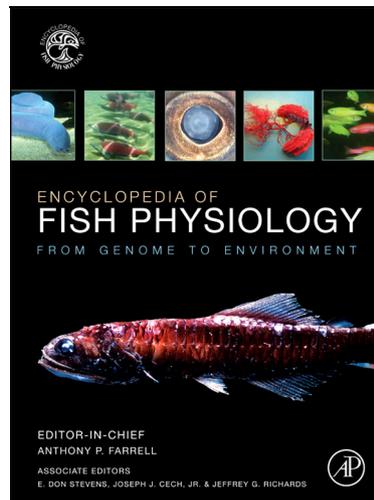


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Parental Care in Fishes

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Introduction

Patterns and Diversity in Parental Care

Explaining the Patterns and Diversity of Fish Parental Care

Physiological Mechanisms Underlying Fish Parental Care

Future Research Directions and Conclusions Further Reading

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.

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, many fishes provide care for their young, and they care for the young in different ways. Which parent provides the care also varies greatly from fish species to fish species. The impressive variation in parental-care tactics has made fishes an excellent group for testing our understanding of how parental care evolves. Indeed, studies with bony fishes have helped shape our theoretical understanding of how sexual selection operates.

In contrast, the physiological mechanisms underlying parental behavior in fishes remain poorly explored. Although to a limited degree prolactin, isotocin, and androgens have all been investigated in the context of parental care, the behavioral physiology of parental care in fishes is very much in its infancy. In this article, we examine the major forms of care and the common patterns of care found 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 much-needed 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 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, for example, defending offspring against predators. This measure 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.

The question of which behaviors to include or exclude when using the terms parental care or parental investment can also be challenging. For example, building and defending a nest may not only increase the chances of attracting a mate (reproductive effort), but also have a positive impact on offspring fitness (parental effort). Many fish species provide eggs with large quantities of yolk before releasing them to the external environment (see also **Social and Reproductive Behaviors: Nutritional Provision During Parental Care**); the largest known fish egg belongs to the coelocanth (*Latimeria chalumnae*) with a diameter between 7.5 and 9.0 cm and a mass of 325 g. Whether or not such provisioning should be considered as parental care or parental investment has been much debated. Females vary considerably (within and across species) 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.

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 way care is performed is highly variable (**Figure 1**). Fish care ranges from hiding of eggs and then abandoning the area, to guarding young in elaborately prepared structures for up to several months, and from carrying young in or on the parent's body cavity to the feeding of young.

The simplest form of fish parental care is hiding of the eggs. Female salmon and trout, for example, will excavate nests (redds) by digging simple depressions with their tails; the eggs that are laid in these redds are fertilized and then buried by the female. 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, 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 (**Figure 1(a)**; see also **Social and Reproductive Behaviors: Sexual Behavior in Fish**).

Guarders are fish species that take parental care a step further than nest builders, by tending and defending eggs, embryos, or larvae until they hatch. Some guarding species 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

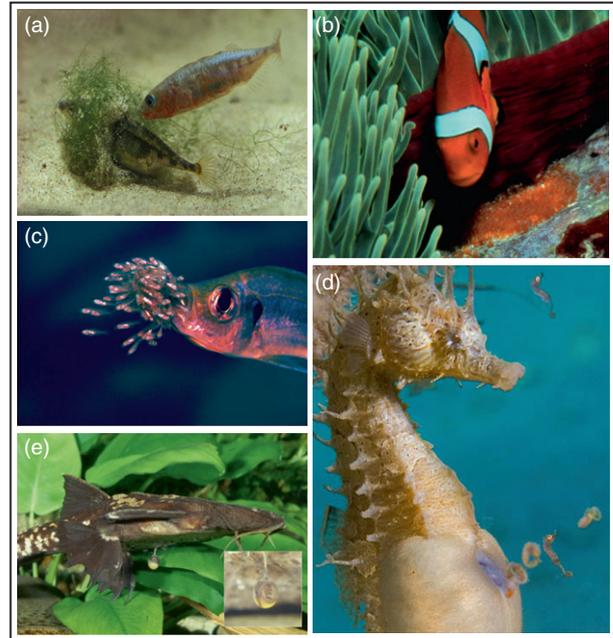


Figure 1 (a) A male three-spined stickleback (*Gasterosteus aculeatus*) observing a female entering his nest; (b) a male clownfish (*Amphiprion percula*), inspecting eggs in its nest; (c) a female mouth-brooding cichlid from Lake Tanganyika, *Haplotaxodon microlepis* collecting young in its mouth; (d)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

