Sperm from the two males (or more) then compete to fertilize eggs. Males are known to act as simultaneous reproductive parasites in at least 159 species in 25 families (Taborsky, 1994, and references therein). In broadcast spawners with no investment in territorial defence or nest construction, stolen fertilizations do no result in alloparental care. In species with pre-spawning investment, usurper males parasitize the time and effort of territorial males that defend a territory, construct a spawning site (nest), and successfully court receptive females. In species with post-spawning care of the eggs and/or free-swimming young, usurper males further parasitize the parental care of cuckolded males. Reproductive success of the parasitic strategy can match or surpass the fitness benefits accrued by territorial males.

Egg dumping

I know of only one example of sneaky egg dumping in fishes, that by the weakly electric fish *Eigenmannia virescens* (Gymnotidae; Hagedorn and Heiligenberg, 1985). In this species, a single female establishes a territory in a dense clump of floating vegetation and defends it against other females. After lengthy courtship with a male involving both electric and acoustic communication, the female and male alternate releasing gametes into the vegetation. While the territorial female is spawning, neighbouring females sneak into the plant thicket and release eggs, sometimes turning off their electrical organ as they do so, presumably to reduce the probability of detection by the territorial female. No post-zygotic parental care of the eggs or young has been reported for this species (Hagedorn and Heiligenberg, 1985).

Many of the cichlid fishes in Africa exhibit maternal mouthbrooding of the eggs (Keenleyside, 1991). Males are typically polygynous (Ribbink, 1990). Males establish a territory, often with the construction of elaborate spawning structures (McKaye, 1991) that they defend against other males and use as a platform for attracting females. Receptive females release eggs on the spawning surface, typically a flat rock or a bowl-shaped sand bower, and pick them immediately. This system would appear to be a prime candidate for intraspecific parasitic egg dumping, such as occurs in birds (Yom-Tov, 1980; Eadie, 1991) and insects (e.g. Tallamy, 1985). Female fecundity is limited by the volume of the buccal cavity, where the relatively large eggs and newly hatched young are incubated (Yanagisawa et al., 1996). During

this time, females generally do not feed, although exceptions to this rule are known (Yanagisawa and Sato, 1990; Yanagisawa and Ochi, 1991; Yanagisawa et al., 1996). In light of the propensity of fishes to evolve mechanisms of alloparental care, the absence of egg dumping in mouthbrooding cichlids is surprising.

Zygote dumping

Mouthbrooding cichlids have been exploited by an egg dumper, but ironically not by a mouthbrooding cichlid species, but rather catfish endemic to Lake Tanganyika in the genus *Synodontis* (Mochokidae), *S. multipunctatus* (Sato, 1986) and *S. petricola* 'dwarf' (Gordon, 1994). *S. multipunctatus* intrudes upon and spawns simultaneously with any one of a number of host mouthbrooding cichlids. The catfish eggs are smaller than cichlid eggs, hatch first and eat the cichlid young while still in the female cichlid's mouth (Sato, 1986; pers. obs.). This is an understudied system! The proximate cues used by the catfish appear to be common to many mouthbrooding cichlids. Even though *S. multipunctatus* is endemic to Lake Tanganyika, Africa, in aquaria this species successfully parasitizes cichlids from any of the African rift valley lakes, i.e. Tanganyika, Malawi and Victoria, as well as *Geophagus steindachneri*, one of the few mouthbrooding cichlids from South America (Loiselle, 1998).

Data collected on the reproductive activity of a male and the socially dominant of two females held in a large cichlid aquarium (125 × 45 × 60 cm) over 18 months reveal that *S. multipunctatus* is a fractional spawner, able to ovulate and release eggs over several days (P. Belanger, unpublished data). The subordinate female *S. multipunctatus* never spawned during this time. Cichlid spawns occurred at median intervals of about 3 days (25, 75 percentiles = 1, 6 days, $n = 133$), of which 65 or 48.9% were successfully parasitized by the breeding pair of *S. multipunctatus*, at a median interspawning interval of 5 days (25, 75 percentiles = 1, 11.5 days, $n = 65$, Figure 1). *S. multipunctatus* successfully parasitized two or more broods within the same day on nine occasions. The median number of *S. multipunctatus* young produced per cichlid brood was 6.6 young (25, 75 percentiles = 5, 10 young, range = 1 to 21, $n = 65$), and was not related to interspawning interval (Spearman rank correlation $r_s = 0.20$, $p > 0.05$, Figure 2). The highest number of *S. multipunctatus* young per cichlid brood occurred for the species *Haplochromis 'piebald'* with a median of 14 young (25, 75 percentiles = 6.5, 17 young) in 10

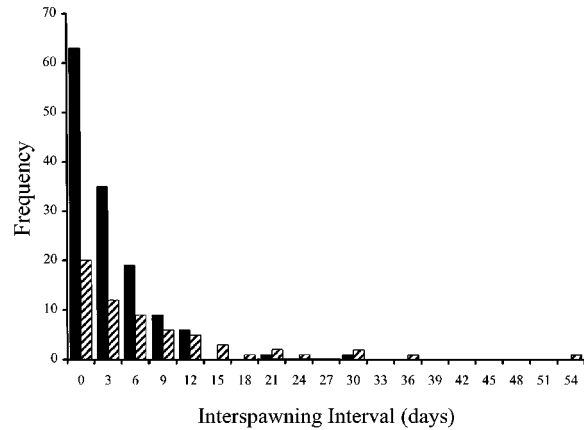


Figure 1. Frequency of spawns with interspawning intervals ranging from zero (more than one spawn in a given day) for a multispecies group of mouthbrooding cichlids from Lakes Victoria and Malawi (solid bars, $n = 133$) and a single breeding pair of *Synodontis multipunctatus* (Mochokidae) (hatched bars, $n = 65$). Only successful parasitisms by *S. multipunctatus* were recorded as spawns for that species.

of 24 cichlid spawns. *Iodotropheus sprengerae* broods contained a median of 6 young *S. multipunctatus* (25, 75 percentiles = 4, 11.5 young) in 3 of 6 cichlid spawns before the switch to an inclined spawning surface. *H. obliquidens* broods contained a median of 6.3 catfish young (25, 75 percentiles = 5, 9.5) in 52 of 103 cichlid spawns. The number of catfish young in *H. 'piebald'* broods was significantly higher than in *H. obliquidens* broods (Wilcoxon–Mann–Whitney test, $z = 2.17$, $p = 0.03$). Successful parasitism of *I. Sprengerae* ceased after that species switched from spawning on a horizontal rock surface to an inclined surface. Although the cichlid hosts in this data set are all endemic to East African rift valley lakes, none are sympatric with *S. multipunctatus*. The two *Haplochromis* species come from Lake Victoria and *I. sprengerae* comes from Lake Malawi. Yet, the number of catfish young per cichlid brood is comparable to data reported for six Lake Tanganyikan cichlids in the field, ranging from 1 to 16 *S. multipunctatus* young per parasitized brood (Sato, 1986). Only 6.3% of the Tanganyikan cichlid hosts reported in Sato (1986) were parasitized, compared with 48.9% in this data set. The enclosed aquarium space may have favoured the *S. multipunctatus*, or Tanganyikan cichlids may have evolved strategies to reduce the incidence of brood parasitism. The possibility of an adjustment of reproductive behaviour to reduce brood parasitism in a Lake Victoria cichlid in this data set is especially intriguing.

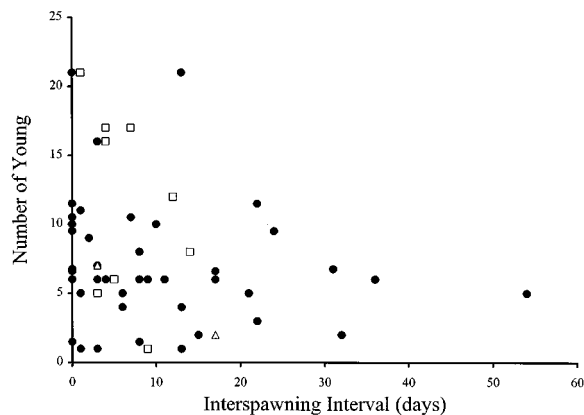


Figure 2. Number of young *Synodontis multipunctatus* (Mochokidae), relative to interspawning interval of the catfish, recovered from the buccal cavities of three species of maternal mouthbrooding cichlids, approximately 10 days (ranged from 7 to 14) after spawning. Cichlid hosts: *Haplochromis obliquidens*, solid circles; *Iodotropheus sprengerae*, open squares; *Haplochromis 'piebald'*, open triangles.

Nest associations occur in a number of fish species, especially North American cyprinids among which at least 35 species deposit their zygotes into the open nests of other species of cyprinids or centrarchids (Johnston, 1991, 1994a, 1994b; Johnston and Page, 1992; Katula and Page, 1998). This is another understudied system and appears in many cases to be a mutualistic relationship between the host and associate species (for exceptions see Baba et al., 1990; Fletcher, 1993). Nest associations have evolved independently many times in minnows (see Figure 7 in Johnston and Page, 1992, for phylogeny of breeding strategies of North American cyprinids) and are likely an evolutionary elaboration of the ancestral widespread pattern of broadcast spawning (Johnston and Page, 1992). Examples of heterospecific nest associates in non-cyprinids are relatively uncommon (Carr, 1942; Shoemaker, 1947; Woynarovich and Entz, 1949; Pflieger, 1966; Goff, 1984; Baba et al., 1990; Page and Johnston, 1990).

