

Social and reproductive behaviors: Parental care in fishes

S. Balshine^a and K.A. Sloman^b, ^aMcMaster University, Hamilton, ON, Canada; and ^bUniversity of the West of Scotland, Scotland, United Kingdom

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Key points

- About 30% of the 500 known fish families show some form of parental care, most often care is provided by only one parent.
- Across families of fish, male care (50%) is more common than female care (30%), with biparental care accounting for only about 20%.
- Care in fishes ranges from hiding eggs and then abandoning them to guarding young in rearing structures, through to carrying young in or on the parent's body cavity, and even to feeding the young.
- In many species that show paternal care, androgen levels are high pre-spawning, fall during spawning, and then rise again during the parental care period.
- The neuropeptides isotocin, arginine vasotocin, prolactin and galanin all play a role in modulating parental care behaviors.

Glossary

Androgen Any natural or synthetic steroid hormone that is principally involved in growth, development, and maintenance of the male reproductive system and secondary sexual characteristics.

Arginine vasotocin A neuropeptide homolog of arginine vasopressin found in mammals. These hormones are released not only at the posterior pituitary gland, but also widely in the brain where they act as neuromodulators.

Isotocin Homolog of the mammalian hormone oxytocin, known to influence social behaviors in fish.

Oviposition An act of laying eggs by oviparous animals (animals laying eggs that develop outside the female's body).

Phylogeny Modification of the structure and function of a species or group of species throughout their evolutionary history.

Prolactin A protein hormone primarily produced in the pituitary acting on ion balance and reproduction.

Sneaker male A male phenotype that sneaks into the territory of a conventional male to mate with a female.

Sperm competition The competition between sperm from two or more males to fertilize the egg of a female.

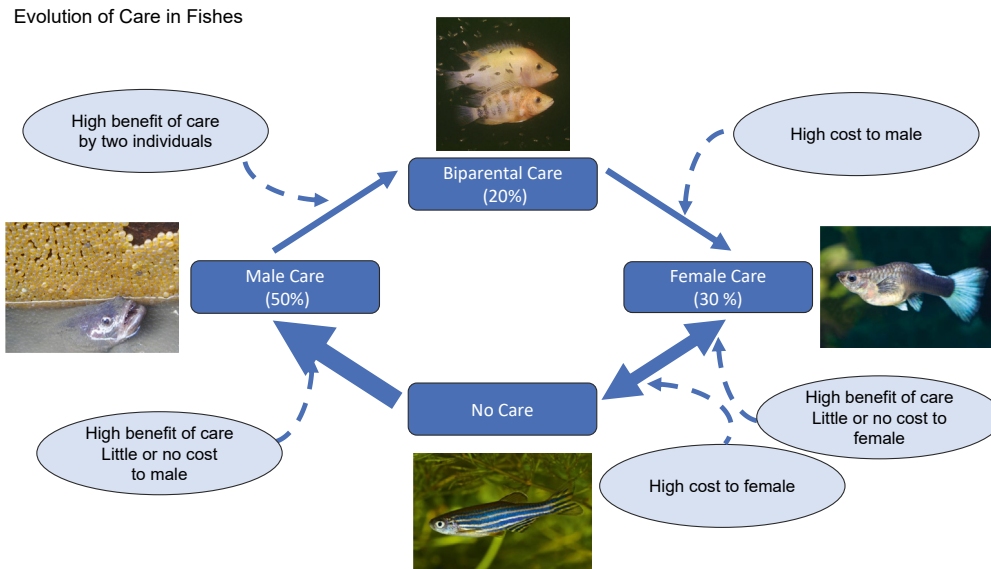
Viviparity The production of live young that develop before being released into the external environment.

Zygote The initial cell of a new organism, usually formed by the joining of an egg and sperm at fertilization.

Abstract

Although parental care is not the norm across fish species, it does occur in some fish species with parents defending, cleaning and aerating young, and even sometimes providing food for young. How much care is provided, and which sex provides care, varies across species and is shaped by life history, phylogeny, benefits (increased survival) and costs (decreased survival, growth and mating) for males versus females. As male care is common in fishes and the sex of the caregiver often varies between closely related species, many fish studies have been conducted to test ultimate theories of parental care evolution. In contrast, the physiological mechanisms underlying care in fishes are less well understood with the neuropeptides isotocin, arginine vasotocin, prolactin and galanin emerging as key modulators of parental care behaviors.

Teaching slide



A traditional stepping stone model of the evolution of parental care in fishes with external fertilization. There are four possible states of parental care: no care, male, female, or biparental care. While most fishes do not provide care for their young (no care), the arrows show the likely direction of evolution among states. Arrow size and direction reflects the number of evolutionary transitions between those two states and the direction of the transitions. The circles with the dashed arrows refer to the selective factors promoting that particular transition in care. While most fishes do not provide parental care for their young, it is thought that transitions occur among fish parental care states. Of the fish families that show care, most (50%) provide male-only care, with female-only care (30%) and biparental care (20%) being less common. The fish families that include species in more than one state were counted more than once. This figure is based on Gross MR and Sargent RC (1985) The evolution of male and female parental care in fishes. *American Zoologist* 25: 807–822, and on a review of 422 families of teleost fish families.