substrate to receive eggs (nest builders), also guard eggs against predation (**Figure 1(b)**). 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*. Many fish species go beyond simple guarding by aerating the eggs using their pelvic or pectoral fins. By fanning the eggs with their fins, parents ensure that fresh, aerated water is passed over the eggs on a regular basis. Many parent fish also clean the eggs, placing their mouths against the eggs and sucking away detritus or removing dead or fungus-ridden eggs.

Although the terms 'brooding' and 'incubation' are commonly used by fish biologists when describing fish parental care, fish 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 viviparous species; see also **Social and Reproductive Behaviors: Nutritional Provision During Parental Care**). Species of fish that

protect or incubate their young internally may do so in their mouths (e.g., marine catfishes and cichlids, **Figure 1(c)**), in ventral brood pouches (e.g., sea horses and pipefishes, **Figure 1(d)**), on hooks (e.g., *Kurtus* spp.), embedded in skin (e.g., American banjo catfish, **Figure 1(e)**), or in gill chambers (e.g., cavefish). Internal brooding is an extremely effective method of protection because the only way a predator can capture or kill young fish is to injure or kill the parent or force the parent to eject its young. For example, male seahorses, *Hippocampus whitei*, receive eggs from their female partners, which the males internally fertilize and then aerate and nourish for a few weeks in an enclosed pouch. The dads eventually give birth (via a series of forward and backward muscular contractions) to young, one at a time.

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. *Symphysodon discus* young as well as the young of some other cichlid species ingest the epidermal mucus from their parents' body. Both male and female parents of the Central American convict cichlid, *Cichlasoma nigrofasciatum*, carefully lift up fallen leaves for their young providing them with benthic prey underneath the leaf litter. Many cichlid 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 until the danger has passed. Finally, in Tanganyikan cichlids, such as *Neolamprologus brichardi* and *Neolamprologus pulcher*, sexually mature young continue to be vigorously guarded.

Sex of Caregiver

In fishes, care can be provided by the female alone (maternal or female-only care), by the father alone (paternal or male-only care), or by both parents together or in sequence (biparental care, **Figure 2**). About 30% of the 500 known fish families show some form of parental care, and most often (78% of the time) care is provided by only one parent (usually the male). Male care (50%, **Figure 2(a)**) is much more common than female care (30%) with biparental care accounting for about 20%, although a more recent comparative analysis suggests that male care may be more common (84%; **Figure 2(b)**). In some species, such as Galilee St. Peter's fish (*Sarotherodon galileaus*) and the brown bullhead (*Ameiurus nebulosus*), parental care is variable with male-only, female-only, and biparental care occurring in the same population.

Explaining the Patterns and Diversity of Fish Parental Care

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

1. *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 biotas, especially shallow ones where fish eggs are typically released, vary tremendously in time and space. Hence, selection of particular spawning locations combined with parental care can have massive impacts on egg development and survival. This benefit has led to male defense of the best or favored female spawning sites and to female egg clumping. 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.