Sixty-eight (71.6%) of the 95 cyprinid species listed in Johnston and Page (1992) are described as broadcast or crevice spawners (no preparation of the substrate) and it is among these where most of the nest-associating species are found. About 41% of these species form spawning associations with other species, either with nest-building minnow species (31 or 77.5% of 40 associations) or nest building and brood guarding centrarchids (9 or 22.5% of 40 associations) (Johnston and Page, 1992). There is a recent

report of golden shiners (*Notemigonus crysoleucas*, Cyprinidae), spawning over nests guarded by male bowfin (*Amia calva*, Amiidae; Katula and Page, 1998). Minnows that construct nests for spawning activity can also act as nest associates at the nests of other species (5, or 18.5%, of the 27 nest-building species listed in Johnston and Page, 1992), and do so in about the same proportion as non-nest builders: 14 or 93% of 15 associations with cyprinid hosts, 1 or 7% of associations with centrarchid hosts (Johnston and Page, 1992). Cyprinids that form nest associations with other species tend to specialize on either cyprinid hosts or centrarchid hosts. Of the 33 nest associates listed in Johnston and Page (1992), only two species (6%) associate with both a cyprinid and a centrarchid host, and one species with a centrarchid and amiid hosts (Katula and Page, 1998). *Nocomis* (Cyprinidae) nests can host up to five (Cooper, 1980) or six (Johnston and Page, 1992) nest associate species simultaneously, while centrarchid nests typically host a single associate species (Johnston and Page, 1992).

Nest associates are attracted to the care-giving heterospecific and not to the physical characteristics of the nest structure *per se* (Reighard, 1943; Hunter and Hasler, 1965; Johnston, 1994b). Artificial nest sites, or nest sites from which the guardian host was absent or had been removed, fail to attract next associates (Hunter and Hasler, 1965; Johnston, 1994b; Shao, 1997a). Movement of a sunfish model, or even a metre stick, was sufficient to attract spawning aggregations of redbfin shiners (*Lythrurus umbratilis*, Cyprinidae) to the vicinity (Hunter and Hasler, 1965), but chemical cues associated with gamete release (milt or ovarian fluids) of the host, green sunfish (*Lepomis cyanellus*, Centrarchidae) were required to induce territorial behaviour in male minnows and spawning (Hunter and Hasler, 1965). Spawning aggregations of redbfin shiners were induced to form over a muck substratum in the absence of either a nest structure or a guardian male sunfish (Hunter and Hasler, 1965). A fascinating hypothesis for the proximate mechanism for the evolutionary origin of nest associations in cyprinids is group spawning behaviour, whereby the presence of (and chemical cues from) spawning minnows attracts other conspecifics to the area. Minnows that spawn in the nests of other species may have evolved to use sex pheromones of other species (minnows, centrarchids, etc.) as the trigger for their own gamete maturation (Hunter and Hasler, 1965; Sørensen and Scott, 1994). Nest-building minnow species that facultatively spawn

in the nests of other minnows are consistent with this hypothesis.

Nest associates may spawn in virtually 100% of their host's nests (Wallin, 1989; Vives, 1990) and all nests of *Nocomis* sp. serve as spawning substrates for other cyprinid species (Vives, 1990). Golden shiners associated with 4% to 94% of active largemouth bass (*Micropterus salmoides*, Centrarchidae) nests and represented 0.6% to 78.4% of all eggs present in those nests (Kramer and Smith, 1960). Redfin shiners associated with up to 93% of green sunfish nests in a study by Hunter and Hasler (1965). Many minnows are obligate nest associates and reproductive success is tied to that of their host; others use heterospecific nest facultatively or opportunistically (Raney, 1940; Johnston and Page, 1992). Host species generally tolerate the presence of nest associates, even when associates form spawning swarms of more than 100 individuals over the nest (Reighard, 1943; Hunter and Hasler, 1965; Johnston, 1991). However, in other instances, tolerance is variable and limited (Kramer and Smith, 1960).

Nocomis nests are typically large mounds (50 × 40 × 6.4 cm high), immediately upstream from a spawning pit or trough (Vives, 1990). The spawning site comprises up to 10,000 or more individually placed pebbles, each measuring 2.5 × 2.5 × 3.2 cm, with an aggregate underwater weight of 40 kg (Reighard, 1943; Lachner, 1952), that are transported from 4 m on average, for a total pebble-carrying distance of more than 25 km to complete one nest (Reighard, 1943). This is significant effort for a single male *Nocomis* measuring only 12 to 17 cm in length (Lachner, 1952), and accomplished in as little as 20–30 h of continuous work over 3 days (Reighard, 1943). Sometimes one to five accessory male subordinates contribute to the nest (Reighard, 1943; Wallin, 1989), spawn concurrently with the dominant male and work together on subsequent nests (Wallin, 1989). The amount of nest building performed by accessory males, and whether their use of the nest for spawning is conditional upon their contribution to the nest, is not known.

Male *Nocomis* court and spawn with sequential females, each time driving its gular region into the gravel to form a trough or spawning cup. After eggs have been deposited and fertilized, the male fills the cup with gravel and prepares a new one immediately downstream from the previous one (Vives, 1990). Nest associates concentrate their spawning efforts over the active spawning cup of the *Nocomis* and thus their

eggs benefit from the protective layer of gravel placed over them by the male *Nocomis* (Vives, 1990). It is not at all clear if, or even how, *Nocomis* may benefit from the presence of nest associates. If the presence of eggs from nest associates imposes little or no cost to survival of *Nocomis* eggs, then there is no justification for expending energy in driving associates away from the spawning area. Conversely, there may be a benefit via the dilution effect (see below) in the presence of egg predators.

Nest take-overs

Males can acquire non-descendant young by successfully evicting a resident male from a spawning territory that already contains eggs. Instead of eating the eggs from the previous male, the victor cares for them because the presence of eggs enhances the victor's attractiveness to females (Unger and Sargent, 1988). Stepfathers guard and tend the inherited eggs along with new clutches that they sire. In fathead minnows (*Pimephales promelas*, Cyprinidae), stepfathers often cannibalize part of their clutch of eggs, preferentially eating non-descendant eggs (Sargent, 1989). In other cases, male *Padogobius martensii* (Gobiidae) from neighbouring territories attempt to intercept females from rival males (Bisazza et al., 1989). After driving away the resident male, the intruder attempts to lead the female to his territory. If the female does not respond to these leads and deposits eggs in the rival male's territory, the intruder fertilizes them and remains to care for them, even if the shelter already contains eggs fertilized by the other male (Bisazza et al., 1989).

Anemone fish (*Amphiprion clarkii*, Pomacentridae) form monogamous pair bonds, and egg care (fanning and mouthing) is performed predominantly by males (Yanagisawa and Ochi, 1986). If the male of a pair is lost to predators (or experimentally removed), females assume responsibility for egg care. New males, usually smaller in size than the first, often replace these males and form a pair bond with the resident female. In mid season, replacement males usually assume care of the eggs sired by the previous male, facilitated by violent head butts by the females directed at the male's belly. Care of non-descendant eggs in this species may be a mechanism for strengthening the pair bond, and by emancipating the female from egg care, she can forage more and reduce the time to the next spawn (Yanagisawa and Ochi, 1986).

Female tessellated darters (*Etheostoma olmstedi*, Percidae) lay eggs on the ceiling of shelters guarded by males (Constanz, 1979, 1985). Egg deposition occurs rapidly and time to hatch is relatively long, resulting in males accumulating eggs (Unger and Sargent, 1988). When their spawning shelter is getting full, they abandon their nest and eggs and find another shelter without eggs. The abandoned eggs are tough and resistant to cannibalism, and the risk of lost fitness is low. Subordinate males take over abandoned nest sites and court females to deposit eggs in the space remaining. In the meantime, they care for the eggs abandoned by the previous male.

Piracy describes the tactic whereby dominant male peacock wrasses (*Symphodus tinca*, Labridae) commandeer a spawning shelter of another male that already contains eggs, use it for spawning, then abandon the shelter (van den Burghe, 1988). The original resident then resumes care of eggs fertilized by both males.

A variation on nest take-overs is shown by the marine sculpins *Artedius harringtoni* (Cottidae; Ragland and Fischer, 1987) and *Alcichthys alcicornis* (Cottidae; Munehara, 1988). Eggs stripped from ripe females developed normally, indicating that fertilization is internal (Ragland and Fischer, 1987). In *A. alcicornis*, females visit males on the male's breeding territory, deposit a few thousand eggs and only then copulate with the male. Using allozyme electrophoresis, Munehara et al. (1990) showed that at least 3 out of 10 egg masses tested were not genetically related to the male providing care. A later study using DNA fingerprinting confirmed that males do not fertilize any of the eggs at the time of copulation (Munehara et al., 1994). Each male therefore cares for eggs fertilized during the previous copulation event, i.e. in some cases by another male. Male care is crucial for egg survival (Munehara et al., 1994), leading the authors to conclude that males guard non-descendant eggs to attract females with which to copulate (Ragland and Fischer, 1987; Munehara et al., 1994) or that females are highly male-specific (Ragland and Fischer, 1987). These data provide partial support for both hypotheses.

Female antarctic plunder fish (*Harpagifer bispinis*, Harpagiferidae) prepare nests, spawn, and guard eggs for 4–5 months (Daniels, 1979). Care is required for egg survival. If the female is removed, she is replaced by a conspecific, usually male, which then cares for the eggs. If that male is removed, another male take his place. This apparent act of altruism cannot be

explained away easily by invoking paternity, kin selection or reciprocal altruism, and remains an enigma for evolutionary ecology (Daniels, 1979).

Up to four males guard the eggs of one female in *Hemilepidotus hemilepidotus* (Cottidae; DeMartini and Patten, 1979). Only one male is thought to have fertilized the eggs; the other males may use the clutch to attract other females. In some cichlids from Lake Tanganyika, Africa, former offspring remain at their parent's nest and assist in egg care and defence of the territory (Taborsky and Limberger, 1981). However, helpers rarely take over the site directly from their parents. This system is described in more detail below.

Zygote stealing

The selective forces that drive nest take-overs may also contribute to zygote stealing. Some male stickleback steal fertilized eggs from the nests of other males and place them into their own nest (van den Assem, 1967; Rohwer, 1978). A preference by female stickleback to deposit eggs in nests that already contain eggs is hypothesized to maintain this bizarre behaviour.

