

Integrative approach on the diversity of nesting behaviour in fishes

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Abstract

Nests are the key elements of the reproductive repertoire of several fish species. Understanding the physiological aspects behind their nesting behaviour is imperative to improve our knowledge about behavioural mechanisms focusing on species conservation. Nevertheless, current knowledge on fish nesting is still underexplored. Here, we show a synthesis based on an integrative approach for understanding the diversity of nesting behaviour in fish. Because a nest sometimes does not involve new buildings (as in birds), we suggest a more comprehensive definition based on the behaviour instead of the structure per se. Forty fish families were recorded as they made nests, which were sorted into six main types: bowls, burrows, foam nests, nests made of plant matter and animal parts, besides nests made on clean rock surfaces. Besides spawning and parental care, these nests also serve as a refuge against predators and male competitors, as targets for sexual selection, including bowers with no parental care function, and badges of social status. We showed that, although it is advantageous to what the Darwinian fitness of the species is concerned, nesting also requires time and energy. We propose an evolution of nest types and functions, from the ancestral bowl used as refuge to derived foam nests with sexual selection functions. Physiologically, nesting is controlled by the HPG axis and particular brain circuits, this probably being the less explored subject. Finally, we highlighted that, in the changing world of the Anthropocene, nesting behaviour emerges as a framework to indicate the quality of the aquatic environments.

KEYWORDS

androgens, nesting evolution, neuropeptides, parental care, reproductive behaviour, spawning

1 | INTRODUCTION

Nest building is a component of the reproductive repertoire in several animal species, although birds are the group of animals that usually come to mind when one thinks about nests. The definition of nest is slightly variable, depending on the author and on its behavioural function; the consensus broadly defines it as a modified place for mating and rearing eggs and young (Breed & Moore, 2015; McFarland, 2006). In fish, the classic definition of nest is similar to that, considering it as a structure in which eggs

are laid and where parental care extends beyond spawning (Balon, 1975). Nevertheless, nests are known to play some other roles in the life of fish species. For example, there is a close link between nests and sexual selection (Barber et al., 2001; Kokko & Jennions, 2008; Vasconcelos et al., 2012); predation avoidance by conspecifics and other fish species (Detrich et al., 2005; Gravel & Cooke, 2013; Zuckerman & Suski, 2013); and identification of the social hierarchy (Östlund-Nilsson, 2000). Thus, considering that different authors alternatively include or exclude different information related with the main function of the nest in reproductive behaviour,

a generally accepted definition of fish nest remains to be determined. It is, therefore, imperative that nest is more clearly defined to assure that studies focus on a similar topic and cover all functions regarding nesting behaviour in fish species.

Even though reproductive behaviour has been well studied in fish, and the role and diversity of nests have been highlighted as a key element in their behavioural repertoire, knowledge on this subject is still underexplored. Whilst some species, such as the Nile tilapia (*Oreochromis niloticus*, Cichlidae), can spawn without adequate substrate (Mendonça & Gonçalves-de-Freitas, 2008), other related species, such as Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae), were reported to engage in vacuum behaviour for digging a nest in the absence of substrate (Galhardo et al., 2008), thus showing strong motivation for nesting only for one of the species. Moreover, due to our incipient knowledge, anthropogenic activities, such as deforestation and pollution, can affect nesting and disturb fish reproduction, reducing the species' Darwinian fitness and threatening their survival (Miranda-Chumacero et al., 2020). Nesting can also be impaired by tourism activity (Bessa & Gonçalves-de-Freitas, 2014), and surely by fishing (see MacLean et al., 2020; Twardek et al., 2017). Therefore, nesting can be an indicator of the individual state and ecological "health" of aquatic environments. In this context, it is necessary to understand how nesting behaviour is controlled. Here, we reviewed the diversity of fish nests and functions, including the physiological control behind them. We also suggest how nesting probably evolved and was selected at a family level. Thereby, this synthesis provides an integrative approach to understanding nesting behaviour in fish species.

2 | DEFINITION OF NESTING

As previously mentioned, nests have different functions, and they are not always associated with a structure built by the animal, although most studies commonly consider nests as part of the reproductive repertoire of fish. Few studies consider nests outside of this scope; one example is that by Nanami and Nishihira (1999), who showed that the Japanese labrid, *Choerodon jordani* (Labridae), builds a nest made of coral branches and other debris to shelter overnight. According to them, the nest is not used for reproduction, but offers protection from predators, whilst the fish is resting. We consider it to be a shelter, not a nest. For this synthesis, we suggest a definition based on the fish behaviour, instead of focusing on the structure per se: "Nesting is an activity of the reproductive repertoire that consists of remodelling the habitat by building a new structure or changing an already existing one, which increases Darwinian fitness." Hence, nesting is associated with reproductive success, such as mating and spawning, brood care, dominance signalling and sexual selection. A site or structure used only as a shelter or refuge, although it increases individual survival, will not be considered a nest herein.

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3 | WHICH FISHES ARE KNOWN TO NEST?

Nests are widespread amongst fish families. Lampreys (Petromyzontidae) are the most primitive fish to have a nesting behaviour. After reaching headwater streams of temperate areas, males of most species dig a nest in the gravel and sand by waving their bodies (Stone, 2006). One or more females may join them later to further enhance the nest before spawning. Chondrichthyes is not known to nest (Musick, 2010). The primitive *Amia calva* (Amiidae) digs a shallow circular nest ranging from 0.35 to 1 m in diameter amid the vegetation. Even though the nest is built by the male and will be visited by one or more females, eggs and young are guarded exclusively by the male parent (Ridley, 1978). Besides these, the highest diversity of nesting is found in several species from 40 fish families, which are summarized in Table 1.

4 | NEST TYPES AND FUNCTIONS

4.1 | Nest types

Nests are constructed in a variety of shapes, using several sorts of materials. We chose to sort them into six main types: bowls, burrows, foam nests; nests made of plant matter, nests made of animal parts, and nests made by cleaning rock surfaces (Figure 1). The most common kind of fish nest is the fry-pan bowl nest (Figure 1a), which is common from lampreys to cichlids. This nest is built either by transporting fine substrate or gravel with the mouth, or by digging

TABLE 1 Nest type, function and nesting behaviour according to fish Family

Fish Family	Nest type	Function(s)	Behaviour	References
Amiidae	Plant matter	Parental care	Males of the bowfin <i>Amia calva</i> dig circular nests using abundant vegetation. After spawning, eggs and young are guarded exclusively by the male parent	Ridley (1978)
Anabantidae	Foam	Parental care	In this family (represented by the labyrinth fish), the male is the main responsible for foam production and nest guarding. Males of this family make bubble nests and aggressively guard them	Ishimatsu et al. (2018), Miller and Jearld (1983)
Ariidae	Burrow Plant matter	Refuge Parental care	Nest-guarding Siluriforms include Ariidae, Ictaluridae and Plotosidae, whose individuals bury their eggs under gravel substrates; doradid catfishes build nests out of leaves. Pimelodidae, Ictaluridae, Bagridae, Doradidae, Aspredinidae, Heteropneustidae and Clariidae also dig burrows in which the eggs are kept by one or both parents	Bruton (1996)
Aspredinidae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae.	Bruton (1996)
Aulorhynchidae	Plant matter Animal parts	Refuge Badge of status Parental care	Aulorhynchidae species share some nesting habits with their close relatives, the sticklebacks. Some species nest amid large kelp algae. Males of <i>Aulorhynchus flavidus</i> guard the eggs, which will hatch from two to three weeks	Limbaugh (1962), Ridley (1978),
Bagridae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae	Bruton (1996)
Batrachoididae	Burrow Animal parts	Badge of status Sexual selection Parental care	Toadfishes nest under rocks inside bivalve or gastropod shells and inside tins. Males of <i>Halobatrachus didactylus</i> have two morphs, a nesting bourgeois male and a satellite non-nesting male. In this species, larger nests predict larger egg clutches. Male parents of the midshipman <i>Porichthys notatus</i> build nests under rocky shelters during the summer season in the intertidal zone of the eastern Pacific. They court females with a long acoustical call ("hum") produced by sonic swim bladder muscles. Males may spawn with several females, then provide paternal care for the eggs in the nest by fanning and brushing them to keep them clean and safe from predators.	Bass (1999), Brantley and Bass (1994), Carriço (2014), Gray and Winn (1961), Knapp et al. (1999), Vasconcelos et al. (2012)
Blenniidae	Burrow Rock surfaces	Refuge O ₂ enrichment Parental care	The <i>Andamia tetradactylus</i> , for example, reproduces in the high intertidal zones in crevices between rocks. The female usually spawns on the air-exposed walls of the nest. The male parent tends the eggs	Ishimatsu et al. (2018)
Callichthyidae	Plant matter Foam	Refuge O ₂ enrichment Sexual selection Parental care	To prevent eggs from drying, some species of the armoured catfish build bubble nests (about 30 cm wide and 6 cm high) on which the eggs are placed and then covered with plant matter. The female may or may not contribute to bubble production, yet she usually stays around and inspects nest building, which takes place during the night. On the next day, the couple expels and fertilizes eggs, which are placed above water level, probably due to low dissolved oxygen. The subfamily Callichthyinae are called "aphrophilic nest-guarding fishes," which means that the parents build and guard a floating bubble nest. The floating nests of <i>Hoplosternum littorale</i> , for instance, are built by the male in shallow, herbaceous swamps during the rainy season, and all females spawn in the nest simultaneously, which results in eggs always of the same age and developmental stage. The fish <i>Callichthys callichthys</i> usually build their bubble nests on the edge of shallow swamps, located in cavities and tree roots, sometimes only accessible through a narrow underwater corridor, which facilitates male vigilance during the fry's protection	Balon (1975), Hostache and Mol (1998), Mol (1993)