Introduction

Parental care, the investment in young after fertilization, may not be a behavior that immediately jumps to your mind when you think of fishes. However, thousands of fish species provide care for their young, and provide care for young in different ways. Which parent provides the care also varies between one fish species and another and even closely related species can have dramatically different care habits (Blumer, 1982). The impressive variation in parental care tactics has made fishes an excellent group for testing our understanding of how parental care evolves and there has been great interest in understanding what drives this variation across fishes (Balshine-Earn and Earn, 1998; Mank et al., 2005; Gross, 2005). Indeed, studies with bony fishes have helped shape our theoretical understanding of how parental care influences sexual selection (Baylis, 1981; Alonzo, 2012). Sex differences in parental investment patterns have long been thought to influence the direction and intensity of mating competition (Trivers 1972). The many fish species with male parental care provided an important counter example and clarified that offspring processing rates more directly influence which sex competes most, and the intensity of that competition (Clutton-Brock and Vincent, 1991).

In contrast, the physiological mechanisms underlying parental behavior in fishes are less explored. Prolactin, isotocin, vasotocin, galanin and androgens have all been examined in the context of parental care (Bukhari et al., 2019; O'Connell et al., 2012; Knapp et al., 1999), but compared to other vertebrates, the proximate control of parental care in fishes is still only beginning to be uncovered. In this article, we describe the common forms of care and patterns related to the sex of the care giver typically observed in fishes. We then provide an explanation for these patterns based on the costs and benefits of parental care. Finally, we review the

current available information on physiological underpinnings of fish parental care behavior, albeit limited, and suggest areas for future research.

Before embarking on a review of parental care in fishes, it is necessary to clarify the terms used when describing behavior of parents toward their young. The term “parental care” is used to describe any behavior performed by parents that appears likely to improve the survival and reproduction of the young. Robert Trivers in 1972 coined a more restrictive term “parental investment” to refer to any action by parents that increases offspring fitness at a cost to parental fitness (because it curtails their ability to invest in future mating, fecundity, survival, or further parental care). The terms parental effort or parental expenditure refer specifically to the time and effort spent on parental care of offspring, again referring to actions that are thought to increase offspring fitness, such as defending offspring against predators. Effort is related to parental investment but does not necessarily imply fitness costs for parents, as the costs of parental care may change with an individual's age, status, or condition.

Which behaviors to include or exclude when using the terms parental care or parental investment can be challenging. For example, building and defending a nest may not only have positive impact on offspring fitness (parental effort) but also may increase the chances of attracting a mate (mating effort) (Stiver and Alonzo, 2009). Many fish species provide eggs with large quantities of yolk before releasing them to the external environment; the largest known fish egg belongs to the coelacanth (*Latimeria chalumnae*) with a diameter between 7.5 and 9.0 cm and a mass of 334 g (Balon, 1991). Whether or not such maternal provisioning should be considered as parental care or parental investment has been much debated. Within and across different species of fishes, females vary considerably in the extent to which they provision eggs, and such provisioning has profound effects on development time, survival of young, and the ability for a female to invest in future young (Gross 2005; Smith and Wootton, 2016). In this article, we use a broad definition of parental care that includes both egg provisioning and nest construction.

Patterns and diversity in parental care

Form of care

Unlike birds and mammals, where offspring require some form of parental assistance, most fish species do not provide parental care. However, in 25% of fish species, care has evolved and the manner in which care is performed is highly variable across species (Fig. 1). Fish care ranges from hiding of eggs and then abandoning the area, to guarding young in elaborately prepared and maintained rearing structures for up to several months, and all the way to carrying young in or on the parent's body cavity and even to the feeding of young (Smith and Wootton, 2016).

The simplest form of fish parental care is the hiding of fertilized eggs. Female salmon and trout, for example, will excavate nests (called redds) by digging simple depressions with their tails; the eggs that are laid in these redds are fertilized and then buried by the female (McPhee and Quinn, 1998). In contrast to the simple pit built by the female salmonids, some fish species are amazing construction workers. Lake Malawi's cichlid, *Cyrtocara eucinostomus*, creates crater-shaped nests that are more than 3 m in diameter (McKaye et al., 1990), while the three-spined stickleback, *Gasterosteus aculeatus*, constructs elaborate nests woven of plant material carefully glued together with a special kidney glycoprotein secretion known as spiggin (Fig. 1A; Smith and Wootton 2016). A contender for the most impressive nest builder of all fish species may be the small white-spotted pufferfish, *Torquigener albomaculosus*, which constructs enormous 2 m ringed sand nests with a series of groves and mountains that looks like a maze from above and take nearly 2 weeks to complete (Bond et al., 2020). The structure of the nest itself will determine its function and whether it is mainly for natural or sexual selection or both. Natural selection benefits include providing protection and hiding areas from predators, to protecting young from harsh environmental factors such as fast currents or changing abiotic conditions.