Mrowka (1987b) observed zygote stealing by female mouthbrooding cichlids. This is opposite to the prediction (above) that zygote dumping, not stealing, should evolve in maternal mouthbrooders. In this instance, females snatch non-descendant zygotes released by other females and incubate them in their buccal cavity. There are several potential costs in lost foraging opportunities, extended interval between reproductive events and reduced fecundity owing to space limitations (Hess, 1993; Smith and Wootton, 1994; Balshine-Earn, 1995; Yanagisawa et al., 1996). A likely benefit of this behaviour might be brood dilution against brood predators that target mouthbrooding cichlids (McKaye and Kocher, 1983) or later when the young become free swimming and exposed to predators (McKaye and McKaye, 1977). Zygote stealing in this context may be a case of zygote 'kidnapping' (McKaye, 1981). Until further study has been conducted, however, maladaptive misdirection of parental care, similar to the failure of female mouthbrooding cichlids to discern between their own eggs and the relatively small eggs of parasitic *Synodontis* catfish, cannot be ruled out. First, the volume of the oral cavity limits fecundity in these fishes. Second, there is strong selection for minimizing the time that eggs are exposed to predators during the spawning act. Female mouthbrooding cichlids have been selected to pick up the eggs soon after they are leaved, in

some cases before the male has had opportunity to fertilize them. Egg-sized yellow or orange spots on the anal fin of many male mouthbrooding cichlid species exploit the strong sensory drive of females to pick up eggs (Wickler, 1962; Mrowka, 1987a). As a female attempts to pick up these false egg-spots on the male's anal fin, she inadvertently inhales sperm that serves to enhance fertilization of the eggs already in her mouth.

Alloparental care of free-swimming young

There are at least seven mechanisms by which parents can acquire non-descendant free-swimming young: for species with post-hatch care of the young, alloparental care of eggs leads to alloparental care of free-swimming young; independent offspring inclusion (*sensu* Taborsky, 1994), in which young separated from, or abandoned by their parent(s), or recently independent juveniles, may join a neighbouring brood guarded by foster parents (Baylis, 1974; Coyne and Sohne, 1978; Lewis, 1980; Ribbink et al., 1980; Yanagisawa and Nshombo, 1983; Lavery et al., 1990; de Gannes and Keenleyside, 1992; Wisenden and Keenleyside, 1992; Ochi and Yanagisawa, 1996; Yanagisawa et al., 1996); kidnapping, in which parents actively sequester non-descendant young, presumably to obtain benefits (see below) of having extra young in their brood (McKaye and McKaye, 1977; Mrowka, 1987b); farming out (Yanagisawa, 1985) or young dumping, in which natural parents actively transfer their young into the care of foster parents (Ribbink, 1977; Ribbink et al., 1980; Yanagisawa, 1985; McKaye et al. 1992; Ochi et al., 1995); brood amalgamation (Eadie et al., 1988), in which families coalesce either in a cooperative manner or by one set of parents dominating the others, gaining sole care of the combined brood (Ward and Wyman, 1975, 1977; McKaye and McKaye, 1977; Ribbink et al., 1981); or philopatric offspring (Taborsky and Limberger, 1981).

Extension of alloparental care of eggs

Kleptogamic events, in which some males fertilize eggs for which other males provide care, occur in the Belontiidae, Blenniidae, Centrarchidae, Cichlidae, Cyprinidae, Cyprinodontidae, Gasterosteidae, Gobiidae and Percidae (Taborsky, 1994; and references therein). In bluegill sunfish (*Lepomis macrochirus*, Centrarchidae), 15% of the males build and defend nests and tend eggs, the remaining males (85%!) act

as parasites (Gross, 1982). Approximately 10% of spawns in *Pseudocrenilabrus philander* (Cichlidae) involve secondary males which fertilize approximately 7% of the eggs (Chan and Ribbink, 1990; Chan, 1987, in Taborsky, 1994). In another African cichlid, *Pelvicachromis pulcher*, satellite males fertilize about half of the eggs spawned by harem males (Martin and Taborsky, 1997). Parasitic male wrasses (Labridae) successfully fertilize about 10–40% of the eggs spawned in territories of territorial males (review: Taborsky, 1994). In salmonids, parasitic male Atlantic salmon (*Salmo salar*) achieve on average 1–5% of fertilizations spawned with territorial males (Hutchings and Myers, 1988), 7% of eggs in Miyabe charr (*Salvelinus malma miyabe*); Maekowa and Onozato, 1986, in Martin and Taborsky, 1997), 25% of eggs in chum salmon (*Oncorhynchus keta*; Schroder, 1981, in Martin and Taborsky, 1997), and 10% in sockeye salmon (*O. nerka*; Chebanov et al., 1983).

Independent offspring inclusion

Central American cichlids are generally biparental substrate spawners with extended defence of their free-swimming young (Keenleyside, 1991). These fish commonly incorporate non-descendant young into their own brood. McKaye and McKaye (1977) reported adoption events for at least four of nine cichlid species in Lake Jiloá, Nicaragua: *Cichlasoma citrinellum*, *C. longimanus*, *C. nicaraguense* and *Neetroplus nematopus*. When guarding pairs of *C. citrinellum* were experimentally removed, their young were adopted by neighbouring pairs of guarding conspecifics and heterospecifics. All broods of *C. citrinellum* older than 5 weeks contained juvenile *N. nematopus*, some broods of *C. longimanus* contained *C. citrinellum* young, and some *C. nicaraguense* broods contained *C. longimanus* young (McKaye and McKaye, 1977). *C. citrinellum* and *N. nematopus* broods increased in number over time, indicating intraspecific brood adoption. Mixed size classes, an indication of intraspecific brood adoption, also occurs in *C. maculicauda* in Lake Gatún, Panama (McKaye and McKaye, 1977).

The number of young in many broods of convict cichlids (*C. nigrofasciatum*) increased over time or two or more distinct size groups formed within the brood, one size class being descendant young of the guardian parents, the other(s) adopted young. Overall, 42% of the 232 broods were involved, as donor or receiver, in the intraspecific exchange

of young (Wisenden and Keenleyside, 1992). A conservative estimate of 15% of 232 broods acted as donors of young to other broods and 29% were receivers (Wisenden and Keenleyside, 1992). Mixed broods contained about 11% adopted young with the mode occurring between 0 and 5%. The transfer of young to neighbouring pairs occurred facultatively, conditional upon the prospects of guarding the young to the end of the period of parental care. Although chiefly biparental, male convict cichlids occasionally desert their mate and brood before the young have reached independence (Wisenden, 1994a). When males from guarding pairs were experimentally removed, lone females had a significantly lower probability of successfully guarding the brood to independence, significantly lower number of young for those broods that remained intact to independence, and significantly higher rates of transfer of young to alloparental care by neighbouring intact broods (Wisenden and Keenleyside, 1992). The mechanism of transfer is most likely independent offspring inclusion by abandonment or the outcome of skirmishes between neighbouring guarding pairs.

In Lake Malawi, most cichlids are maternal mouthbrooders that typically guard their young for 7–11 days (up to a month in one species) after the young are released from the mother's mouth (Ribbink et al., 1980). Interspecific brood care occurs among these fishes (Lowe, 1952, in McKaye, 1981). For example, broods of *Haplochromis polystigma*, *H. macrostoma*, and *Serranochromis robustus* were all found, without exception, to include heterospecific cichlid young, at least some of which were identified as *H. chrysonotus* (Cichlidae; Ribbink, 1977). *H. chrysonotus* are planktivorous cichlids that orally incubate their young in the surface waters above the rock-dwelling alloparental hosts. In follow-up studies, the number of Lake Malawi cichlids that act as alloparents was increased from 3 to 13 (Ribbink et al., 1980). On average, 34% of broods in these species were found to contain adopted young. The percentage of an individual brood that was adopted young ranged from less than 5% (mode) to 50% adopted young. These data are strikingly similar to data for *C. nigrofasciatum* from Central America (Wisenden and Keenleyside, 1992). In addition of *H. chrysonotus*, the young from 3–5 other *Haplochromis* cichlids were among those found tended by alloparents; up to three different 'guest' species were found in the same brood. Intraspecific brood adoption was also noted among these species (Ribbink et al., 1980). Transfer of young

was not observed in this instance, but 'farming out' (Yanagisawa, 1985) is a leading possibility. Ribbink et al. (1980) hypothesized that *H. chrysonotus* (and other pelagic zooplanktivores, or 'utaka') females descend from the surface waters when the young are ready for independent life and release them among the rocks on the bottom. From there, some of the young independently find and join broods guarded by other cichlid species (independent offspring inclusion). For rock-dwelling species that have well-developed parental care, predation events that involve groups of brood predators that overwhelm the defensive capabilities of the guardian parent can cleave and disperse the brood over a wide area. Fragments of a dispersed brood may independently join neighbouring conspecific or heterospecific broods.

Although the mechanism of brood transfer is as yet undetermined, intraspecific brood mixing occurs in the Lake Malawi mouthbrooder *Protomelas* cf. *spilopterus* (Kellogg et al., 1998). Four of six broods examined contained young that did not possess microsatellite alleles of the female carrying them. Multiple paternity was also documented. Reproductive behaviour of this species is not well known.

Young dumping (farming out)

About a third of the 170 cichlid species in Lake Tanganyika guard free-swimming young after guarding or mouthbrooding eggs (Ochi and Yanagisawa, 1996). This pattern of care is hypothesized to be the principal source of mixed broods in Lake Tanganyika cichlids (Ochi et al. 1995). The term 'farming out' was coined by Yanagisawa (1985) to describe the transfer and subsequent abandonment of free-swimming young by females of the Lake Tanganyikan intermediate-mouthbrooding cichlid *Perissodus microlepis* into neighbouring broods guarded by conspecific pairs. This term is in common usage and is used here.