(Continues)

TABLE 1 (Continued)

Fish Family	Nest type	Function(s)	Behaviour	References
Centrarchidae	Bowl	Refuge Badge of status Parental care	Some Centrarchidae species, such as <i>Lepomis megalotis</i> , tend to nest. They breed in large colonies with nests clumped together and neighbours intruding on each other's nests to try to fertilize available eggs. The bluegill sunfish (<i>Lepomis macrochirus</i>) digs high-density nests—as many as 300 per colony—where the eggs are kept and juveniles are raised to independence. In the smallmouth bass, <i>Micropterus dolomieu</i> , males build their nests in shallow waters composed of sand, gravel, or rocky bottoms; then male and female swim over the nest, rubbing and nipping each other, and spawning (<i>per se</i>) for only 5 s. This mating behaviour takes 2 h, after which the female leaves, and the male guards the eggs and fry	Cargnelli and Neff (2006), Keenleyside (1972), Scott and Crossman (1973)
Characidae	Bowl Plant matter	Communal parental care	Reproductive behaviour, including nesting in characid fish, is largely understudied. Nevertheless, there is evidence of some species with nesting behaviour, such as the red-bellied piranha. Its nest is a bowl around 15 cm wide and 5 cm deep dug in the substrate. The eggs are attached to the roots and leaves inside the nest and are placed closely together, so that communal parental guarding may be done	Lima and Britski (2006), Uetanabaro et al. (1993)
Channidae	Plant matter	Parental care	Snakeheads create an open circular area for spawning buoyant eggs on the water surface, by arranging the vegetation in this area. The eggs will remain in the centre of this “floating nest” surrounded by plant debris. In the Asian genera <i>Channa</i> , both parents guard these buoyant eggs and aggressively defend them from any approach, including human ones	Ishimatsu et al. (2018), Landis and Lapointe (2010), Rüber et al. (2020)
Cichlidae	Bowl Plant matter Animal parts Rock surfaces	Refuge O ₂ enrichment Sexual selection Parental care	Cichlids are some of the best-known nest builders. Nests are even known for fossil specimens from Plio-Pleistocene. The nests, when present, are built by the male parent alone or both. They can be placed in mollusk shells, plant matter, or dug in the sandy or muddy substrate as a shallow pot. Some cichlids of the New World may also deposit their eggs on leaves, carrying them around to safer areas when necessary (<i>e.g.</i> <i>Aequidens paraguayensis</i> ; <i>Cichlasoma paranaense</i> (personal observation)). A special kind of nest was described for the African cichlid <i>Neolamprologus mondabu</i> , whose female is thought to dig nests to expose benthonic invertebrates consumed by the fry otherwise unable to consume such items.	Barlow (2002), Dupuis and Keenleyside (1982), Feibel (1987), Keenleyside (1991), Konings (2002), Ota and Kohda (2014)
Clariidae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae	Bruton (1996)
Claroteidae	Bowl Animal parts	Parental care	Males of the catfish <i>Auchenoglanis occidentalis</i> brood and guard their eggs in saucer-like depressions covered with shells and gravel. Another catfish species (<i>Dinotopertus cunningtoni</i>), may parasite <i>A. occidentalis</i> 's nests, using the host to tend for its fry	Ochi, Kanda, et al. (2001), Ochi, Onchi, et al. (2001)
Cyclopteridae	Bowl Burrow	Refuge Sexual selection Parental care	The lumpfish, <i>Cyclopterus lumpus</i> , nests in crevices or substrate depressions dug by the male, who settles a territory before females arrive inshore. The nest is tended by the male (fanning and predator avoidance). Nests of this family may include pebbles and vegetation, and their position may be concealed. Nevertheless, none of these characteristics influence egg-hatching	Goulet and Green (1988)

TABLE 1 (Continued)

Fish Family	Nest type	Function(s)	Behaviour	References
Cyprinidae	Bowl Plant matter Rock surfaces	Badge of status Parental care	Several species of carps build nests, such as the fallfish minnow <i>Semotilus corporalis</i> , which form a mound by carrying gravel from the river's bottom using their mouth. Few males make nests in this species, and most of the smaller and younger individuals act as satellites. In <i>Fundulus heteroclitus</i> and <i>Semotilus atromaculatus</i> , satellites are rare, yet nests are built similarly. Other nest types are described for minnows, such as pits (genus <i>Luxilus</i> , <i>Compstoma</i>), saucers (<i>Agosia</i>), pit and ridge (<i>Semotilus</i>), mound (<i>Nocomis</i> , <i>Exoglossum</i>), egg-clumping in defended crevices (<i>Rhinichthys</i>), and egg-clustering under rocks and logs (<i>Pimephales</i> , <i>Codoma</i> or <i>Opsopoeodus</i>). Nevertheless, at least 35 species of North American minnows spawn in other individuals' nests, probably due to the advantage of using an already constructed nest and saving their own energy; in the nests of bigger fish, these minnows face a lower probability of having their small eggs predated, besides obtaining the parental care provided by the builder of the nest	Johnston and Page (1992), Katula and Page (1998), Ross (1977, 1983), Taylor et al. (1977)
Cyprinodontidae	Bowl	Badge of status Sexual selection Parental care	Although many Cyprinodontidae species have internal fertilization, some of them nest. Nests are placed in aggressively defended territories, which are only occupied during the day by species such as the <i>Cyprinodon rubrofluvialis</i> . The flagfish <i>Jordanella floridae</i> nest in a variety of environments, from fresh to brackish waters. The <i>Cyprinodon pecosensis</i> correlates its reproductive success not only to male nuptial colour, but also to how complex the bottom of its nest is	Echelle (1973), Hale and St Mary (2007), Kodric-Brown (1983)
Doradidae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae.	Bruton (1996)
Erythrinidae	Burrow	Parental care	The erythrinid <i>Hoplias malabaricus</i> digs a burrow in shallow, slow-flowing sandy parts of the river. The couple or the male stays in the nest to guard an average of eight thousand eggs adhered to the nest bottom	Prado et al. (2006)
Gasterosteidae	Plant matter Foam	Refuge Badge of status Sexual selection Parental care	Sticklebacks (<i>Gasterosteus aculeatus</i>) are perhaps the best-studied nest-building fish, probably a heritage from Niko Tinbergen's seminal studies regarding the innate releaser mechanism. The male of this 4.5 cm long fish knits a tube-shaped nest. Firstly, the male delimits and defends a territory, then digs a pit and fills it with plant material, such as aquatic grasses or filamentous algae. The male glues the plant material together using a renal secretion and opens a passage through it by forcing his snout through the plant mesh. After the nest is completed (~ 5 hours), the male starts courting the female that swims through the nest whilst laying the eggs; afterward, the male also swims through the nest fertilizing the eggs. Males, then, stay inside the nest guarding, it aggressively, excluding dead eggs or embryos, and fanning the eggs until they hatch	Barber et al. (2001), Östlund-Nilsson (2007), Tinbergen (1974), Wootton (1976)
Gobiidae	Burrow Plant matter Animal parts Rock surfaces	Refuge Sexual selection Parental care	Gobiids have a variety of nests, such as empty mollusk shells, rock surfaces, coral, algae crevices and burrows. Gobiid mudskippers such as <i>Boleophthalmus pectinirostris</i> , <i>Periophthalmodon schlosseri</i> and <i>Periophthalmus modestus</i> are known to spawn in hypoxic intertidal mudflats excavated burrows, which requires adjustments for successful incubation, and it is probably the ancestral condition for this group. During the reproductive season, the water-filled burrow may extend into a J-shape or U-shape, providing space for an egg chamber. This chamber may be filled with air by the male, one mouthful at a time, during a low tide. The air storage is monitored by the male and replaced even during a high tide, when the burrow entrance is underwater. When the male parent perceives that the embryos are ready to hatch, it removes the air of the incubation chamber and immerses the eggs in water, allowing the fry to emerge freely. Some gobiids, such as the Australian reef <i>Paragobiodon</i> , form monogamous couples, which farm an algal nest to conceal the eggs, which, in turn, will be tended by both parents.	Ishimatsu et al. (2018), Ishimatsu and Graham (2011), Lassig (1976), Lee et al. (2005), Mück et al. (2013)