Some fish species take parental care a step further than simply building a nest by tending and defending the eggs, embryos, or larvae until they hatch. Such guarding species sometimes build their own nests, while others choose an area (cavity, cave or natural burrow, underside of a rock, or log) to use as a spawning and guarding site. Typically, fish species that significantly modify the substrate to receive eggs (nest builders), also guard their eggs against predation (Fig. 1B). The amount of time spent protecting young varies from 1 day in the Sacramento perch, *Archoplites interruptus*, to over 4 months in the Antarctic plunderfish, *Harpagifer bipinis* (Mathews, 1965; White and Burren, 1992). Many fish species go beyond simple guarding by aerating the eggs using their fins. By fanning the eggs with their fins, parents ensure that fresh, aerated water is passed over the eggs on a regular basis. Parent fishes will often clean their eggs, placing their mouths against the eggs and sucking away detritus or removing dead or fungus-ridden eggs (Smith and Wootton 2016).

Although the terms “brooding” and “incubation” are commonly used by fish biologists when describing fish parental care, fishes do not truly incubate eggs, as heat is not transferred to the eggs by parents. However, many fish species protect their young internally, and some even have live births (known as live-bearing or viviparity, Weller et al., 2022; Goodwin et al., 2002). Species of fish that protect or incubate their young internally may do so in their mouths (e.g., marine catfishes and cichlids, Fig. 1C), in ventral brood pouches (e.g., seahorses and pipefishes, Fig. 1D), on hooks (e.g., *Kurtus* spp.), embedded in skin (e.g., American banjo catfish, Fig. 1E), or in gill chambers (e.g., cavefishes). Internal brooding is an extremely effective method of protection because the only way a predator can capture or kill young fishes is to injure or kill the parent or force the parent to eject its young. For example, male seahorses and pipefishes receive eggs from their female partners, which the males internally fertilize and then aerate and nourish for a few weeks in an enclosed pouch (Wilson et al., 2003; Whittington and Friesen, 2020). In addition to providing nourishment, paternal brood pouches of male pipefishes have distinct microbial communities and there is microbial transfer from parents to

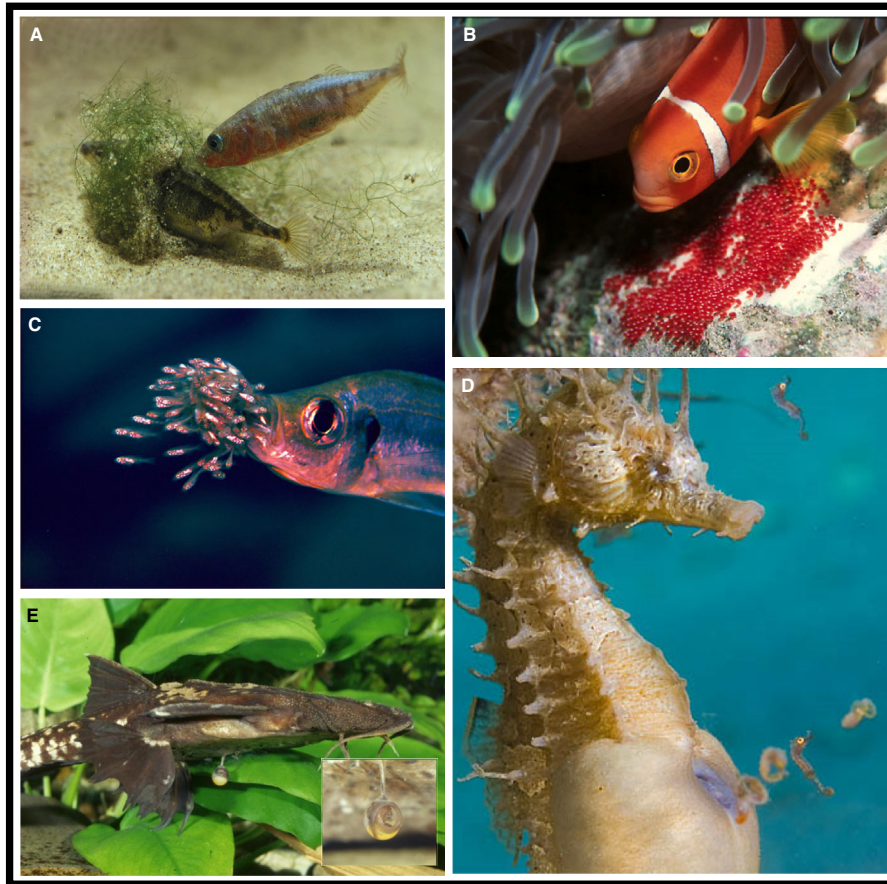


Fig. 1 Examples of parental care in fishes. (A) A male three-spined stickleback (*Gasterosteus aculeatus*) observing a female entering his nest; (B) a male clownfish (*Amphiprion percula*), inspecting eggs in its nest; (C) a female mouth-brooding cichlid from Lake Tanganyika, *Haplotaxodon microlepis* collecting young in its mouth; (D) an unnamed seahorse, *Hippocampus* spp. giving birth to live young; and (E) a female eel-tailed banjo catfish, *Platystacus cotylephorus*, carrying young embedded on the skin of her abdomen. (A) Reproduced with permission from Photolibrary. (B) Reproduced from Buston, P.M., Balshine, S., 2007. Cooperating in the face of uncertainty: A consistent framework for understanding the evolution of cooperation. *Behav. Processes* 76, 152–159, with permission from Elsevier. (C) Reproduced with permission from <http://www.deeblestone.com> (E) Reproduced with permission from Ingo Seidel.