Female *P. microlepis* orally incubate their young for 9–11 days after which the free-swimming young, about 7 mm in length, are released and guarded by both parents for 7 weeks until the young reach 30 mm in length and become independent from parental care (Yanagisawa and Nshombo, 1983). During this time, the young continue to seek refuge in the buccal cavity of either parent during times of danger. When the male was experimentally removed from a guarding pair of *P. microlepis*, the female was less successful in defending the brood against brood predators than

when assisted by her mate (Yanagisawa, 1985). In response to male removal, some females used calling behaviours to induce her young (up to 30 at a time) to seek shelter in her mouth. She then swam to a nearby conspecific brood guarded by two parents, spat her young into the foster brood and abruptly left (Yanagisawa, 1985). Lone females repeated this sequence until all the young were farmed out. The young were often transferred to more than one foster brood. When females were experimentally removed, lone males performed farming out, but less frequently than did females. Alloparents became agitated by the addition of young to their brood but they did not attack the introduced young. Seven of nine broods guarded by intact pairs collected by Yanagisawa (1985) and over 85% of 61 broods collected by Ochi et al. (1995) contained 2–7 size classes of young, of which only one size class were descendant young of the pair providing care. This strongly suggests that farming out occurs frequently under natural conditions. Farming out by intact pairs of *P. microlepis* was not observed, leading Yanagisawa (1985) to conclude that farming out was an adaptive response to the loss of their mate to desertion or predation, but a less successful strategy than guarding the young themselves. However, a detailed cost/benefit analysis for alloparents and donors has not been done on this system. Interestingly, farming out behaviour is exhibited by intact pairs of *Xenotilapia flavipinnis* (Yanagisawa, 1986), suggesting that farming out may be conditional upon factors in addition to mate assistance, such as the interaction between the costs of parental care and brood size, predation pressure or remating opportunities.

High levels of interspecific brood mixing also occur among Lake Tanganyikan cichlids (Ochi and Yanagisawa, 1996). Size differences between young of ‘host’ and ‘guest’ species suggest that some heterospecific young were adopted before they became independent from their own parents (farmed out) while other adoptions occurred after (independent offspring inclusion). Foraging requirements of host and guest species were similar in all cases (planktivores) and likely played a role in host-species selection by parents that farmed out their young. Conversely, species with benthic, highly aggressive young were rarely selected as hosts by planktivorous species that farmed out their young (Ochi and Yanagisawa, 1996). Females of the Tanganyikan cichlid *Microdontochromis* sp. orally incubate their eggs until the young have grown to about 10 mm in length, then transfer half of the brood to the presumed father for him to orally

incubate (Yanagisawa et al., 1996). This doubles the total volume of buccal cavity for the young to continue to grow and feed on plankton ingested by the parents (Yanagisawa et al., 1996). At this size, young also begin to appear as adopted young in cichlid broods guarded by *Perissodus microlepis* and *Lepidolamprologus elongatus*. This suggests the possibility that farming out may be derived from biparental or partial mouthbrooding, where instead of transferring the young to the male, the young are transferred to heterospecific broods.

Kidnapping

The only known example of kidnapping of non-descendent free-swimming young was reported by McKaye and McKaye (1977). Here, a male *C. citrinellum* with young aged 3 weeks, cleaved off 50 young from a neighbouring conspecific brood and shepherded them into his own brood of about 150 young. The authors invoke the ‘dilution effect’ argument (see below) as the selection pressure that gave rise to, and maintains, kidnapping in cichlids. Kidnapping may be an extension of communal care (below) or misdirected care.

Brood amalgamation

A less common phenomenon is cooperative care of a multifamily brood by more than one set of biological parents (McKaye and McKaye, 1977; Ward and Wyman, 1975, 1977; Ribbink et al., 1981). The likely reason for the relative rarity of this pattern of alloparental care is that there is often likely to be selection favouring all but one of the attending parents to desert (Trivers, 1972; Bristow, 1983; McKaye, 1985; Lazarus, 1990). In addition, parents are typically intolerant of other adults in close proximity to their brood, and care of a combined brood may be left to the largest, most dominant parents by default (Baylis, 1974). Communal care may have arisen and been facilitated by limited nursery habitat (Taborsky, 1984), or greater antipredator vigilance by multiple adults (Wallin, 1989; Taborsky, 1994; Mappes et al., 1995). Increased efficiency of brood defence is thought to be a major selective force in the evolution of biparental care from uniparental male care (Barlow, 1974; Keenleyside, 1978; but see Wisenden, 1994a, 1995). Communal care arises when more than one set of parents remain near the combined brood, tolerate each other’s presence, and jointly defend the young.

Communal care among cichlids occurs in species in Central America (McKaye, 1977; McKaye and McKaye, 1977), Africa (Lake Malawi: Ribbink et al., 1981, and Ribbink, 1990; Lake Tanganyika: Taborsky and Limberger, 1981) and Asia (Ward and Wyman, 1975, 1977). Three pairs of *Cichlasoma citrinellum* were observed guarding a large shoal of young in the late stages of brood development (McKaye and McKaye, 1977). When danger approached, the adults went their separate ways and the young appeared to follow the closest parent without regard to relatedness. When danger had passed, the three families coalesced and mixed freely. Much the same pattern has been reported from Lake Malawi for *Tilapia rendalli* (Cichlidae; Ribbink et al., 1981). Four adults (two monogamous pairs) were observed guarding a combined brood of about 500 young comprising two distinct size classes. Half of the young were about 20 mm, the other half about 40 mm. When danger approached, the brood split, one half with about 30% large and 70% small young went with one set of parents, the rest with the other set. Cooperative care is also reported in the mouthbrooding cichlid *Cyrtocara taeniolata* from Lake Malawi (Ribbink, 1990). Here, parents set up protective stations in close proximity to each other and the young move freely among them.

Green chromide cichlids (*Etoplus suratensis*) are one of the few cichlids from Asia. Of 28 families (adults with young) observed, three were guarded by more than one pair of adults (Ward and Wyman, 1977). Several sets of parents may guard a combined brood of up to 2000 free-swimming young (Ward and Wyman, 1975, 1977). Among the adults, there can be one pair that dominates and leads the shoal of young and occasionally attempts, in vain, to drive away the other tending adults (Ward and Wyman, 1975, 1977). Subdominant adults station themselves near the margins of the brood. All adults participate in brood defence and allow young to consume epidermal mucus secretions from their sides (Ward and Wyman, 1977).

An unusual example reported in the literature is that of herbivorous cichlid fish, with no young of their own, defending the young of their predator (McKaye, 1977). McKaye (1977) observed seven broods of *Cichlasoma dovii* (Cichlidae; large piscivore) being defended by male *C. nicaraguense* (small herbivore) against predatory attacks from *C. nigrofasciatum* and *Gobiomorus dormitor* (Eleotridae) for about 3 weeks each. Alloparental care from the smaller species benefited the *C. dovii* parents. The

presence of heterospecific alloparents was correlated with improved brood survival, and lower defence effort by the true parents. McKaye (1977) hypothesized that this alloparental care could be maintained by natural selection if increased production of the predator species has a more adverse effect on competitors of the alloparental species than on the alloparental species itself. *C. nicaraguense* compete with both *C. nigrofasciatum* and *Neetroplus nematopus* for nest sites. *C. dovii*, *C. nigrofasciatum*, and *N. nematopus* co-occur in rocky areas where *C. dovii* preys on the other two. *C. nicaraguense* lives in sandy areas when it is not breeding (in the rocks) and is relatively free from predation by *C. dovii* for much of the year.

Cichlid parents 'farm out' their young into broods of the catfish *Bagrus meridionalis* (Bagridae) from Lake Malawi (McKaye et al., 1992) and in half the cases, the cichlid parents remain near by and assist in brood defence (McKaye and Oliver, 1980; McKaye, 1985). The proportion of catfish broods that contained cichlid young varied with the age of the catfish young from none (when catfish were < 20 mm) to 100% (when catfish young were 20–40 mm) and levelled off to about 70% of broods 40–80 mm in length (McKaye, 1985). Overall, more than 50% of catfish broods contained cichlid young. Cichlids adopted by these catfish were young of *Cyrtocara pleurostigmoides*, *C. pictus* and *Rhamphochromis* sp. Broods of *C. pleurostigmoides* and *C. pictus* were never observed independent of a catfish brood, suggesting that this mutualism may have co-evolved. Such co-evolved behavioural mutualisms are known among cichlids and well within the realm of credibility (Wyman and Ward, 1972). It is unknown why these particular species, but none of the dozens of other similar cichlids in the vicinity, have come to associate with catfish broods.

Philopatric offspring

Helpers at the nest is one of the more intriguing phenomena in the study of reproductive behaviour of fish, noted to occur in cichlids endemic to Lake Tanganyika, Africa, *Lamprologus brichardi*, *L. pulcher*, *L. savoryi* and *Julidochromis marlieri*, *J. ornatus* and *J. regani* (Taborsky and Limberger, 1981; Taborsky, 1984, 1985; Yamagishi and Kohda, 1996) and two species of anabantid fish, *Betta brownorum* and *B. persephone* (Witte and Schmidt, 1992). Here, offspring from previous breeding efforts remain in the natal territory and assist the breeding pair (usually

their parents) in raising subsequent broods (Taborsky and Limberger, 1981; Taborsky, 1984, 1985). Helping behaviour in *L. brichardi* is best known. Helpers engage in intra- and interspecific territory defence, and territory maintenance behaviours. The presence of multiple size classes of helpers suggests that offspring from up to four previous breeding efforts remain at their natal territory before being expelled by the breeding adults. A typical brood cycle is 2–4 months, resulting in helpers remaining at their natal nest for up to a year (Taborsky, 1984). Helpers tend to remain in their natal territory until forcefully evicted by the breeding pair (Taborsky, 1985).

Evolution of alloparental care in fishes: low cost, high benefits

Why is alloparental care so prevalent in fishes? The answer seems to be a combination of low costs and high potential for benefits. Parental fish are relatively free from the costs associated with feeding their young and predation risk to themselves incurred during brood defence (although see Magnhagen, 1992). Parental care in fishes is essentially antipredator behaviour in the form of brood defence. Energetic constraints associated with feeding their young are largely absent in fishes. This gives rise to a cost–benefit dynamic very different from that of mammals and birds, and has important consequences for the evolution of alloparental care in fishes as an evolutionary solution to the problem of predation on eggs and young (McKaye, 1981).