(Continues)

TABLE 1 (Continued)

Fish Family	Nest type	Function(s)	Behaviour	References
Gymnotidae	Foam	O ₂ enrichment Parental care	In the Gymnotidae family, males of the Amazonian poraquê <i>Electrophorus electricus</i> build a bubble nest by using their richly vascularized mouth epithelium (also used for air-breathing) and guard the eggs and the fry	Assunção and Schwassmann (1995), Johansen et al. (1968)
Heteropneustidae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae.	Bruton (1996)
Hypoptychidae	Plant matter Animal parts	Parental care	Tube-nose females (<i>Aulichthys japonicus</i>) lay eggs in the peribranchial cavity of an ascidian during early summer. Males establish distinct territories around the nest to tend the fry. In <i>Hypoptychus dybowskii</i> , males establish a reproductive territory around sargassum seaweed on which females spawn egg masses.	Akagawa et al. (2004), Narimatsu and Munehara (2001)
Ictaluridae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae	Bruton (1996)
Labridae	Plant matter Animal parts	Refuge Badge of status Sexual selection Parental care	Labrids build nests using coral branches, plant debris and algae. Differently from <i>Choerodon jordani</i> , which uses the modified place as refuge only, males of the <i>Symphodus</i> genera build their nests for reproduction and parental care, vigorously defending them from satellite males	Taborsky et al. (1987), Nanami and Nishihira (1999), Milazzo et al. (2016)
Lepidosirenidae	Burrow Plant matter	Refuge O ₂ enrichment Parental care	The Amazonian lungfish piramboia (<i>Lepidosiren paradoxa</i>) builds a nest in weeds and plant debris in burrows at the bottom of the swamp.	Carter and Beadle (1930)
Loricariidae	Burrow	Refuge Parental care	Another group of armoured catfish, the loricariids, may dig deep burrows on the banks of rivers. The genus <i>Pterygoplichthys</i> digs 75 cm deep burrows slightly inclined downwards along the waterline of the rivers in aggregations. As this species tolerate a broad range of environmental conditions, they usually build burrows in clay soil and tolerate low oxygen levels. This type of nest probably protects the brood from predators that do not tolerate such variation. Two interesting morphological adaptations were described in loricariids related to nesting. One of them is that the snout tentacles in reproductive males would serve as mimics of <i>Ancistrus</i> fry inside a nest, thus attracting females, as they usually choose to mate males guarding offspring. The second description is about the rostroventral position of another <i>Ancistrus</i> species, considered to be an adaptation to grasping the roof of the burrow in fast-flowing rivers despite the presence of a voluminous ventral yolk sac. Many Loricariidae species dig burrows such as those described above	Bruton (1996), Geerinckx et al. (2008), Goymann et al. (2019), Kokko and Jennions (2008), Kraak and Weissing (1996), Lienart et al. (2013), Sabaj et al. (1999)
Osphronemidae	Foam	Badge of status Parental care	In this betta fish family, the male is the main responsible for the production and guarding of their bubble nests	Rainwater (1967), Ishimatsu et al. (2018)
Osteoglossidae	Bowl	Refuge Parental care	The Amazonian giant <i>Arapaima gigas</i> builds concave bowl nests up to 50 cm in diameter and 12 cm depth in shallow parts of the river, especially amid the riparian vegetation. Nests take 3-5 days to be built by both parents, after which the couple spawns and female leaves. Males will take care of the juveniles for the following three months	Castello (2008), Gurdak et al. (2019)
Petromyzontidae	Bowl	Refuge Parental care	This family is the most primitive one known for building nests. Males mainly build the nest by themselves, yet females may join them later to further help to build it and spawn	Linville et al. (1987), Stone (2006)
Pimelodidae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae	Bruton (1996)
Plotosidae	Burrow Plant matter	Refuge Parental care	See the information described above in the Behaviour description of Ariidae.	Bruton (1996)

TABLE 1 (Continued)

Fish Family	Nest type	Function(s)	Behaviour	References
Pomacentridae	Bowl Plant matter Animal parts Rock surfaces	Refuge O ₂ enrichment Badge of status Parental care	Several species of marine fish make an algae nest by removing non-interesting species with their mouth and letting only their preferred species grow, knowingly red and green filamentous algae. Instead of farming algae, the anemonefish, <i>Amphiprion melanopus</i> , herd anemones to cover its nest by biting them. The Mediterranean damselfish <i>Chromis</i> forms colonial nests with several males nesting side by side. Denser colonies reduce the chances of nest predation; however, there are increased chances of sneaking neighbours stealing fertilizations from the guarding male. In the <i>Stegastes acapulcoensis</i> , male parents can also guard a compound nest, characterized by a single nest divided into sections of fertilized eggs attached to different rocks that are distant from each other up to 10 cm.	Limbaugh (1964), Navarrete-Fernández et al. (2014), Picciulin et al. (2004), Ross (1978), Saunders et al. (2013), Urbiola-Rangel and Chassin-Noria (2019)
Protopteridae	Burrow Plant matter	Refuge O ₂ enrichment Parental care	The African species <i>Protopterus aethiopicus</i> builds a breeding nest in hypoxic swamps composed of densely matted roots/soil sediment, in which the opening may or may not be exposed to air	Greenwood (1958)
Salmonidae	Bowl	Sexual selection Badge of status Parental care	Salmonid males swim up the rivers to reproductive areas, where they fight for the best territories, established according to water speed, depth and riverbed gravel. Females evaluate these territories to select a partner and then dig a nest using their pectoral fins; they also compete for the best territories. As a semelparous species, females may stay and guard the eggs against predation before dying. Usually, salmonid species have a very distinctive nest from the surrounding elevations in the stream, built in an ellipsoidal erosion-deposition pattern, also known as "redds"	Adkison et al. (2014), Roncoroni and Lane (2019)
Synbranchidae	Burrow Foam	Refuge Parental care	Eels from this family reproduce inside burrows. Species of the <i>Synbranchus</i> genus build 15 cm wide and 30 cm deep galleries guarded by an aggressive male. It is not known if the high number of eggs inside the nests is from multiple spawning of the same female or, more likely, if many females mate with the guarding male. In the <i>Monopterus albus</i> , an interesting combination of a burrow and bubbles are used for the males to construct their nests.	Blumer (1982), Favorito et al. (2005), Ishimatsu et al. (2018)
Tetraodontidae	Bowl Plant matter	Sexual selection Parental care	Pufferfish are less known as nest builders, although they have recently received a lot of attention due to the beautiful bowers of the <i>Torquigener</i> species, built 30 m to 137 m deeper, depending on the location. In the pufferfish (<i>Canthigaster valentini</i>), females, instead of males, dig nests, yet no further parental care is provided. In this species, males have territorial harems that overlap numerous females' territories	Bond et al. (2020), Gladstone (1987), Kawase et al. (2013), Sikkell and Sikkell (2012)
Zoarcidae	Burrow	Refuge Parental care	Zoarcid fishes build burrows to protect the eggs from predation. The female is the sole one to provide parental care, although the nest is dug by both parents by body coiling. These individuals may even perform reproductive migrations to sites with suitable nesting sediment	Ferry-Graham et al. (2007), Matallanas et al. (1990)

it with the snout or head (Johnston & Page, 1992). Other kinds of dug nests can be made by moving body and fins, such as the 2 m wide circular nest of the *Torquigener* sp. (Tetraodontidae) pufferfish (Kawase et al., 2013).