offspring (Roth et al., 2012). The dads eventually give birth (via a series of forward and backward muscular contortions) to young, one at a time (Wilson et al., 2003).

The most complex or elaborate parental care behaviors found in fishes are undoubtedly the feeding of young post-hatch and caring for nutritionally independent young. Both male and female parents of the Central American convict cichlid, *Cichlasoma nigrofasciatum*, carefully lift up fallen leaves for their young to provide them with benthic prey found underneath the leaf litter (Keenleyside, 2012). *Symphysodon discus* young as well as the young of some other cichlid species ingest the epidermal mucus from their parents' body (Buckley et al., 2010). In many mouth brooding species, parents appear to be able to signal imminent danger to their young by using a specific jolt or calling behavior that consists of open-and-shut snapping of the pelvic fins while swimming backward with the head pitched downward. The young respond to these warning movements by settling down into the substrate or swarming and entering the parents' mouths where they can be kept safely hidden until the danger has passed (Keenleyside, 2012). Finally, in Tanganyikan cichlids, such as *Neolamprologus brichardi* and *Neolamprologus pulcher*, even sexually mature young continue to be vigorously guarded by their parents (Dey et al., 2017).

Sex of the caregiver

In fishes, care can be provided by the female alone (maternal or female-only care), by the male alone (paternal or male-only care), or by both parents together or in sequence (biparental care, Fig. 2). About 30% of the 500 known fish families show some form of parental care, and most often (78% of the time) the care is provided by only one parent (Gross and Sargent, 1985; Mank et al., 2005). Usually in fishes it is the male who provides care; male care (50–84%, Fig. 2A) is much more common than female care (up to 30%) with biparental care accounting for up to 20%, (Fig. 2B, Mank et al., 2005). In some species, such as Galilee St. Peter's