Fish are poikilothermic and have a relatively low metabolic rate compared with homeotherms. Consequently, fish generally do not provision their young with food. Reproductive strategies in mammals must consider resources devoted to lactation (Jennions and Macdonald, 1994). Altricial birds spend a great deal of time, energy and risk foraging for food for their young (Rohwer and Freeman, 1988). As such, alloparental care in mammals or birds is costly to care givers (Riedman, 1982). In birds, precocial species amalgamate broods, but alloparental care in altricial species is generally parasitic in nature and associated with a high fitness penalty (Yom-Tov, 1980; Eadie et al., 1988; Rohwer and Freeman, 1988, 1992; Lyon and Eadie, 1991; Cooper and Miller, 1992; Sorenson, 1992).

Having made the assertion that fish generally do not feed their young, it bears considering that there are

a number of examples of post-hatch food provisioning by parental fish. Large male cichlids of the species *Cichlasoma maculicauda* use their size to monopolize good feeding areas for the young (Perrone, 1978). Parents of 28 species, including 24 in the Cichlidae, provide food to their free-swimming young by secreting an extra-thick layer of mucus on their body for their young to consume (Thistlethwaite, 1947; Hildemann, 1959; Ward and Barlow, 1967; Noakes and Barlow, 1973; Noakes, 1979; Ferraris, 1991). These secretions are obligatory for offspring survival in *Symphysodon* sp. (Cichlidae) and parental mucus of cichlids generally seems to have nutritional value for the young (Kishida and Specker, 1994; Takemura, 1994; Schütz and Barlow, 1997). While guarding mobile broods of young, convict cichlids engage in leaf-lifting and fin-digging behaviour at greatly elevated levels that assist young in foraging (Williams, 1972; Wisenden et al., 1995). In some species of mouthbrooding cichlids, females browse on algae or plankton for the benefit of the developing young inside their buccal cavity (Bradley, 1980; Yanagisawa and Sato, 1990; Yanagisawa and Ochi, 1991; Yanagisawa et al., 1996). In bagrid catfish from Lake Malawi, females provide sterile ‘trophic eggs’ for their young to use as forage, and males leave the brood to forage for benthic invertebrates that are then brought to the brood area for the young to eat (McKaye, 1986). This same catfish species also provides direct nourishment to adopted cichlid young by allowing them to feed on parental skin secretions (McKaye et al., 1992). However, these exceptions aside, it is generally true that the evolution of parental care in fishes has been shaped largely by strong selection pressure exerted by predation on the eggs and young.

The dynamic between brood predators and guardian parents in fish is different from that in birds and mammals. Newly hatched fish are proportionately much smaller compared with their parents than are young birds or young mammals relative to their parents. Consequently, unlike birds and mammals, predators of fish broods generally do not pose a predation threat to adults.

Parental care in fishes is largely an unshareable form of parental investment (Lazarus and Inglis, 1986). In other words, brood defence benefits all young equally, and broods with many young are as easy to defend as broods with few young. While this may hold for species that guard eggs, it is not always true for species with extended post-hatch care of their young. A test on fish (Wisenden and Keenleyside,

1995) and a similar test on parent bugs (Mappes and Kaitala, 1994) indicate that efficacy of brood defence is lower for large broods than small broods. In both systems, large females lay more eggs (Mappes and Kaitala, 1994; Wisenden, 1995) and are more effective in brood defence (Mappes and Kaitala, 1994; Wisenden, 1994b) than small females. In experimentally manipulated broods of convict cichlids, or reciprocal transplant experiments in parent bugs, parents with an augmented clutch size incurred greater losses to predation than control broods (Mappes and Kaitala, 1994; Wisenden and Keenleyside, 1995) and an increase in brood survival for subnormal clutch sizes (Mappes and Kaitala, 1994). Parents appear to lay as many eggs as they can economically defend.

Even with this evidence for a constraint on brood size imposed by the demands of brood defence, it is important to keep in mind that fecundity for animals such as fish and insects is much greater than that for birds and mammals. Starting brood sizes in convict cichlids ranged from 70 to 150 free-swimming young and in the study on parent bugs, from about 44 to about 52 eggs. Most care-giving fishes are much more fecund than this. The increment in cost associated with caring for one additional offspring is small for animals with young that do not need post-hatching assistance in procuring food. These aspects of fish reproductive biology have allowed alloparental care to evolve independently many times in fishes.

Because in most cases an alloparent is already caring for its own young, the costs of alloparental care are only those above the costs of conventional care (Smith and Wootton, 1995). Among these costs are consumption of host eggs by donor parents (Fletcher, 1993), adopted young eating host eggs (Sato, 1986), adopted eggs contributing to host egg mortality from fungal infection (Shao, 1997b), or risk of hybridization (Raney, 1940; Reighard, 1943).

Opposing these costs are at least seven potential mechanisms for fitness benefits that may promote alloparental care by natural selection: acquisition of mates (Taborsky, 1994); the confusion effect (Taylor, 1976; review: Pitcher and Parrish, 1993); the dilution effect (McKaye and McKaye, 1977); the selfish herd effect (Hamilton, 1971; McKaye et al., 1992; Johnston, 1994a); the selfish shepherd effect (Wisenden and Keenleyside, 1992); kin selection (Hamilton, 1971; Taborsky, 1984), and reciprocal altruism (Trivers, 1971) or 'pay to stay' (Taborsky and Limberger, 1981; Taborsky, 1985).

Acquisition of mates

Females in many species prefer to lay eggs in nests that already contain eggs (e.g. darters: Knapp and Sargent, 1989; Page and Bart, 1989; Lindström and Sargent, 1997; minnows: Unger and Sargent, 1988; blennies: Kraak and van den Burghe, 1992; Kraak and Groothuis, 1994; Santos, 1995; sculpins: Marconato and Bisazza, 1986; damselfish: Petersen, 1989; Petersen and Marchetti, 1989; Sikkel, 1989, 1994; stickleback: Rohwer, 1978; Ridley and Rechten, 1981). The probable selective pressure driving this preference is partial and/or total filial cannibalism by guardian males. For species in which there is male-only care (i.e. the majority of fishes with care, Blumer, 1979), males are limited in their opportunities for foraging over extended periods of courting females and tending and defending eggs. Males in a number of these species cannibalize eggs, presumably to sustain themselves until the end of the period of parental care of the remaining eggs (e.g. darters: Knapp and Sargent, 1989; minnows: Unger and Sargent, 1988; blennies: Santos, 1995; Apogonidae: Okuda and Yanagisawa, 1996; stickleback: Belles-Iles and FitzGerald, 1991; sculpins: Marconato and Bisazza, 1988; damselfish: Petersen and Marchetti, 1989; cichlids: McKaye, 1983; but see Smith, 1992, for opposing viewpoint). The eggs most likely to be consumed are the first, and the last eggs deposited in a male's nest. Males with nests containing eggs close to hatching may cannibalize the youngest eggs in their nest to sustain themselves until their oldest eggs have hatched and dispersed. If a male succeeds in acquiring only one clutch, then he might abandon the effort and cannibalize the entire clutch. Alternatively, cannibalizing old eggs (first ones laid) may be favourable if the male accrues a net gain by receiving more new clutches than he needs to sustain himself at the spawning site to rear them. Thus females that avoid being the first to spawn in a nest reduce the risk of their eggs being eaten. If other eggs are already in the nest, the statistical probability of their eggs being cannibalized is diluted by the total number of eggs in the nest. So great is the potential benefit from exploiting female preference for nests with eggs that territorial males steal eggs (van den Assem, 1967; Rohwer, 1978) or take over established nests (Unger and Sargent, 1988; van den Burghe, 1988) to acquire eggs. To the degree that female preference for nests with eggs is driven by mate-choice copying by females (Dugatkin, 1992; but see Jamieson, 1995), the acquisition of non-

descendant eggs may give a male the appearance of past reproductive success (being chosen by previous females) and may enhance females' perception of his value as a mate.

In contrast, alloparental care in tessellated darters is driven by males that benefit from guarding spawning sites with large areas of available space for egg deposition (Constanz, 1979, 1985). Males defend flat-bottomed rocks, the undersides of which serve as spawning shelters. The supply of such rocks constrains male reproductive success. Females deposit eggs directly onto the bare rock surface on the underside of the spawning site. The value of the spawning site to a male is reduced when part of its area is filled by a clutch of eggs. After spawning, dominant males abandon their nest and eggs and monopolize a new site without any eggs. The new site offers greater potential for new eggs than what remained of the old site. Subordinate males occupy spawning sites abandoned by dominant males and prepare the remaining area of egg-free rock for a spawn of their own. In so doing, they inadvertently clean and guard the eggs of the previous male. Once water hardened, eggs of tessellated darters are resistant to cannibalism, decreasing the cost of abandonment to the first male and obliging the subsequent male to care for them lest they become diseased and infect new eggs fertilized by the second male (Constanz, 1979, 1985).

Piracy is a tactic in which a dominant male takes over the nest of a rival male that contains eggs, attracts females and spawns, then abandons the area, leaving the resident male to care for clutches sired by both males (van den Burghe, 1988). Pirates achieve 2.5 to 10 times the fitness pay-off of males that use other reproductive tactics (territorials, satellites, interceptors), an estimate based upon number of eggs fertilized, energy savings in brood care, and higher foraging opportunities (van den Burghe, 1988). The resident male does not desert because he has much fitness to gain by remaining to care for descendant eggs.

Territorial males can benefit from the presence of cuckolded males if these males assist in defence of the territory and/or harem (Kodric-Brown, 1977; Warner and Lejeune, 1985; Taborsky et al., 1987; Santos and Almada, 1987; Wallin, 1989; Martin and Taborsky, 1997), act as mate insurance in protandric species (e.g. anemone fish, *Amphiprion clarkii*) if one of the monogamous pair is lost to predation (Fricke, 1979), or help attract more females than would have been otherwise the case (Kodric-Brown, 1977; Ross and Reed, 1978; Dominey, 1981). In most cases it is not

known if these benefits surpass the cost of lost fertilizations. In some cases, parasitic males are tolerated only because it is too expensive to chase them away (Barlow, 1961; Kodric-Brown, 1977).