Burrow nests are found in many fish species, which dig their burrows in a similar way to how bowl nests are built. However, burrows are usually deeper in the ground and narrower in the surface (Figure 1b). This type of nest is commonly built on riverbanks by armoured catfishes, such as the loricariids *Pterygoplichthys* sp. (Loricariidae) (Lienart et al., 2013). Some Japanese gobiids, however, have a rare method for constructing theirs. These fish form

a symbiotic association with digging shrimps, sharing the burrow and using it as a site for spawning in shallow water rivers. This association has been described between the snapping shrimp (*Alpheus bellulus*, Alpheidae), and the *Amblyeleotris japonica* (Gobiidae) fish (Yanagisawa, 1984), and between the mud shrimp *Upogebia yokoyai* (Upogebiidae) and the goby *Eutaeniichthys gilli* (Gobiidae) (Henmi & Itani, 2014).

Foam nests are bunches of bubbles produced by mucus and air and placed on the water surface, so they are usually floating nests. In the Siamese fighting fish (*Betta splendens*, Osphronemidae; Figure 1c), for example, the male has a wrinkled pharyngeal organ

whose epithelium contains more mucous goblet cells compared to those in females. As the fish capture atmospheric air with its mouth, these cells cover the air volume with mucus to produce, one by one, the bubbles that compose the nest (Kang & Lee, 2010). On the other hand, the armoured catfish (*Haplosternum littorale*, Callichthyidae) produces the same kind of nest by expelling mucus through the gills and using the pectoral fins to mix it with air, whilst swimming upside down (Andrade & Abe, 1997). Males of this species cover the foam with eggs and then place plant debris over the set (Hostache & Mol, 1998; Mol, 1993). An interesting burrow/bubble nest combination is found in the *Monopterus albus* (Synbranchidae) (Figure 1b). Males deposit bubbles in the U-shaped burrow where fertilized eggs are attached to (Ishimatsu et al., 2018; Wu & Liu, 1942).

Two other types of nests are structured by using organic material available in the environment: plants and animal parts. A well-known example of nests made of plant matter is that of the three-spined stickleback fish (*Gasterosteus aculeatus*, Gasterosteidae; Figure 1d). This species uses algae mixed with mucus to build a tubular nest (Rushbrook et al., 2008). Nests made of animal parts are usual in *Lamprologus callipterus* (Cichlidae) species (Figure 1e), whose males collect snail shells from their surroundings and gather them to form a nest (Sato, 1994).

Some species also modify a rock surface by rubbing and cleaning it, so that later they can attach adhesive eggs that will be tended by the parents. Males of the Batrachoididae family (e.g. the midshipman fish (*Porichthys notatus*, Batrachoididae) and the Lusitanian toadfish (*Halobatrachus didactylus*, Batrachoididae) care for eggs attached to the roof of rocks cleaned by the females during reproduction in intertidal zones (Alderks & Sisneros, 2013; Carriço et al., 2014; Vasconcelos et al., 2012). This same pattern of nest construction and male parental care can be observed in cyprinid minnows (Katula & Page, 1998). Cichlids, such as *Pterophyllum scalare* (Cichlidae) and *Cichlasoma dimmerus* (Cichlidae), may also attach their adhesive eggs onto clean surfaces, although plant matter, such as leaves, seem to be the preferred place for nesting (Alonso et al., 2011; Cacho et al., 1999).

4.2 | Nests for protection and refuge

A widespread role conferred to fish nests is that of refuge against predators for eggs and larvae (Dominey, 1981; Stein & Philipp, 2015); it is considered the most ancient function for fish nests (see Figure 2). A representative example is the nest of the fifteen-spined stickleback (*Spinachia spinachia*, Gasterosteidae), which is placed in safer positions, up high in the vegetation, aiming at preventing egg-predator crabs from finding the fish's offspring (Östlund-Nilsson, 2000). Similarly, reef blennies from Noumea, New Caledonia, plug the nest entrance with their bodies in order to protect the eggs from predation by the *Emydocephalus annulatus* (Elapidae) sea snake (Goiran & Shine, 2015). In some cases, as nests protect the offspring, this refuge can also reduce the predation risk of the adult fish. The *Lipophrys pholis* (Blenniidae), for

instance, build their nests in burrows of rocky platforms in the intertidal zone. These rocks are characterized by the presence of a large number of appropriate shelters in the shape of holes or crevices, which may be used as both nests and/or refuges by this species (Martins et al., 2017).

Some protecting nests are suitable places, which satisfy offspring's specific requirements. Foam nests of the Anabantidae, Osphronemidae and Callichthyidae families, for example, provide an oxygen reservoir for eggs and larvae besides reducing egg exposure, thus protecting them from predators (Balon, 1975; Hostache & Mol, 1998; Mol, 1993). The guarding male parent regularly supplies the nest with fresh foam to avoid its deterioration (Mol, 1993). If they do not make foam nests, parents may provide oxygen by fanning the eggs with their fins. Pomacentrids, such as *Abudefduf saxatilis* (Pomacentridae) and *Stegastes fuscus* (Pomacentridae), have this behaviour when they fan over the eggs inside the nest, thus providing oxygen and avoiding dust deposition (Bessa & Sabino, 2012).

Nests can also protect the pair from interference during mating behaviour. For example, the two-spotted goby (*Gobiusculus flavescens*, Gobiidae) nests in mussel shells or amid kelp (Amundsen & Forsgren, 2001), which reduces male-male aggression and mating interruptions in more complex habitats (Myhre et al., 2013). Azorean rock-pool blennies (*Parablennius sanguinolentus*, Blenniidae) nest in crevices defended by the male during the reproductive season. The area opened for the nest is the main characteristic evaluated by females when choosing their mates, since narrower openings help the couple to avoid egg predators and intrasexual interferences more easily (Oliveira et al., 2000).

4.3 | Mouthbrooding: A booster in parental care when associated with nesting behaviour

According to Balshine and Sloman (2011), "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." Several fish species that build nests may also tend the brood inside their mouth at some point of the offspring's development. This type of parental care, called mouthbrooding, can be provided by one parent alone (i.e. more commonly female- or male-only care) or by both parents (i.e. more rarely biparental mouthbrooding care). Mouthbrooding is considered to have evolved from an ancestral state of parental care provided in the substrate, offered by species called "substrate spawners," or "substrate brooders," a type of care usually provided by both parents inside a nest (Goodwin et al., 1998).

In the Channidae family, the majority of the species are floating-egg guarders, and a few species are mouthbrooders with male-only parental care (Rüber et al., 2020). In the Synbranchidae family, only one species is known as mouthbrooder, the *Monopterus albus*. The males of this facultative air-breather species are bubble nesters, which care for the fry inside their mouths after the eggs hatch (Ishimatsu et al., 2018; Matsumoto & Iwata, 1997).