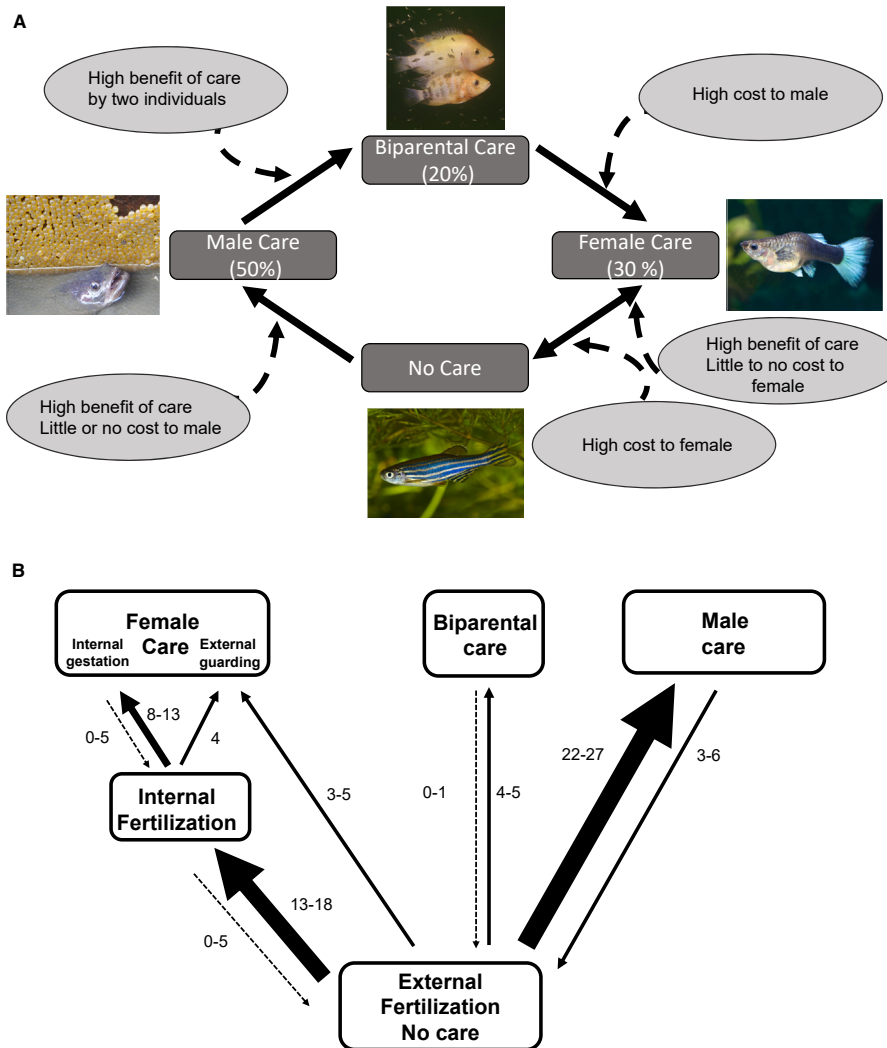


Fig. 2 Evolution of parental care in fishes. (A) The commonly accepted stepping-stone model of parental-care evolution in fishes with external fertilization (the data are based on 422 families of teleost fish families). There are four possible states of parental care: no care, male, female, or biparental care. The arrows show the likely direction of evolution among states. The dashed arrows refer to the selective factors promoting transitions in care. The percentage of teleost families in each state is shown, and families including species in more than one state are counted more than once. (B) An alternative evolutionary model for transitions among parental care states. Arrow size reflects the number of evolutionary transitions and the numbers by each arrow refer to the minimum and maximum number of possible transitions. The analysis is based on data for 228 families of ray-finned fishes (Actinopterygii). (A) Reproduced from Gross, M.R., Sargent, R.C., 1985. The evolution of male and female parental care in fishes. *Am. Zool.* 25, 807–822, by permission of Oxford University Press. (B) Reproduced from Mank, J.E., Promislow DEL, Avise, J.C., 2005. Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. *Evolution* 59, 1570–1578, with permission of John Wiley and Sons.

fish (*Sarotherodon galileus*) and the brown bullhead (*Ameiurus nebulosus*), parental care is labile with male-only, female-only, and biparental care occurring in the same population (Balshine-Earn and Earn, 1998; Blumer, 1986).

Explaining the patterns and diversity of fish parental care

Many interesting questions arise from exploring the observed patterns in fish parental behavior. For example, (1) why is male-only (paternal) care so common in fishes? (2) why is female-only (maternal) care typically associated with internal bearing in fishes? and (3) why do so many more freshwater fishes provide care (57% of freshwater fish families) compared to marine species (only 16%)? This next section addresses these related questions about who should care, and we also provide a review on our current understanding of the costs and benefits associated with parental care in fishes:

1. *Why so much male-only (paternal) care in fishes?* A lot of theory has centered on why, in contrast to other groups of animals, it is the males among fishes that usually provide care. Initially, it was thought that higher rates of paternity would be associated with

external fertilization, and so external fertilization predisposed male fishes to care (Trivers, 1972; Blumer, 1982); however, it turns out that external fertilization does not protect against paternity loss. Strong sperm competition and sneaker reproductive tactics have evolved many times in external fertilizing fishes, and paternity is not necessarily more certain in external fertilizers (Neff and Gross, 2001; Mank and Avise, 2006). Later, it was argued that the order in which gametes are released predisposes male fish to care. The idea proposed was that in external fertilizing fishes, females will shed eggs before males release sperm, effectively providing females with an opportunity to desert their partners. Hence, male externally fertilizing fishes are abandoned in the cruel bind and are left in charge of the babies by females who have an opportunity to abandon first (Dawkins and Carlisle, 1976); however, in the majority of externally fertilizing fishes, both males and females release gametes simultaneously (Keenleyside, 2012). In some species (e.g., black gobies), caring males release sperm before females lay their eggs (Locatello et al., 2007) and still don't desert, while in other species, females provide care even when males release their gametes last (Williams, 1975).

A third idea, known as the association hypothesis (Williams, 1975), is currently considered to be the most parsimonious for explaining the preponderance of male care in fishes. Williams (1975) argued that when there are benefits to providing care, it will be the sex with the lowest costs associated with care that will provide the care. He surmised that this will usually be the sex that is already more closely associated with the young. For example, it will be the female in most internal fertilizing fishes, because the female retains the embryos inside her body; however, it will be the male in species with male territory defense. If males already must defend a territory in order to mate and attract females, then defending young on that territory will not represent a large increase in energy or time over and above the cost of defending a territory (Ah King et al., 2005). Moreover, male reproductive rates are not necessarily curtailed by providing care, because multiple females may spawn with a single male (Stiver and Alonzo, 2009). Male fish can often care and court. This is especially true when females are attracted to particular spawning areas because of reduced offspring mortality. In fact, in some fish species, females are most attracted to caring males that already have eggs in their nests (Jamieson, 1995). In contrast to males, the provisioning and protection of young can severely impact female growth and fecundity (Balshine-Earn, 1995). Given that a male holding a territory can attract and mate with several female fish at once, the extra costs of providing care for young in an already defended territory often will be lower for males than for females, favoring male-only care.