Confusion effect

The success of an attack declines with increasing group size of shoaling prey (Neill and Cullen, 1974; Milinski, 1977) because predators cannot visually isolate individual prey as easily when prey are in a large group as when the prey are in a small group or alone (Magurran and Pitcher, 1987; Godin and Smith, 1988; review: Pitcher and Parrish, 1993). Theoretically, the addition of adopted young to a brood should enhance this effect and reduce losses to brood predators for descendant young. Adoption of heterospecific young that differ visually from descendant young would help predators to isolate individual adopted young (i.e. an example of a selfish shepherd), deflecting predator pressure away from descendant young. To my knowledge, there has not yet been any demonstration of the confusion effect or the visual oddity effect accruing benefit in the context of alloparental care.

Dilution effect

The inclusion of non-descendant young into a brood dilutes the probability that any given attack by a brood predator will succeed in taking one of the descendant young (McKaye and McKaye, 1977).

The dilution effect seems to be an important selective force driving nest associations by cyprinids and their hosts (Johnston 1991, 1994a, 1994b) and this system is ripe for future experimental work. Large-mouth bass nests that contained eggs of lake chub-sucker (*Erimyzon sucetta*, Catostomidae) were more likely than bass nests without sucker eggs to receive bass eggs (5/6 vs. 14/22), hatch bass eggs (5/6 vs. 6/22) and have young bass survive to independence (4/6 vs. 1/22) (Carr, 1942). Golden shiner reproduction was greatest in successful bass nests and least successful in bass nests that failed (Kramer and Smith, 1960). Six of 10 smallmouth bass (*Micropterus dolomieu*, Centrarchidae) nests that contained eggs of longnose gar (*Lepisosteus osseus*, Lepistosteidae) successfully produced bass larvae compared with a success rate of only 19 out of 59 nests without gar eggs (Goff, 1984). Gar eggs found at the perimeter of smallmouth bass nest experienced greater losses

to predators than eggs in the nest centre (Goff, 1984).

Unfortunately, without experimental manipulation, the anecdotal correlation between the presence of non-descendant eggs and host success in the preceding examples does not necessarily imply a causal relationship. These data cannot distinguish between two possibilities: (1) that nest associates select the best sites for egg survival; and (2) that non-descendant eggs enhance survival of host eggs.

A well-controlled experiment showed that in the presence of predators, green sunfish broods with redfin shiner nest associates had more surviving young than hosts without associates (Johnston, 1994a), primarily through the dilution effect. Large male pumpkinseed sunfish (*Lepomis gibbosus*, Centrarchidae) had more broods per season, and males with nest associates had more broods per year than males without nest associates (Shao, 1997b). However, pumpkinseed sunfish nests with golden shiner associates had no net benefit (Shao, 1997b). Fertilization success of sunfish eggs was significantly lower in nests with associates (43%) than in nests without associates (73%). These unfertilized eggs, and unfertilized eggs of the shiners, created conditions favouring the pathogenic fungus *Saprolegnia* that can spread to healthy fish eggs. These costs were offset by significantly decreased predation on sunfish larvae through the dilution effect (Shao, 1997b). Fungal infection from roach (*Leuciscus rutilus*, Cyprinidae) eggs is inferred to have a similar negative effect on the eggs of the host *Lucioperca sandra* (Percidae; Woynarovich and Entz, 1949–50).

Involvement of a third species can change the nature of the relationship between the host species and nest associate. Reproductive territories of male *Siniperca kawamebari* (Serranidae) are used by the nest associate *Pungtungia herzi* (Cyprinidae) as a place to deposit eggs (Baba et al., 1990). Egg survival for both species is low if the territorial male *S. kawamebari* is removed. A specialized egg predator, *Zacco temminckii* (Cyprinidae) resembles *P. herzi* and gains unfettered access to nests by tagging along with spawning groups of *P. herzi*. *Z. temminckii* eats eggs of the host and presumably also the associate, and thereby manifests an indirect net fitness cost of alloparental care to the host species (Baba et al., 1990).

Another demonstration of the effectiveness of brood dilution on survival of the alloparent's descendant young comes from a brood manipulation experiment in the field on convict cichlids (Wisenden and

Keenleyside, 1994). Descendant young in experimentally enlarged broods had significantly higher survival than similar-sized descendant young in control broods.

Selfish herd effect

The selfish herd effect describes differential predation of young by spatial variation in predation risk (Hamilton, 1971). Young at the brood periphery are subject to greater rates of predation than those in the brood centre (Burchard, 1967; McKaye and Oliver, 1980; Goff, 1984; McKaye 1985; McKaye et al., 1992; Johnston, 1994a). Alloparents that force adopted young to occupy peripheral positions greatly reduce the number of predator attacks directed at descendant young and thereby increase their reproductive success. Descendant and adopted young are spatially segregated in mixed broods guarded by the African cichlid *Tilapia mariae* (host) and *T. melanopleura*. The swarm of young “while retaining its unity as a swarm is neatly polarized, with the *T. mariae* fry [young] among the plants and those of *T. melanopleura* spread out over the adjacent sand surface!” Burchard (1967, p. 127). Mouthbrooding cichlids in Lake Malawi retrieve their young into their mouth during times of risk. In mixed broods, descendant young were usually the first to enter their mother's mouth while adopted young were among the stragglers (Ribbink et al., 1980). Thus the adopted young are at greater risk of predation than host young. However, in one instance, the addition of adopted young rendered the brood too large to fit into the finite volume of the mother's mouth. Descendant young not able to enter their parent's mouth as a result of crowding may represent a cost to parental fitness (Ribbink et al., 1980).

Bagrid catfish that force cichlid young associated with their brood to occupy peripheral positions in the mixed shoal of cichlid and catfish young, do so presumably to insulate descendant young from brood predators with a protective buffer of cichlid young (McKaye and Oliver, 1980). Indeed, video analysis revealed that 87% of attacks by brood predators on mixed broods were made on cichlid young positioned at the periphery of the brood and only 13% were directed at the catfish young in the brood centre (McKaye et al., 1992). In an earlier test of this hypothesis, adult catfish were removed from pure catfish broods or from mixed cichlid–catfish broods (McKaye, 1985). Catfish young were consumed faster when in pure broods than when in mixed broods.

However, catfish in the pure broods were 2.2 cm in length (relatively small, weak swimmers) compared with 5.9 cm for catfish in the mixed broods tested. This size difference confounds the test and therefore does not constitute an unambiguous demonstration of the selfish herd effect. An unexplored alternate hypothesis is that parental catfish push cichlid young to the brood periphery to exclude them from access to trophic eggs released by female catfish or invertebrates retrieved and released into the nest by the male (McKaye, 1986). While defence of an area is a form of unshareable parental investment (i.e. benefits all young equally) for which cost is more or less independent of the number of young in the brood, trophic eggs are a form of direct, shareable parental investment, i.e. the more young that share a resource the smaller the benefit to each (Lazarus and Inglis, 1986). Therefore, catfish should be selected to take measures to ensure that relatively costly trophic eggs contribute directly to their fitness and are not wasted on non-descendant young.

Johnston (1994a) found significantly more redbfin shiners eggs (nest associate) on the periphery of sunfish nests than sunfish eggs, and significantly more sunfish eggs in the nest centre than shiner eggs. This could potentially confer a selfish herd benefit to guarding sunfish. The mechanism of egg distribution is not known.

Selfish shepherd effect

The selfish shepherd describes differential predation by variation in antipredator competency among young in a mixed brood, formerly referred to as the 'differential predation effect' (Wisenden and Keenleyside, 1992). When there is more than one size class of free-swimming young in a brood, the small sizes that have the least developed antipredator competencies (Fuiman and Magurran, 1994) suffer a higher rate of predation relative to the other subgroups of young (Wisenden and Keenleyside, 1992, 1994). In a typical case of brood predation (by attrition – Wisenden, 1994b), a predator darts into the shoal of young and captures, at most, one young before the guardian parents drive the predator away. In this short interval, the predator selects the prey for which capture success is most likely, that is, the smallest, weakest individuals in the brood.

Brood-guarding Central American cichlids adopt non-descendant conspecific and/or heterospecific young into their care when the new young are similar

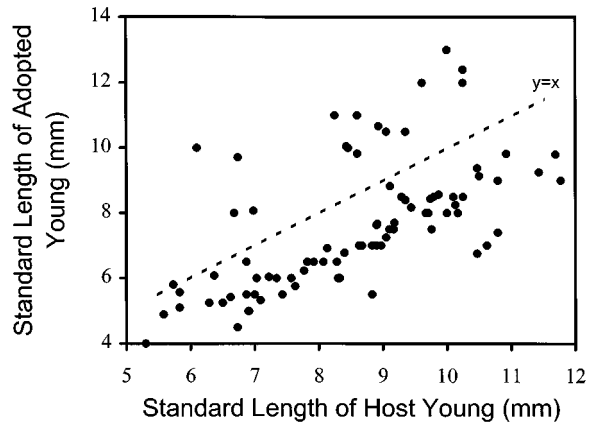


Figure 3. Standard length (mm) of adopted conspecific young relative to the length of the young related to the parents providing the care for 84 broods of convict cichlids in natural populations in Costa Rican streams. Broken line is line of equality: the majority of adopted young were smaller than host young ($p < 0.05$). Data from Wisenden and Keenleyside (1992).

in size to, or smaller than, the alloparent's young. This occurs in the laboratory (Greenberg, 1963; Myrberg, 1964; Noakes and Barlow, 1973; Fraser et al., 1993; Fraser and Keenleyside, 1995; Fraser, 1996) and in the field (McKaye and Hallacher, 1973; McKaye and McKaye, 1977; Wisenden and Keenleyside, 1992; Figure 3). A field test confirmed the selfish shepherd effect (Wisenden and Keenleyside, 1994). Convict cichlid broods were manipulated to a standard number of 40 young, then 20 additional young were added to half of the broods. The size difference between the two groups of young was carefully set at 1.5 mm, the average size difference between size classes of young in naturally occurring mixed broods. For test broods with natural young sized 8.0 mm standard length (SL) and adopted young sized 6.5 mm SL, survival of the alloparents' descendant young was significantly greater relative to control broods than could be accounted for by the effect of brood dilution acting alone (Figure 4). This demonstrated a fitness benefit to alloparents through differential predation on adopted young based on variation in antipredator competency (Wisenden and Keenleyside, 1994).