Most (if not all) cichlid species show nesting behaviour. The majority of African species are mouthbrooders, whose parental care is preceded by a male building a nest, usually a spawning site (Fryer & Iles, 1972). On the other hand, most of New World's cichlids are substrate guards (Barlow, 2002; Goodwin et al., 1998). Mouthbrooding may have evolved from a form of oral transportation of the brood by substrate guards that retained the fry inside their mouth for some time to avoid predation, for example (Baylis, 1981; Lowe-McConnell, 1959). Along with the evolution of mouthbrooding, the eggs may have lost adhesive structures, species may have had reduced fecundity, whilst eggs increased in size, consequently achieving a better brood survival rate inside their parents' mouths (Baylis, 1981; Goodwin et al., 1998).

4.4 | Nests as targets for sexual selection

Some types of nests were selected as an element for mating choice, as some characteristics of the nest may reduce egg predation and increase the reproductive success of the guarding male. Nests with smaller and better-hidden entrances, for instance, are preferred by spawning females (Reynolds & Jones, 1999). The territory complexity that females seek in a partner's nest may function for egg protection (Klug et al., 2005). Conglomerates of nests such as those seen in fallfish minnows (*Semotilus corporalis*, Cyprinidae) have been linked to an opportunity for females to assess many males at the same time (Ross, 1983). If not the nest itself, nesting-related behaviours are highly important in sexual selection, as nest-tending indicates how likely a male is to spawn (e.g. the flagfish *Jordanella floridae* (Cyprinodontidae); Hale & St Mary, 2007).

Barber et al. (2001) found correlations between nest structure, male fertility and health in sticklebacks. An indirect measure of androgen production (i.e. relative kidney weight) was correlated to nest neatness and compactness. Male health, measured through spleen weight, correlated to the amount of material used in the nest, its compactness and neatness. In that same species, Östlund-Nilsson and Holmlund (2003) observed that females were more attracted to males that decorate their nests with sticks and spangles, than to males with undecorated nests, another behaviour probably related to paternal skills that were selected in sticklebacks. In the fifteen-spined stickleback, *Spinachia spinachia*, females are attracted to the male's nest, considered as an honest sign of good genes and health, as males who feed better produce a more densely mashed nest (Östlund-Nilsson, 2001). Besides ornamentation, sticklebacks exposed to predation risks are more selected by females if they build hidden nests, than when the nests are in an open site (Candolin & Voigt, 1998; Kraak et al., 1999).

In another fish species, the damselfish (Pomacentridae), males build their nests by using algae and females use cues from the nest to choose which male to mate with. Females prefer to mate with males whose nests are more densely covered by algae, particularly green and red filamentous algae, whereas males with a less dense algae

material are less prone to courting females. Algae is also thought to be an egg disguise since in manipulated nests in which algal cover is removed from one side, females only lay eggs on the covered side (Sikkel, 1995).

Some fish also make bowers, which are complex structures built by males exclusively to attract females, with no role in egg-guarding, such as those built by bower birds (Borgia, 1995). Therefore, a bower is characterized based on its sexual selection function, not on its shape, which can vary. Some examples of fish that are known to build bowers are the numerous species of sand-dwelling cichlids of Lake Malawi (McKaye et al., 2001; York et al., 2015). *Copadichromis* spp. (Cichlidae), for example, is a complex of 13 cm cichlid species that carry sand with the mouth, building 25 cm high mounts as shown in Figure 1f (Taylor et al., 1998). Amongst the African cichlids of Lake Malawi, York et al. (2015) observed that the hypothesis of the speciation by sexual selection can be an evolutionary model in this group, since female preference for bower-building behaviour in males may be driving speciation in the lake. Mitchell et al. (2014) suggested that the accumulated shells collected by the male work as a bower in the cichlid *Lamprologus callipterus*. Although this fish is a shell-nester (i.e. use animal parts), males tend to make a collection of small shells and shell fragments as well, unsuitable for spawning. Moreover, female preference is correlated to the diversity of shell types in a male's collection (Mitchell et al., 2014). Nest density is also crucial for female choice in the *Lamprologus* cichlids, allowing them to assess numerous males at the same time (Schütz et al., 2016). Another example of bower-building fish is the *Torquigener* pufferfish, with no function of parental care, yet associated with female mate choice (Kawase et al., 2013; Matsuura, 2015). This pufferfish swims from a central point rubbing its stomach on the sand and builds beautiful 2 m wide circular bowers (see Table 1).

Despite the above mentioned, selecting partners based on nest quality is not mandatory. In the lumpfish (*Cyclopterus lumpus*, Cyclopteridae), the nest characteristics did not predict hatching success (Goulet & Green, 1988). In this case, there is evidence that nests have no function in sexual selection (Goulet & Green, 1988), as the authors found no correlation between female preference and nest structure. Similarly, Li et al. (2015) studied the specific characteristics of the nest and its occupying male in the cichlid *Julidochromis transcriptus* (Cichlidae), by relocating alpha and betta males in step-nests. In that case, female preference was associated with social rank instead of nests. Similar results have been reported for Azorean rock-pool blennies (Oliveira et al., 2000).

4.5 | Nests as badges of status and aggression reducers

Nests may also function as badges of status, signalling dominant individuals and avoiding frequent hierarchical disputes. This has been suggested for the role of bowers in the Malawi cichlid *Hemitalapia oxyrhynchus* (Cichlidae) (Genner et al., 2008). In that species, bowers