2. *Why is female-only or maternal care associated with internal bearing in fishes?* Internal gestation is rare in fishes (11% of families) but has evolved independently at least eight times and is strongly associated with female care (Mank et al., 2005). Once internal fertilization has evolved, the retention of eggs for longer periods would have required little re-organization and would confer a substantial protection and survival benefit to young. A protracted association between females and the zygote is thought to be the basis for selection of internal fertilization and is considered an irreversible condition (Mank et al., 2005). In families with internal fertilization and care, the female that provides the care in 86% of the cases. In contrast, when external fertilization and parental care co-occur, it is usually the male that provides care (76% of cases).
3. *Why so much more care in freshwater species?* The open ocean provides a relatively stable, safe, and homogeneous environment for egg development, egg predators are relatively rare, and water conditions do not fluctuate quickly. In contrast, freshwater environments, especially shallow ones where fish eggs are typically released, vary tremendously in time and space. Hence, selection of particular spawning locations can have massive impacts on egg development and survival. This benefit (most often observed in highly heterogeneous habitats) would have led to male defense of the best or favored female spawning sites and to female egg clumping (Baylis, 1981; Gross, 2005). Under these conditions (male territoriality and multiple females being attracted to the same spawning site), guarding eggs in addition to a territory would not be particularly costly (Ah-King et al., 2005).

Costs and benefits of parental care

The answers to all of the above questions rely on understanding both the costs and benefits of care. The main benefit of parental care is that it improves survival and development of young. The three main costs of parental care are (1) decreased parental survival; (2) increased time until the next breeding attempt; and (3) reduced future fecundity (via suppressed feeding and growth) (Baylis, 1981; Gross and Sargent, 1985; Gross, 2005). Experiments with various fish species have provided support for these costs and benefits. For example, when parent sticklebacks and cichlids have been experimentally removed, eggs and young fail to survive (Smith and Wootton, 2016). Experiments that have manipulated the benefits (relatedness and number of young) have shown that parents usually can dynamically adjust the level of care in relation to these changes in benefits (Neff, 2003). Experimental manipulations have also quantified the costs of care. First, brooding male pipefish (*Syngnathus typhle*) are less likely to survive than non-brooding males (Svensson, 1988). This may be because parents are more conspicuous or take bigger risks, or because caring is energetically costly while limiting foraging time, which in turn reduces body condition and makes parents more susceptible to predators, disease, and starvation. Second, in the cichlid fish, *Sarotherodon galileus*, caring males and females have longer inter-spawn intervals (Fig. 3A) and fewer opportunities to feed than noncaring fish (Balshine-Earn, 1995). Caregivers also have a lower body mass, which reduces female fecundity as a result of smaller subsequent clutches compared to those that spawn eggs but do not provide care (Fig. 3B and C; Balshine-Earn, 1995). Third, in another biparental cichlid, *Herotilapia multispinosa*, by varying sex ratios it has been shown experimentally that males desert their clutches far more frequently in female-biased areas, where their probability of mating again is high (Keenleyside, 2012).

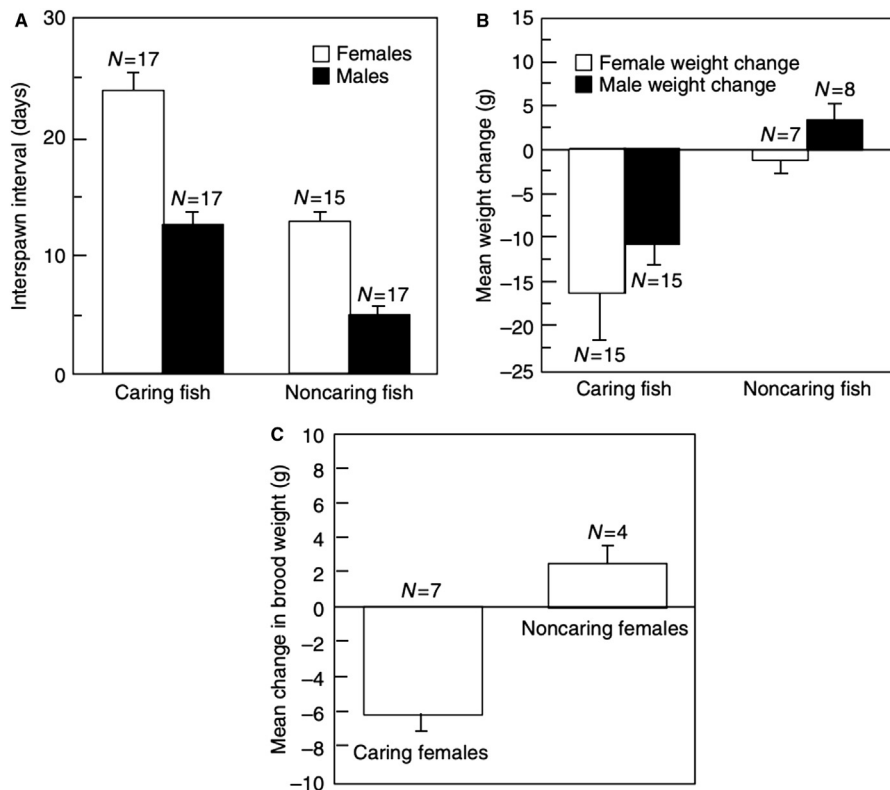


Fig. 3 Parental care in Galilee St Peter's fish. (A) The inter-spawn interval for caring versus noncaring male (in black) and female (in white) Galilee St. Peter's fish. (B) Body mass change for caring versus noncaring St. Peter's fish. (C) A decrease in fecundity was observed for caring but not for noncaring female St. Peter's fish. Reproduced from Balshine-Earn, S., 1995. The costs of parental care in Galilee St. Peter's fish *Sarotherodon galilaeus*. *Anim. Behav.* 50, 1–7, with permission from Elsevier.