2. *Why is female-only or maternal care associated with internal bearing in fishes?* Internal gestation is rare in fishes (11% of families) and is strongly associated with female care. Once internal fertilization has evolved, the retention of egg requires little re-organization and would confer a substantial survival benefit to young. A protracted association between females and the zygote is considered to be the basis for selection of internal fertilization. In families with internal fertilization and care, in 86% of the cases it is the female that provides the care; 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 male-only (paternal) care in fishes?* A lot of theory has centered on why, in contrast to other animals, in fish, it is the males that usually provide care. Initially, it was thought that higher rates of paternity, associated with external fertilization in fishes predisposed males to care. However, external fertilization does not protect against paternity loss; sneaker tactics and strong sperm competition have evolved many times in fishes and paternity certainly does not cause male care. Later, it was argued that the order in which gametes are released predisposes male fish to care, because in external fertilizing fishes, females shed eggs before males shed sperm, effectively providing females with an opportunity to desert their partners. Hence, male externally fertilizing

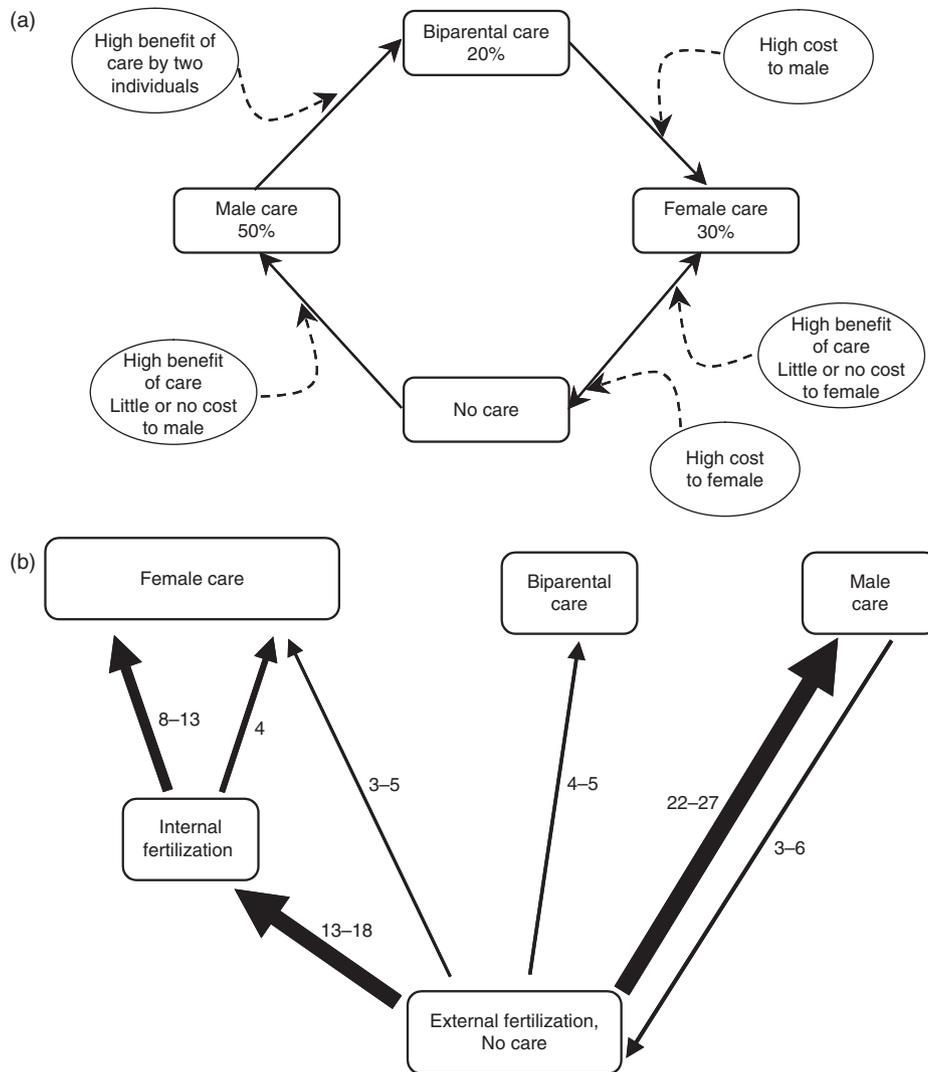


Figure 2 (a) The commonly accepted stepping-stone model of parental-care evolution in fishes with external fertilization (the data are based on 422 families of teleost fish families). There are four possible states of parental care: no care, male, female, or biparental care. The arrows show the likely 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 MR and Sargent RC (1985) The evolution of male and female parental care in fishes. *American Zoologist* 25: 807–822, by permission of Oxford University Press. (b) Reproduced from Mank JE, Promislow DEL, and Avise JC (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 are abandoned in the cruel bind of being left in charge of the babies. However, for the majority of externally fertilizing fishes, both males and females release gametes simultaneously. In some species (e.g., black gobies), caring males release sperm before females lay their eggs and in other species, females provide care even when males release gametes last.