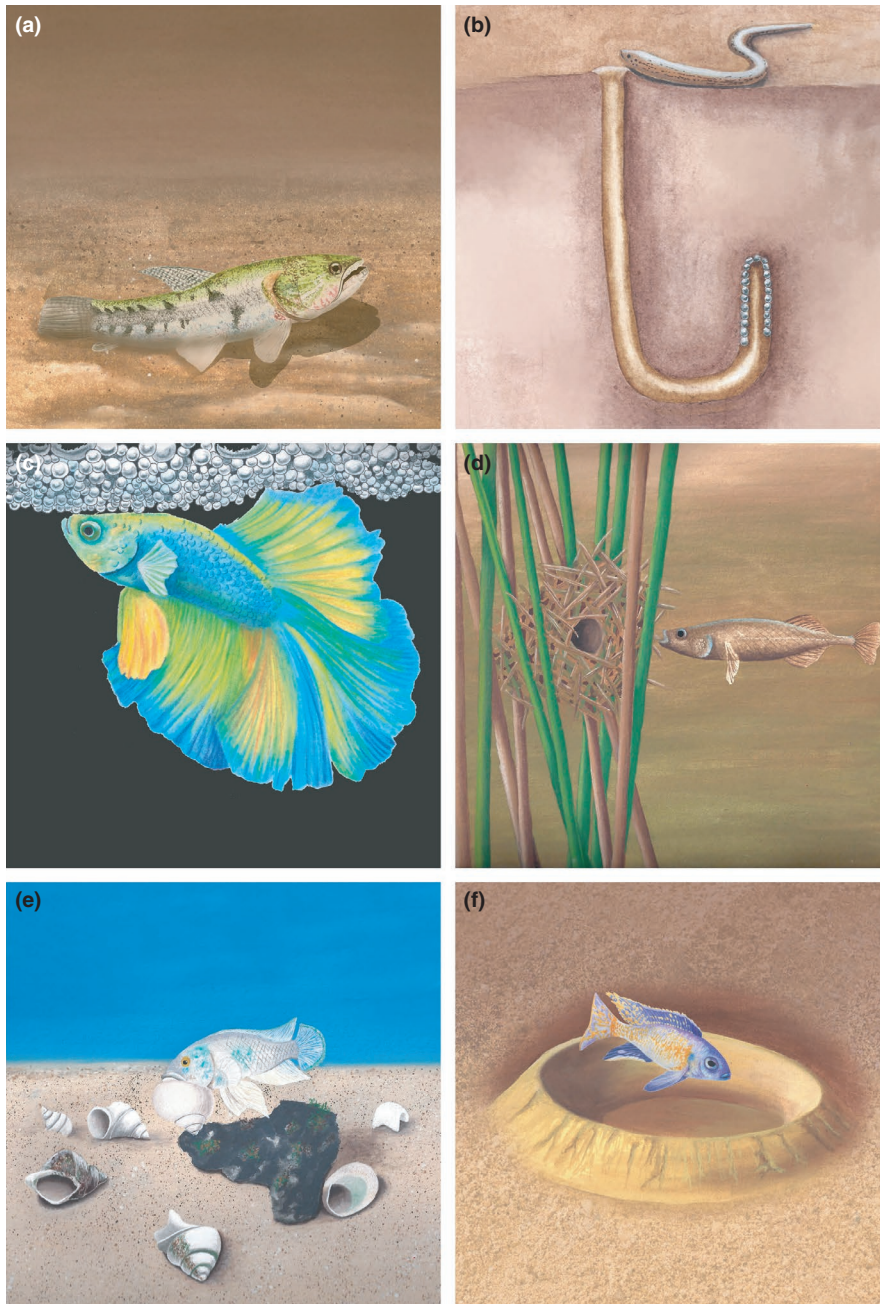


FIGURE 1 Types of nests. (a) a bowl of *Hoplias malabaricus* (Erythrinidae); (b) a burrow/bubble nest of *Monopterus albus* (Synbranchidae); (c) The bubble nest of a *Betta splendens* (Osphronemidae); (d) a *Gasterosteus acculeatus* (Gasterosteidae) plant matter nest; (e) snail shells used as nests made of animal parts by *Lamprologus callipterus* (Cichlidae); (f) the mount-shaped bower of *Copadichromis* spp (Cichlidae). Watercolour paintings by Marcos Silva-Ferraz

serve for intrasexual selection more than for female choice and are correlated with body characteristics linked to aggression and success in agonistic disputes. In the Ambon damselfish (*Pomacentrus amboinensis*, Pomacentridae), only the most dominant males guard nests, which also guarantees mating with dominant females (McCormick, 2016). In another pomacentrid, the colonial-nesting *Chromis chromis* (Pomacentridae), the more central the nest is placed within the colony, the more dominant the male is (Picciulin et al., 2004).

Higher status, signalled by badges of status, results in reduced aggression towards dominant fish (Volpato et al., 2003). If nests may be used as badges of status, they should also result in reduced attacks. That was observed in the ocellated wrasse (*Symphodus ocellatus*, Labridae), whose nesting males were less attacked than non-nesting males (Stiver et al., 2019). Males of two

southern Atlantic pomacentrids (the sergeant major (*Abudefduf saxatilis*, Pomacentridae) and the dusky damselfish (*Stegastes fuscus*, Pomacentridae)) holding nest sites perform much less defensive behaviours than individuals without one (Bessa & Sabino, 2012). Thus, other benefits of nesting in fish may be social rank signalling, reducing time and energy spent in agonistic contests.

5 | COSTS AND CONSTRAINTS OF NESTING

Considering the nesting functions explored here, it is clear that nesting brings advantages to the Darwinian fitness of the fish. However, a nest can also be costly, as energetic expenditure increases during

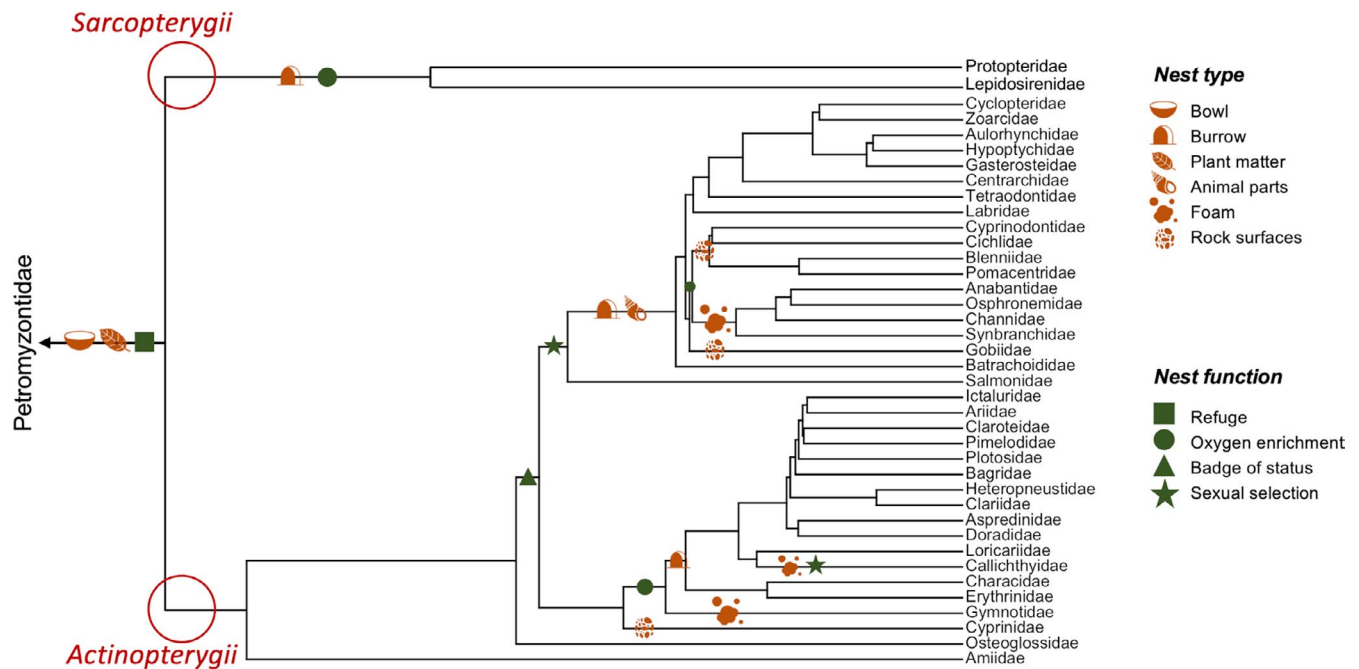


FIGURE 2 Cladogram suggesting how the main nest types and nest functions may have evolved in bony fishes, from a more primitive ancestry of nests made of bowl and plant matter, functioning as a refuge, present in lampreys. This cladogram was organized using the previously published work of Rabosky et al. (2018) and Betancur-R. et al. (2013)

the reproductive season with gamete production, secondary sexual characters, and reproductive behaviour, including nesting (Wootton, 1985). For instance, the male largemouth bass (*Micropterus salmoides*, Centrarchidae) digs bowl nests by swimming open-mouthed with powerful fin movements. This results in peaks of energy expenditure during muscle contraction only comparable to spawning and egg-predator chasing (Cooke et al., 2001). Moreover, males of a congeneric fish, *M. dolomieu* (Centrarchidae), lose almost 3% of their body mass within eight days of parental care (including other behaviours besides nest-building; Gillooly & Baylis, 1999). Nest-digging also results in a six-fold increase in energy expenditure in the African cichlid *Neolamprologus pulcher* (Cichlidae) (Grantner & Taborsky, 1998). Therefore, it is possible to conclude that nesting is an expensive behaviour in terms of energy consumption.

Besides the energetic cost, nests can bring additional constraints, as they attract more satellite males, *that is*, sexually mature individuals that do not nest, therefore, reproducing by alternative tactics (Ross, 1983). This author observed that only around 20% of the males in the fallfish minnow, *Semotilus corporalis*, build nests and that most of their life's reproductive success is due to sneaking satellite behaviours guided towards successful nests. In fact, most of the nest invasions occurred whilst the male was busy building, fixing, or protecting its nest. Similarly, colonial-nesting males of *Chromis chromis* damselfish were more liable to nest parasitism by opportunistic neighbours in a denser colony (Picciulin et al., 2004). However, colonial nesters can attract more females, and females may prefer to reproduce with males that can succeed in a competitive colony (Young et al., 2009), possibly assessing multiple males at once, as observed in *Lamprologus callipterus* (Schütz et al., 2016), although males must

be prepared to deal with sneakers that mimic females (Li et al., 2015). Nesting males can adjust their nesting behaviour in response to parasitic males. In the cichlid *Lamprologus lemairei* (Cichlidae), males used shells with a narrower opening to prevent sneaking competitors (Ota & Kohda, 2014).