Evolutionary trajectories of parental care among fishes and phylogenetic comparisons

Parents and their young have often co-adapted to particular levels of care (constraining care tactics) so that sensible manipulative experiments to tease apart the causes and consequences of care are not always feasible. Fortunately, developments in fish phylogenies have allowed phylogenetic-based comparative studies (studies that compare across species while controlling for shared ancestry) to provide a complementary, and powerful way to understand the evolution of parental care (Goodwin et al., 1998; Mank et al., 2005).

For 40 years, the most widely accepted hypothesis for the evolution of parental care in fishes has been a stepping-stone model in which care evolved from an ancestral state of no care to biparental care via two intermediate stages of female-only and male-only care (Fig. 2A; Gittleman, 1981). While within-family phylogenetic-based comparative studies have largely supported this stepping-stone model, a cross-family comparison by Mank and co-workers, with representatives across 228 fish families, found no evidence for the stepping-stone model (Fig. 2B). Instead, they showed that both female and male care have arisen from the precursor state of no care in fishes (Mank et al., 2005).

Transitions between care states are thought to have arisen via changes to the costs and benefits of parental care (Gross and Sargent, 1985). For example, biparental care is thought to arise from male-only care when females lay very large eggs and the benefits of defense by two parents outweighs the female-fecundity costs of care (Gross, 2005). Biparental care is argued to lead to female-only care when male future mating opportunities increase (Keenleyside, 2012). Female-only care is thought to have evolved from no care when the fecundity costs of providing care decrease and the benefits of care in terms of offspring survival surpass these costs. Comparative studies can test these ideas by examining what factors promote transitions in care, and exploring the direction of change (Mank et al., 2005). For example, an analysis of 222 genera of cichlid fishes revealed 21–30 shifts from biparental to female-only care within the Cichlidae family (Goodwin et al., 1998). This removal of male care from the biparental state is related to a reduction in the need for biparental defense.

Physiological mechanisms underlying fish parental care

There are still major gaps in our understanding of parental care regulation in fishes. We know that a number of social, environmental, and physiological factors work together in a complex fashion to influence parental care. To date, few species have been

physiologically studied, and only a small handful of hormones and neuropeptides have been investigated in terms of how they mediate parental behavior.

Nest building

Nest building can be considered a parental behavior because a well-placed, well-built nest can enhance the development of young. Nest building often occurs with territoriality and courtship in male fishes and has been associated with high plasma androgen levels ($0.85\text{--}400\text{ ng mL}^{-1}$) (Jakobsson et al., 1999). For example, when male Siamese fighting fish, *Betta splendens*, build mucus-lined bubble nests and male three-spined sticklebacks weave vegetation nests together with glue from the special kidney protein spiggin, both of these actions are thought to be under the control of androgens (Fig. 1A; Bessa et al., 2022). Following nest building in male Siamese fighting fish, androgen levels and aggression become lower than in males that have not built nests (Agues-Barbosa et al., 2022).

Defense

Male caring fishes, such as sticklebacks, damselfish, girabali, bluegill sunfish, plainfin midshipman, and the black-chinned tilapia, have high plasma androgen levels (testosterone and 11-ketotestosterone) during pre-spawning or at spawning (Magee et al., 2006), when males compete for territories, construct nests, and court females. The androgen levels then gradually drop following spawning while males provide care (Knapp et al., 1999). This was believed to indicate an androgen-mediated trade-off between aggression and parental care and a minimal role of androgens during parental care. Recent studies, however, show that androgen levels often rise again to pre-spawning levels once eggs have hatched. For example, in black chinned tilapia, *Sarotherodon melanotheron*, androgen levels are high pre-spawning, decrease with initiation of mouth-brooding, but then rise to surpass pre-spawning levels by the end of mouth-brooding. Removal of the eggs from males eliminates this drop in androgens, suggesting that the presence of the eggs in the mouth inhibits the pituitary-gonadal axis and that, potentially, the eggs are releasing a chemical signal to delay initiation of the next brood (Specker and Kishida, 2000).

Other studies show that androgens remain high in the early stages of care, and are correlated with the frequency of parental care/defense of young in the biparental cichlid *N. pulcher*. In addition, experimental elevation of androgen levels does not inhibit paternal behavior in several fish species (Ros et al., 2004), suggesting that elevated androgen levels are not necessarily incompatible with the expression of paternal behavior (Magee et al., 2006). This may be true of fishes in general, but not other vertebrates. Male fishes often continue to court and attract females even after they have begun to provide care, but in other taxa, the mating/courtship phase of reproduction is commonly temporally separated from the parental phase (Stiver and Alonzo, 2009). Fishes do not typically feed young, but instead defend young against predators (and sometimes fan the eggs); so, high androgen levels might, in fact, be beneficial and necessary for the aggression needed during parental care. More research is needed to clarify the role of androgens in mediating parental behavior. At the same time, the importance of estrogens in modulating female care remain understudied.