A third hypothesis, known as the association hypothesis, is currently favored for explaining the preponderance of male care in fishes. The simple notion is that the sex with

the lowest costs of care will provide care and that these costs of care are lower for the sex already associated with the young. This is the female for internal fertilizing fishes, while it is the male for external fertilizing species with male territory defense. Defending young does not represent a large energetic or time increase over and beyond the cost of defending a territory. Moreover, male reproductive rates are not necessarily curtailed by providing care, because multiple females may spawn with a single male. 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 males that already have eggs in their nests. In contrast to males, the provisioning and protection of young can severely impact female growth and fecundity. Therefore, male care is more common in fishes because the costs of providing care are lower for males than for females.

Costs and Benefits of Parental Care

The answers to all of the above questions rely on understanding the costs and benefits of care. The 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). Experiments with various fish species have demonstrated these costs and benefits.

When parent sticklebacks and cichlids have been experimentally removed, eggs and young fail to survive. Experiments that have manipulated the benefits of parental care (relatedness and number of young) have shown

that parents usually can dynamically adjust the level of care in relation to these changes in benefits.

Experimental manipulations have also quantified the costs of care. First, brooding male pipefish (*Syngnathus typhle*) have been shown to be 11 times less likely to survive than nonbrooding males. 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 galileaus*, caring males and females have longer interspawn intervals (Figure 3(a)) and fewer opportunities to feed than noncaring fish. 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 (Figures 3(b) and 3(c)). Third, in another biparental cichlid, *Herotilapia multispinosa*, Miles Keenleyside showed by varying sex ratios that males desert their clutches far more frequently in female-biased areas, where their probability of mating again is high.