Competing males often reduce their rivals' reproductive potential by destroying their nests, a behaviour intensified when male density increases (Stanley & Wootton, 1986). Males defend a territory more fiercely if a nest is built inside it, revealing that the nest increases the value of the territory (Stanley & Wootton, 1986). Another option for rival males is to expel a smaller male from the nest the latter has built to dominate several nests at once. These so-called "pirate males" were observed in high-density nesting colonies in the shell-brooding Tanganyika cichlid *Telmatochromis vittatus* (Cichlidae) (Ota et al., 2012).

Nest-caring is so demanding that when the male anemonefish, *Amphiprion clarkia* (Pomacentridae), disappears from a biparentally guarded nest, the female may accept a new partner, but she will persuade him to help with nest maintenance by hitting him with the head (Yanagisawa & Ochi, 1986). Another risk of nesting for an anemone is that these cnidarians can move to other locations. Territorial males are thought to follow their guarded anemones, which can move to a more suitable microhabitat and substrate for laying eggs or, on the contrary, to places which are inadequate for anemonefish to reproduce (Mitchell, 2003).

Nests can attract visually or chemically oriented predators. Turtle-headed sea snakes can use olfactory cues to locate nests and prey on small fish and eggs placed in large areas of coral reefs in New Caledonia (Shine et al., 2004). The purple eggs of the sergeant

major *Abudefduf saxatilis* are easily found by predators, hence nesting males spend more time averting egg predators than *Chromis multilineata* (Pomacentridae), another pomacentrid that conceals eggs amid algae (Bessa & Sabino, 2012). A cooperative interaction between *Stegastes fuscus* damselfish and the dusky grouper (*Epinephelus marginatus*, Serranidae) was reported, in which the damselfish benefits from sharing its territory with a grouper because this serranid feeds on egg predators attracted by the nest (Bessa, 2011). Finally, predatory fishing also benefits from knowing nesting habits. Fish from the genus *Arapaima* (Osteoglossidae) are a target for fishers mainly during spawning and parental care, when parents are easily visible on the surface tending the young (Gurdak et al., 2019).

It is common that adult fish migrate for reproducing, that is, they seek sites with better conditions for egg and fry success (Pitcher, 2012). Specific nest requirements may force nesting species to perform reproductive migrations to sites where nest material is available, such as described in the pelagic deep-water eelpouts (*Lycodes* genus, Zoarcidae), which migrate towards the substrate to spawn (Ferry-Graham et al., 2007). The catfish *Auchenoglanis occidentalis* (Claroteidae) searches for adequate granulometry of sediment and the presence of mollusc shells (Ochi et al., 2001). Siltation is pushing endemic Lake Malawi cichlids away from their nesting grounds (Ngochera, 2014) and increasing energy costs of reproduction for that catfish due to egg fanning (Ochi, Kanda, et al., 2001).

In the Callichthyidae family, the bubble nests of the genera *Hoplosternum* and *Callichthys*, represented by species inhabiting tropical standing waters deprived of oxygen, are considered very important in providing an oxygen-rich environment for the developing eggs and larvae (Carter & Beadle, 1930). Floating bubble nests of *H. littorale* are associated with the annual flooding of shallow swamps (Machado-Allison & Zaret, 1984; Mol, 1993).

6 | PHYSIOLOGICAL MECHANISMS UNDERLYING NEST BUILDING

Physiological control of behaviour occurs in two main ways: a neural one that organizes and coordinates behaviour, and a hormonal one that acts upon the nervous system, modulating animal behaviour. Gonadal steroid hormones, for instance, influence the reproductive behaviour of vertebrates through an organizational effect in early development, or an activational effect, particularly during breeding seasons (Moore et al., 2020; Nelson & Kriegsfeld, 2016). Similarly, gonadal hormones are released in fish through the activation of the hypothalamus-pituitary-gonad (HPG) axis, with a neurosecretion of gonadotropin-releasing hormone (GnRH) by the hypothalamus, which, in turn, stimulates type I and type II gonadotropins from the anterior pituitary. These gonadotropins stimulate gonads to release estradiol and two androgens, namely testosterone (T) and 11-ketotestosterone (11KT), the latter being the main androgen in teleost fishes (Borg, 1994; Borg & Mayer, 1995). These hormones activate reproductive behaviour both in tropical species throughout the year, such as African cichlids (Oliveira, 2004; Oliveira et al.,

2002) and in species inhabiting regions where seasons are well-defined, such as the three-spined stickleback (Borg & Mayer, 1995); smallmouth bass (*Micropterus dolomieu*, Centrarchidae) (O'Connor et al., 2012); Lusitanian toadfish (Amorim et al., 2016); and seasonal breeding males in general (Goymann et al., 2019). In either case, reproductive hormones are involved in nesting behaviour.

In the three-spined stickleback, *Gasterosteus aculeatus*, the nest is shaped by adding spiggin, a protein that acts as an adhesive. Spiggin is produced in the kidney of sticklebacks, with androgen stimulation, specifically 11KT (Jakobsson et al., 1999). Moreover, the stickleback's kidney has a great number of androgen receptors (Hoffmann et al., 2012). Spiggin, as well as the nesting activity, is reduced by anti-androgen pesticides (Sebire et al., 2009) and flutamide (Sebire et al., 2008). Furthermore, castration reduces nesting behaviour, which can be restored by implanting 11KT (Hoffmann et al., 2008), thus showing that 11KT indeed controls nesting behaviour in *G. aculeatus*. In Mozambique tilapia, castrated males show decreased nesting behaviour (Almeida et al., 2014). As castration is followed by a reduction in both T and 11KT, this indicates that nest building is controlled by androgens in Mozambique tilapia (Almeida et al., 2014). Treatment with 11KT or methyltestosterone induces a male-specific nest-building behaviour in female Mozambique tilapia, thus showing an androgen-dependent regulation of nest building in this species (Kuramochi et al., 2011).

Besides androgens, there is some evidence that oestrogens and estrogenic-like substances are involved in the regulation of nesting behaviour in fish. Clotfelter and Rodriguez (2006), for example, studied the effect of estradiol and phytoestrogens on the reproductive behaviour of the Siamese fighting fish, including nesting. They reported that males exposed to 17 β -estradiol were less likely to build a nest, although the nests (when built) were 84% higher than the control group. On the other hand, phytoestrogens increased both the probability of nest building and nest size. This study indicates that sexual hormones can control both motivation and persistence in nesting behaviour.

Additionally to the effect of the sexual steroids, the inactivation of GnRH III also affects nesting behaviour by reducing nest activity and nest size in Nile tilapia males (Ogawa et al., 2006), which is modulated by the olfactory system (Uchida et al., 2005). In another fish species, the blue gourami (*Trichogaster trichopterus*, Osphronemidae), nest-building males show higher levels of the pituitary adenylate cyclase-activating polypeptide (PACAP) mRNA than non-nest-building males and juveniles (Levy et al., 2009). PACAP is known to regulate reproductive behaviour by stimulating the transcription and release of LH and FSH from pituitary cells in teleost fishes (Chang et al., 2001). Therefore, the hormonal mechanism controlling nest behaviour involves the whole HPG axis and seems to be conservative in teleost fishes.

Whilst several studies showed the effect of hormones controlling nesting behaviour, the brain circuits are less known. Pioneering studies on fish reproductive behaviour were carried out by Overmier and Gross (1974), who observed that a telencephalic ablation reduced nest-digging activity in Mozambique tilapia.

Similarly, Davis et al. (1976) studied the effect of bilateral ablation of the telencephalon on the reproductive behaviour of paradise fish (*Macropodus opercularis*, Osphronemidae). The authors found that lesioned males performed species-typical displays at the beginning of spawning; nevertheless, they did not build nests. These studies brought some insights on the neural control of fish nesting behaviour, even though ablation produces major lesions leading to several behavioural alterations.