Fanning and brooding

The internal physiological mechanisms determining parental fanning behaviors remain largely unexplored. Prolactin stimulates fanning behavior in the three-spined stickleback, and administration of a prolactin inhibitor in bluegills reduces fanning and defense of offspring (Páll et al., 2004; Kindler et al., 1991). In the mouth-brooding cichlid, *Oreochromis niloticus*, elevated levels of prolactin are seen in the pituitary and plasma during the brooding period (Tacon et al., 2000), and in the cichlid, *Symphysodon discus*, injections of prolactin cause an increase in egg fanning and the production of mucus secretions on which newly hatched fry feed (Buckley et al., 2010). In *S. discus*, prolactin may, therefore, increase the production of mucus for young to feed from, in a manner similar to the role of prolactin in increasing milk production in mammals (Khong et al., 2009). Other neuropeptides that have been associated with reproductive behaviors include arginine vasotocin (AVT), isotocin and galanin (Fischer et al., 2019; DeAngelis et al., 2018; Bukhari et al., 2019; Cunha-Saraiva et al., 2021) and investigations into their role during parental care are warranted.

In anemone fish, *Amphiprion ocellaris*, nurturing behaviors, such as tending to eggs and defense behaviors (e.g., egg guarding), are controlled by isotocin and AVT, respectively (Barbasch et al., 2022). Blocking of isotocin receptors reduces parental fanning and tending of eggs, whereas blocking of AVT receptors resulted in a shift of parental behavior away from defense, allowing more time to be allocated to nurturing behavior (DeAngelis et al., 2017). Galanin is another neuropeptide that may play a role in parental care. Galanin is involved in the regulation of food intake, and female *Neolamprologus pulcher* caring for young show a greater expression of galanin receptors in the hypothalamus compared to non-caring females (Culbert et al., 2022). Further investigations into the role of neuropeptides during parental care represent an exciting area for future study.

Parental care and the microbiome

In other vertebrate classes, there is increasing evidence for interaction between the parental microbiome and parental care behaviors. Both the physiology (e.g., hormone levels) and behavior (e.g., aggression) of parental care can be influenced by the gut microbiome (Cusick et al., 2021). This may be particularly important for mouth-brooding species where there is evidence for changes in buccal

microbiota in relation to parental care (Keller et al., 2018). The role of the microbiome represents an under-explored area in the context of parental care of fishes.

Future research directions and conclusions

This article makes two main points. First, nowhere in the animal kingdom is the diversity of parental-care habits greater than among fishes. This diversity means that fishes will continue as extremely useful model organisms for clarifying our theoretical understanding of the evolutionary origins of parental care (i.e., who cares?) and revealing key factors influencing the adaptive amount of care (i.e., how much to care?). The idea of reproductive trade-offs (i.e., care, but at what cost?) has provided a rich theoretical test bed for exploring the evolution of parental care in fishes. This approach has moved parental care research from a descriptive qualitative science into a strongly quantitative and predictive one.

Fishes also offer a wonderful opportunity to explore the strong and intimate link between parental care and sexual selection. Parental care promotes the survival and vigor of young (and so will clearly be influenced by natural selection), but in fishes, parental care is often strongly influenced by sexual selection as well—the best parent, the one providing the most vigorous care, is often preferred as a mating partner. A fruitful avenue for future parental care fish research will be to clarify the interactions between natural and sexual selection, and more specifically, to investigate the degree to which parental care (egg tending, defense, and nest building) can be viewed as a sexual ornament enhancing mate attraction.

The second main point in this article is that we know little about the physiology modulating care behavior in fishes. The scarce research in this area has largely focused on androgens and paternal care, while the neuropeptides that modulate parental care remain largely unexplored. There is an urgent need to expand physiological studies to encompass a larger range of hormones and neuropeptides, across more model fish species with different care behaviors (e.g., fanning, offspring retrieval, and feeding). New brain-imaging techniques and the sequencing of entire genomes may provide powerful new insights into neurophysiological systems and molecular changes that occur during parental care. An integration between ultimate and proximate analyses will undoubtedly shed light on the “how” and “why” of parental care in fishes. In other vertebrates, a link between gut microbiome and parental care behaviors is being revealed; given the great variety in fish parental care tactics, this a particularly exciting area for further research. Understanding the physiological processes of fish parental behavior and their link to population biology and the health of fisheries will arm us with a valuable roadmap to navigate the possible impacts of all too frequent anthropogenic changes to environments and ecosystems.

See Also: Conserving the next generation: Perspectives in elasmobranch reproductive research; The diversity of reproductive styles exhibited by fish; Unique aspects of reproductive energetics and endocrinology among chondrichthyes.

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