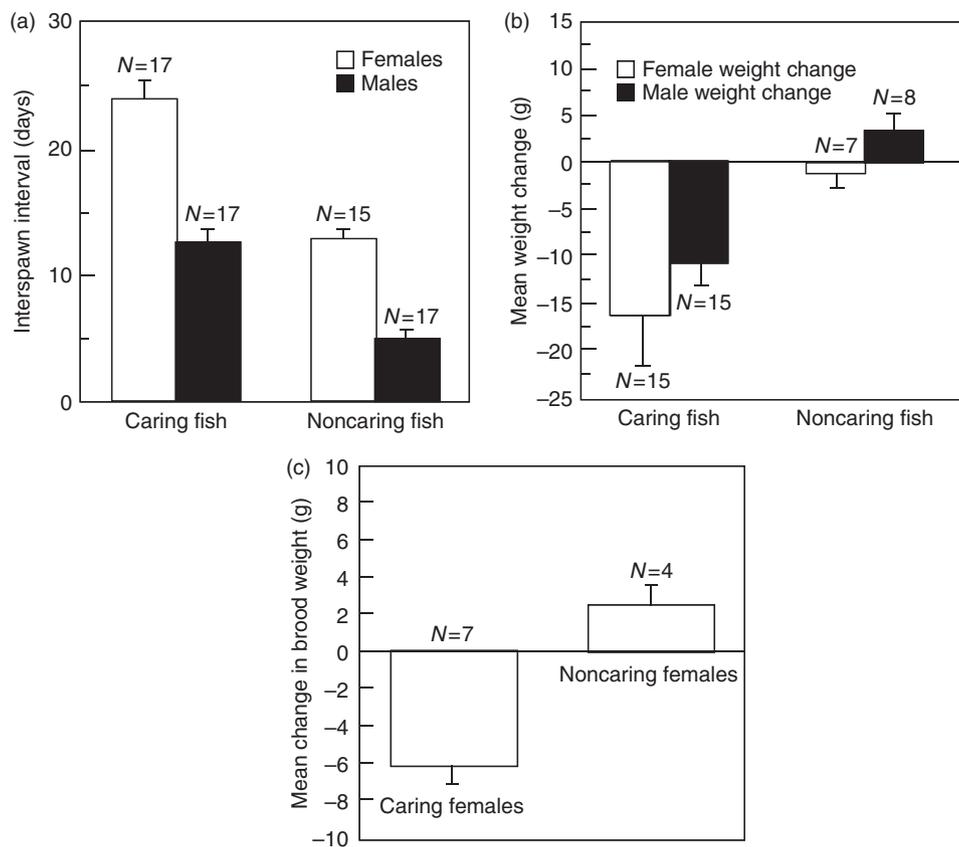


Figure 3 (a) The interspawn interval for caring vs. noncaring male (in black) and female (in white) Galilee St. Peter's fish. (b) Body mass change for caring vs. noncaring St. Peter's fish. (c) A decrease in fecundity was observed for caring but not for noncaring female St. Peter's fish. Reproduced from Balshine-Earn S (1995) The costs of parental care in Galilee St. Peter's fish *Sarotherodon galileaus*. *Animal Behavior* 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, recent developments in fish phylogenies have allowed phylogenetic-based comparative studies to provide a complementary, powerful way to understand the evolution of parental care.

For 30 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 (Figure 2(a)). While within-family phylogenetic-based comparative studies have largely supported this stepping-stone model, a recent cross-family comparison by Mank and co-workers, with representatives across 224 fish families, found no evidence for the stepping-stone model (Figure 2(b)). Instead, they showed that both female and male care have arisen from the precursor state of no care in fishes.

Transitions between care states are thought to have arisen via changes to the costs and benefits of parental care. 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. Biparental care is argued to lead to female-only care when male future mating opportunities increase. 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, examine what factors promote transitions in care, and explore the direction of change. For example, an analysis of 222 genera of cichlid fishes revealed 21–30 shifts from biparental to female-only care within the Cichlidae family. 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 (0.85–400 ng ml⁻¹). 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 (see Figure 1(a); see also Social and Reproductive Behaviors: Sexual Behavior in Fish).

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, when males compete for territories, construct nests, and court females. The androgen levels then gradually drop following spawning while males provide care. This was believed to indicate an androgen-mediated trade-off between aggression and parental care and a minimal role of androgens during parental care.

However, recent studies show that androgen levels often rise again to pre-spawning levels once eggs have hatched. Other studies even show that androgens remaining high in the early stages of care, 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 a number of fish species, suggesting that an elevated androgen level is not necessarily incompatible with the expression of paternal behavior. This may be true of fish in general, but not other vertebrates. Male fish 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. Fish 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 with the importance of estrogen and mechanisms that modulate female care remaining particularly 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 in bluegills, where administration of a prolactin inhibitor reduces fanning and defense of offspring. In the mouth-brooding cichlid, *Oreochromis niloticus*, elevated levels of prolactin are seen in the brain and plasma during the brooding period, 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 (see also **Social and Reproductive Behaviors: Nutritional Provision During Parental Care**). 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. Other hormones that have been associated with reproductive behaviors include arginine vasotocin (AVT) and isotocin (see also **Social and Reproductive Behaviors: Socially Controlled Sex Change in Fishes**) and investigations into their role during parental care are warranted.

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 has meant 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 (the costs and benefits of care) 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 predictive one.

Fishes also offer a wonderful opportunity to explore parental care's strong and intimate link with sexual selection. Parental care promotes the survival and vigor of young (so will clearly be influenced by natural selection), but in fishes can be 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.

Second, 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 neuroendocrinological mechanisms and genetics modulating biparental and female care remain largely

unexplored. There is an urgent need to expand physiological studies to encompass a larger range of hormones, more model fish species, and 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 on the 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. 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: **Social and Reproductive Behaviors: Nutritional Provision During Parental Care; Sexual Behavior in Fish; Socially Controlled Sex Change in Fishes.**

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