The sizes of host and adopted young in Lake Tanganyikan cichlids do not show the consistent pattern observed in convict cichlids (Yanagisawa, 1985; Ochi et al., 1995; Ochi and Yanagisawa, 1996; Yanagisawa et al., 1996). One notable difference between Tanganyikan cichlids and convict cichlids is the duration of parental care. Convict cichlids typically care for their free-swimming young for no more

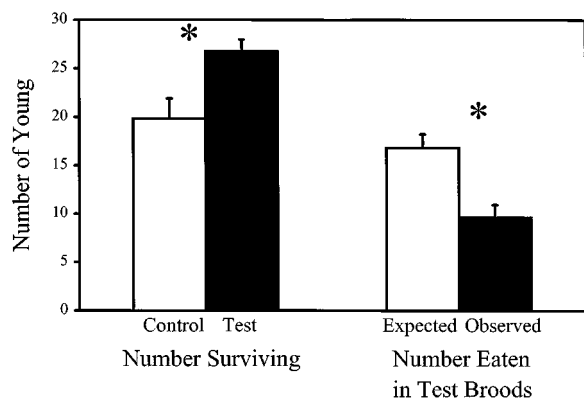


Figure 4. Mean number of descendant young of convict cichlid broods surviving 10 days after brood size was increased from 40 young (control) to 60 young (test) by the addition of 20 non-descendant young sized 1.5 mm smaller than host young; and the mean number of descendant young eaten in test broods compared with that expected based on the effect of brood dilution alone. T-bars denote SE; asterisk, $p < 0.05$. Data from a field study in Costa Rica by Wisenden and Keenleyside (1994).

than 4 weeks and a maximum size of 10 mm before dispersal (Wisenden, 1994a, 1995) while Tanganyikan species care for free-swimming young for up to 7 weeks in *Perissodus microlepis* (Ochi et al., 1995) to 12 weeks in *Lepidolamprologus attenuatus*, or more than 12 weeks in *L. elongatus* (Nagoshi and Gashagaza, 1988; Ochi and Yanagisawa, 1996). Size at independence from parental care in Tanganyikan species can exceed 30 mm (*P. microlepis*) and 40 mm (*L. elongatus*) (Ochi et al., 1995; Ochi and Yanagisawa, 1996). Adoptions in Tanganyikan species do not begin to occur until after the host young are at least 10 mm (Yanagisawa 1985; Ochi et al., 1995; Ochi and Yanagisawa, 1996). At these relatively large sizes, young of different ages may not differ markedly in their antipredator competencies and differential predation on the basis of size may be unimportant. Differential predation on size-stratified broods of convict cichlids breaks down at later stages of development because the differences in antipredator competencies are no longer large (Fraser and Keenleyside, 1995). For parents tending a brood of young of 8 or 9 mm in length, acceptance of larger young benefits parental fitness through the dilution effect (Fraser and Keenleyside, 1995; Fraser, 1996). This creates a trade-off for broods of intermediate development between the benefit of brood dilution and the cost of accepting larger adopted young (Fraser, 1996).

Kin selection

If alloparental care benefits kin, and a predisposition to perform alloparental care has a genetic basis, then increasing survival of kin will promote the genotype shared by the alloparent and non-descendent young, and thereby increase the frequency of genes for alloparental care (Hamilton, 1964). In *Lamprologus brichardi*, the degree of relatedness (r) between helpers and the eggs they cared for ranged from 0.25 to 0.5, decreasing with age of the helper, thus the opportunity for kin selection to promote helping behaviour is apparent (Taborsky and Limberger, 1981).

Of 60 families examined, three (5%) had no young, five (8.3%) had young of one size class, 13 (21.6%) had two size classes of young, 25 (41.6%) had three size classes of young, and 14 families (23.3%) had four size classes of young. The smallest size class was new offspring, the larger sizes served as helpers. Helpers cleaned the territory and removed snails (egg predators). Helpers engaged in territory defence, the largest helpers did as much (intraspecific attacks) or more (interspecific attacks) than the parents (Taborsky and Limberger, 1981). Extreme intraspecific aggression by young ≥ 1.5 cm precludes interfamily exchange of young. In addition, breeders recognize individual helpers and reject similar-sized fish from elsewhere, even if the unfamiliar fish acted as helpers in another family (Hert, 1985).

Reciprocal altruism (pay to stay)

In this situation, breeders tolerate costs associated with the presence of alloparents in exchange for benefits they provide (Trivers, 1971). Although the contribution of helpers did not affect survival of eggs and free-swimming young *per se*, female *L. brichardi* with helpers spent less time on territory maintenance. The energy thus conserved translated into larger clutch sizes and number of free-swimming young for females with helpers than for females without helpers (Taborsky, 1984). In *Julidochromis marlieri*, females with a helper spent only 25% of their time near the nest compared with 70% for females without a helper, and males (the dominant care giver) attacked predators less frequently when assisted by a helper (Yamagishi and Kohda, 1996).

The largest male helpers may become sexually mature before being expelled by the dominant male of the breeding pair, giving the helper an opportunity to usurp some of the dominant male's reproduc-

tive potential in terms of stealing fertilizations and cannibalizing eggs fertilized by the dominant breeder (Taborsky, 1985). When competition for nest sites is particularly intense, sexually active helpers are tolerated by the breeding pair because the helpers, by virtue of their large size, greatly improve the family's chances of retaining control of the breeding territory.

After leaving their natal territory, juvenile and subadult *L. brichardi* form roving shoals where individuals grow until large enough to acquire a nest site of their own. The largest helpers are not yet large enough to effectively defend a nest site and rarely inherit territories directly from the role as a helper. Helpers remain at their natal site and continue to provide alloparental care, even after a turnover of the breeding pair, and exchange alloparental care for sanctuary from predation (pay to stay).

Alloparenting as misdirected parental care

Coyne and Sohn (1978) raised the question of whether or not brood adoption in cichlids is simply a case of misdirected parental care, i.e. that parents cannot distinguish between descendant and non-descendant young. Misdirected care is common among birds where kin discrimination does not appear to be well developed (Kempnaers and Sheldon, 1996). Indeed, in many situations in fishes such as stolen fertilizations and nest associations, parents do not actively discriminate against non-descendant eggs, either because the cost of keeping them is very low or the cost of eliminating them is too high. However, in many cases, parents can and do discern between descendant and non-descendant eggs and offspring, usually on the basis of chemical cues alone (MacGinitie, 1939; Kühme, 1963; Cole and Ward, 1970; McKaye and Hallacher, 1973; Myrberg, 1975; McKaye and Barlow, 1976; Loiselle, 1983; Hert, 1985; Lutnesky, 1989; Sargent, 1989; but see Reeb and Colgan, 1992). Young, on the other hand, are strongly attracted to parental fish but do not seem to distinguish between their own parent(s) and other conspecific adults in breeding colour, nor can they distinguish between their own mother and another guarding female on the basis of chemosensory cues (Baerends and Baerends von Room, 1950; Cole and Ward, 1969, 1970; Barnett, 1977; Hay, 1978). Instead, the young are attracted to the parent that engages in the most parental behaviours (de Gannes and Keenleyside, 1992).

In brood transplant experiments in the field, convict cichlid parents quickly attacked and chased away experimentally added young that were larger than descendant young, but accepted young that were smaller than their own (Wisenden and Keenleyside, 1992). Fraser et al. (1993) showed that convict cichlid parents rejected large adopted young long before the added young posed a direct risk of injury or predation to descendant young. Both of these studies indicate that parents detect the presence of non-descendant young in their brood but have been selected not to evict small ones, presumably because of the fitness benefits that accrue.

Synthesis and future directions for research

Alloparental care is of interest to evolutionary ecologists because investment in non-descendant young is potentially maladaptive and presents a challenge to evolutionary theory. No pattern of parental care is completely resistant to the evolution of alloparental care, and alloparental care has arisen independently many times in disparate fish taxa. The relatively low cost of post-zygotic parental investment has freed parental care in fishes from the high fitness penalties typically associated with alloparental care in homeotherms. Thus, even when there is no kin relationship between alloparent and non-descendant offspring, substantial fitness benefits can accrue (Table 1). One way of summarizing selection pressure on the evolution of alloparental care is to assign to the cases in Table 1 a value of -1 for parasitic relationships, 0 for commensalisms and $+1$ for mutualisms. The sums of these scores show that alloparental care is under a net positive selection pressure for almost all of the general types of care exhibited by fishes (Figure 5). This statement is especially true for substrate brooders with extended care of free-swimming young. Reproductive success of mouthbrooders is constrained by the volume of the oral cavity, thus limiting the benefit of adopting unrelated eggs or embryos.

Alloparental care appears wherever there is parental care. Parental care is best developed among species of the Cichlidae (Keenleyside, 1991) and accordingly, so too is alloparental care (Table 1). Substrate brooders in particular, both New World and Old World species, have incorporated alloparental care as a major and routine part of their reproductive ecology. Brood mobility during care is likely a predisposing factor contributing to the prevalence

Table 1. Distribution of costs and benefits associated with alloparental care in fishes, organized by the patterns of care of the host species. Relationship between host and donor parents: P, parasitic; M, mutualistic; C, commensalistic; Mal, maladaptive misdirection of parental care. **Benefits** that maintain mutualism: 1, assistance in territorial maintenance and defence; 2, acquisition of mates; 3, kin selection; 4, assistance in brood care; 5, dilution effect; 6, group predator vigilance among young or among attending adults; 7, selfish herd effect; 8, confusion effect; 9, selfish shepherd effect. **Costs** that result in parasitism: 10, cuckoldry; 11, young consumed by non-descendant young; 12, risk of hybridization; 13, adult nest associates eat host eggs; 14, increase in egg mortality owing to fungal infection; 15, reduced growth of descendant young; 16, limited room in buccal cavity. See text for descriptions and source references

Pattern of Alloparental care	Pattern of parental care of host species				
	Nest builders	Paternal care substrate spawners	Biparental substrate spawners	Partial mouthbrooders	Maternal mouthbrooders
Alloparental care of eggs					
Sperm dumping	P – 10	P – 10 M – 1, 2	P – 10 M – 1, 3, 4, 6	P – 10?	P – 10 M – 1, 2?, 6?
Egg dumping	C?				
Zygote dumping	P – 12, 13 M – 1, 2?, 5?, 6?, 7?, 8?, 9?	P – 13, 14 M – 1?, 2?, 5, 6?, 7, 8?, 9?			P – 11
Nest take-overs		P – 10 M – 2, 4, 5?, 6?			
Zygote stealing		M – 2, 5? C?			Mal – 16? M – 5?
Alloparental care of free-swimming young					
Extension of egg care	P – 10 M – 5, 6?, 7, 8?, 9?	P – 10 M – 5?, 7, 8?, 9?	P – 10 M – 1, 3, 4, 5?, 6	P – 10 C?	P – 10, 11 M – 5? C?
Independent offspring inclusion			P – 15 M – 5, 6, 7, 8?, 9	P – 16 M – 5, 6, 7, 8?, 9?	
Kidnapping			M – 5, 7?, 8?, 9?		
Larvae dumping (farming out)			M – 1, 5, 6, 7, 8?, 9	P – 16 M – 5, 6, 7?, 8?, 9?	
Brood amalgamation			M – 1, 4, 5, 6, 7?, 8?	M – 1, 4, 5, 6, 7?, 8?	
Philopatric offspring			M – 1, 3, 4, 5?, 6		

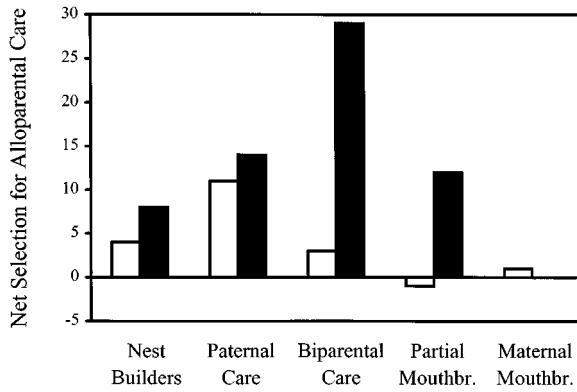


Figure 5. Selection pressure for alloparental care across general classes of parental care exhibited among fishes. Open bars, alloparental care of eggs; solid bars, alloparental care of free-swimming young. Data are summed arbitrary scores calculated from Table 1 (see text for further explanation).

of alloparental care (Figure 1). Has alloparental care played a role in the evolution of egg size and/or clutch size in these fishes (Wisenden and Keenleyside, 1995)? Much of the fitness equation hinges upon relative antipredator competence of young in broods of mixed sizes (Wisenden and Keenleyside, 1992, 1994; Fraser et al., 1993; Fraser and Keenleyside, 1995; Fraser, 1996). Size at hatching is variable in cichlids, within a clutch, within a species and among species (Coleman and Galvani, 1998; Lagomarsino et al., 1988). Size at hatch also affects antipredator competence (Warkentin, 1995). If larger eggs produce larger hatchlings, then alloparental care could favour the evolution of big eggs.

Costs associated with alloparental care of free-swimming young in cichlids have received less attention than benefits. There is a finite number of young that parents can defend (Wisenden and Keenleyside, 1995), which produces an optimal clutch size (Wisenden, unpublished data). However, mixed broods in nature rarely exceeded more than 25% adopted young, so it would seem that the combined number of young in a mixed brood does not frequently exceed the parent's ability to defend it. Although parental effort is constrained by food supply (Townshend and Wootton, 1985; Mrowka, 1986; Lavery and Kieffer, 1994; review: Smith and Wootton, 1995), the cost of alloparental care above that which would have been incurred without incorporating non-descendant young, has never been quantified. Descendant young showed suppressed growth after the addition of extra young (Wisenden and Keenleyside, 1994, 1995), but

there is not yet any measure of how this may translate to offspring survival or parental fitness.

The species of Lake Tanganyika are understudied, but intriguing patterns have already emerged that merit further investigation. Why do some Lake Tanganyikan species have such high levels of alloparental care while others have little or none? How does the cost/benefit ratio of alloparental care change across species? What factors determine spatial and host-species variation in rates of alloparental care (Ochi and Yanagisawa, 1996)? Does the nature of the cost/benefit relationship depend on the species involved? How have these species groups co-evolved *vis à vis* forage specialization and fry-retrieval behaviour? In the bagrid catfish–cichlid communal care system (McKaye et al., 1992), why do cichlids contribute to care in some cases but not in others?

Why are there no known examples of egg dumping among mouthbrooding cichlids? The high investment per egg typical of mouthbrooders may have contributed to this. Spawning *Synodontis* catfish brazenly intrude upon cichlids spawning on open, flat surfaces (pers. obs.) and parasitize gametic investment and parental care of the female. If these catfish can successfully exploit this system, then why not conspecific and heterospecific mouthbrooders? Perhaps multiple maternity recently discovered with orally incubated broods of a Lake Malawi cichlid (Kellogg et al., 1998) may prove to be such a case.

Among the forms of alloparental care summarized in Table 1, some are clearly parasitic, some are suspected, or have been demonstrated, to be mutualistic, while others are perhaps commensalistic. For the majority, however, the nature of the alloparental relationship is simply not known. This knowledge is critical for a complete understanding of the evolutionary mechanisms that gave rise to and maintain alloparental care. Careful tests of cost and benefits associated with alloparental care should be given priority in future studies. This is major gap in our present knowledge.

Molecular techniques such as DNA fingerprinting, having made substantial contributions to the study of parental care in birds (Birkhead and Moller, 1995; Avise, 1996; Westneat and Sherman, 1997), are now being applied to alloparental care in fishes (Munehara et al., 1990, 1994; Philipp and Gross, 1994; Colbourne et al., 1996; Kellogg et al., 1998).

Nest associations among cyprinids have been known for over a century (Cope, 1869) and yet this fascinating phenomenon has only recently received serious attention (Johnston and Page, 1992; John-

ston, 1994a, 1994b; Shao, 1997a, 1997b). The fact that nest associations occur on or near most university campuses makes this neglect of basic fish biology very surprising. Instead, the majority of work on alloparental care has focused on exotic species from tropical climes (e.g. Wisenden and Keenleyside, 1992). Much work remains to be done. In particular, more research on the costs and benefits to hosts and associates, such as recent work by Baba et al. (1990), Fletcher (1993), Johnston (1994a, 1994b) and Shao (1997a, 1997b) would be very helpful. Open nests constructed on loose gravel appear to be vulnerable to opportunistic spawners (Table 1). The widespread nature of the phenomenon suggests that the cost of tolerating associates is low or that the cost of ejecting them is high. There are many questions for future study. What factors determine host species selection? Hunter and Hasler (1965, p. 280) note that redbfin shiners were attracted to the territory of a breeding pair of the Central American cichlid species *Cichlasoma bimaculatus*. How specialized are nest associates for any particular host species? Under what ecological conditions do some minnow species that act as nest associates decide instead to construct their own nests (Johnston and Page, 1992)? Is this facultative opportunism or an alternative reproductive strategy subject to frequency-dependent selection? Hosts sometimes tolerate swarms of nest associates, other times they drive them away (Kramer and Smith, 1960). Is the relationship (mutualistic, parasitic) between associates and host contingent upon extenuating environmental conditions? Some minnows cooperate in nest construction (Wallin, 1989). What is the nature of the relationship and pay-offs among these males?

Alloparental care raises questions that are at the core of evolutionary theory: how can investment in non-descendant young be maintained by natural selection? Attendant to finding solutions to these challenges are the rewards of uncovering basic natural history of some fascinating fishes, of which surprisingly little is known. It is my hope that this review will stimulate future work in this direction.

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Appendix

In the course of researching this review, it became apparent that the classifications of many species associated with alloparental care have undergone recent name changes. This has been a result of reassignment to new or reinstatement of old taxonomic classifications, or of incorrectly used classifications (i.e. invalid or misidentified species). Fishes with different classification from that given in the text are listed below as the given name followed by the currently accepted name (Eschmeyer et al., 1998). Names in the text not listed here remain unchanged. Name differences that appeared to be spelling errors and not a reclassification event, are corrected in the text (i.e. two 'i's in *Zacco temminckii*, and *Padogobius martensii*).

- Cichlidae: *Cichlasoma bimaculatus* corrected to *Cichlasoma bimaculatum*; *Cichlasoma citrinellum* and *C. longimanus* assigned to *Amphilophus citrinellus* and *A. longimanus*; *Cichlasoma dovii* assigned to *Parachromis dovii*; *Cichlasoma maculicauda* assigned to *Vieja maculicauda*; *Cichlasoma nicaraguense* assigned to *Hypsophrys nicaraguensis*; *Cichlasoma nigrofasciatum* assigned to *Archocentrus nigrofasciatus*; *Cyrtocara pictus* mislabelled, valid as *Ctenopharynx pictus*; *Cyrotocara pleurostigmoides* assigned to *Copadichromis pleurostigmoides*; *Geophagus steindachneri* a junior synonym of *Geophagus honda*; *Haplochromis polystigma* assigned to *Nimbochromis polystigma*; *Haplochromis macrostoma* assigned to *Tyrannochromis macrostoma*; *Haplochromis chrysonotus* assigned to *Copadichromis chrysonotus*; *Lamprologus attenuatus* and *L. elongatus* assigned to *Lepidiolamprologus attenuatus* and *L. elongatus*; *Lamprologus brichardi*, *L. pulcher*, and *L. savoryi* assigned to *Neolamprologus brichardi*, *N. pulcher*, and *N. savoryi*; *Tilapia melanopleura*, junior synonym of *Tilapia zillii*.
- Cyprinidae: *Nocomis umbratilis* mislabelled, valid as *Lythrurus umbratilis*; *Leuciscus rutilus* assigned to *Rutilus rutilus*.

- Percidae: *Lucioperca sandra* junior synonym to *Sander lucioperca*.
- Serranidae: *Siniperca kawamebari* assigned to *Coreoperca kawamebari*.

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