Recently, some studies investigated the role of the neurotransmitter serotonin in nest activity. The fathead minnow (*Pimephales promelas*, Cyprinidae), for instance, makes a nest that does not involve a structural building. Males just clean up a surface to which females will be attracted and eggs will be attached (Kottelat & Freyhof, 2007). In this species, fluoxetine, a selective serotonin reuptake inhibitor, increases time spent under the nest site as well as time spent cleaning the nest (Weinberger & Klaper, 2014), thus suggesting some influence of serotonergic pathways controlling the nesting behaviour of fish. On the other hand, exposure to a high concentration of fluoxetine increases cortisol levels and reduces nest quality in male *G. aculeatus* (Sebire et al., 2015), showing a more complex neural mechanism controlling nesting, or revealing species differences regarding the serotonergic control of nesting behaviour. Despite the neurotransmitter mechanism, *G. aculeatus* males' brains are 23% heavier than females', which is attributed to their complex reproductive repertoire, such as building an ornate nest (Kotrschal et al., 2012). Buechel et al. (2019) observed that, during the reproductive cycle, the brain of a male stickleback may increase 24% in size on average when compared to a female's brain during the same period. This supports the idea that the cognitive demands of reproduction, such as nest construction and parental care, are of great adaptive value in selecting for brain size (Buechel et al., 2019).

Other peptides also act as neural modulators in nesting behaviour. Arginine-vasopressin (AVT), isotocin (IT), prolactin (PRL) and galanin (GAL) are highly involved in mating and parental care in fish (Batten et al., 1990; Dulac et al., 2014). Indeed, in males of *G. aculeatus* showing nuptial coloration, IT levels were much higher in aggressive individuals with nests than in non-reproductive males (Kleszczyńska et al., 2012). Higher AVT levels, as well as larger AVT cells in the preoptic area (POA) of the brain, were also related to males that tend the eggs in contrast with males without a nest (Foran & Bass, 1998; Kleszczyńska et al., 2012). In this same species, an intensive PRL synthesis was linked to aggressive males tending the eggs (Slijkhuis et al., 1984) or fanning the nest, even though there were no eggs in it (*i.e.* exogenous PRL, (de Ruiter et al., 1986)). It seems that AVT induces PRL secretion from the pituitary, which again suggests an AVT action in nesting behaviour through PRL regulation (Liu & Ben-Jonathan, 1994).

Finally, GAL is still little known in comparison to the other neuropeptides cited here. Although in midshipman fish, *Porichthys notatus*, GAL presented no relation to nesting behaviour (Tripp et al., 2020), in the cichlid fish *Astatotilapia burtoni* (Cichlidae), the activation of GAL neurons in the POA were related to maternal mouthbrooding

care (Butler et al., 2020). Midshipman male fish care for the fry in the nest, not in their mouth, although substrate brooding requires more aggressive displays than mouthbrooding (Butler et al., 2020). Thus, the behavioural differences observed in *A. burtoni* and *P. notatus* involving GAL action may indicate that this peptide is more related with the agonistic part of the reproductive behaviour. It is worth mentioning that similar processes concerning these neuropeptides, the POA and its homologous brain area in other vertebrates, are also linked to nesting behaviour in other animals, such as mammals and birds (see Jacobson et al., 1980; Kingsbury et al., 2015; Tripp et al., 2020; Wu et al., 2014). This well-conserved pattern of nesting behaviour can be related to the fact that different brain regions present homologies across vertebrate taxa (O'Connell & Hofmann, 2011). Overall, the studies mentioned herein have manipulated hormones and brain mechanisms associated with reproductive behaviour and, in turn, reported alterations in nesting, as it is part of the reproductive repertoire (*e.g.* Almeida et al., 2014; Ogawa et al., 2006). However, specific hormonal and neural pathways regulating nesting behaviour in fish are still little understood, therefore, there is abundant room for further research in this field.

7 | A PROPOSITION OF NESTING BEHAVIOUR EVOLUTION

We present herein a proposition of how nesting behaviour might have evolved in fish, by using two molecular phylogenies of bony fishes based on Betancur-R. et al. (2013) and Rabosky et al. (2018). From these molecular data, we built a new cladogram encompassing all the families mentioned in this review and suggested how nest types and functions could have evolved amongst these families (Figure 2). The cladogram was organized by using the free software R, version 3.6.3 (<http://www.r-project.org>), and the packages "ape" (Paradis & Schliep, 2019) and "phytools" (Revell, 2012). Since the nest function of parental care was common to every family presented in this cladogram since lampreys, we chose not to include this information for rendering the cladogram as clear as possible.

The Petromyzontidae family, represented by the lampreys, is the external group, in which bowl and plant nests functioning as a place of parental care seem to be the ancestral state. On the other hand, nests made of foam and mucus, working to enhance the oxygen supply for the eggs, seem to be a more derived type of nest. Considering Sarcopterygii and Actinopterygii together, nests being also used as a place of refuge is the primitive state in nest function. Therefore, it seems plausible to suppose that nest types evolved from an ancestral state of a bowl nest, going through nests made of plant matter, burrows and crevices, then using animal parts, cleaning rock surfaces, and, finally, made of foam produced by the parents (Figure 2). The function of the nest might have evolved from a commonplace of refuge, being followed by the oxygen enrichment of the eggs in the Sarcopterygii, and a badge of status conferred to the building males in Actinopterygii, then functioning as a target for sexual selection according to the quality of the nest (Figure 2).

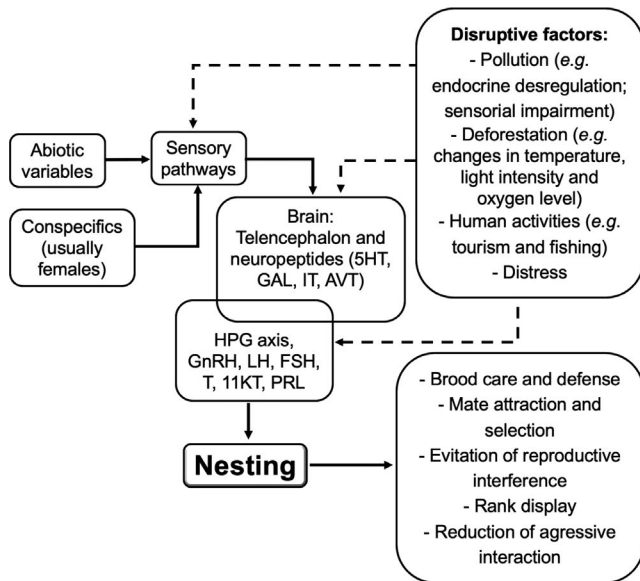


FIGURE 3 Schematic overview showing integrated environmental abiotic variables and the neuro-endocrine mechanism controlling nesting behaviour (solid arrows), as well as the disruptive factors acting upon nesting (dashed arrows)

8 | CONCLUDING REMARKS

We showed herein that nests are part of the reproductive behaviour of several fish species, whose functions are mate attraction and sexual selection, social dominance exhibition, avoidance of reproductive interference, brood care and predator avoidance. After this synthesis, we conclude that defining a fish nest is not an easy task, given the fact that form, function and behaviour vary amongst species. Hence, we suggest a new definition based more on the fish behaviour than on the nest as a structure.

During our synthesis, we identified some topics that need further research. It is fundamental to deepen our understanding of two aspects in particular: how nests can be part of sexual selection and how they may signal social status in different fish species. Another topic of interest is how environment, nest architecture and function are correlated across taxonomic groups. Our phylogenetic analysis will help bring light and interest to this research topic, yet linking nest architecture to environmental characteristics (e.g. water flow, substrate granulometry, dissolved oxygen) can shed light on how nests function. Physiological control mechanisms of nest-building have been studied only in a few species; therefore, more widespread taxonomic coverage of this topic would result in a more comprehensive understanding of nesting. Finally, there are more studies on the hormonal control of nesting than on neural pathways. Thus, studies involving brain areas and neural pathways of nesting would be essential for a complete understanding of the proximate causes of nesting.

Regarding the environmental changes we are facing nowadays in the Anthropocene, it is urgent to understand how nesting behaviour can be affected by environmental impacts. These impacts include, for instance, deforestation and climate change, which increase siltation

(Zeni et al., 2019) and may cover eggs and nests. Such factors may increase the costs of nesting or, on the contrary, prioritize nesting species, which control the environment where eggs develop (Jones et al., 1999). Chemical pollution may disrupt hormonal axes that regulate nesting (Sebire et al., 2008, 2009). Changes in community composition (Ilarri et al., 2008) may influence competition for nesting grounds and increase the risk of predation on eggs or breeding adults. Fishing (MacLean et al., 2020; Twardek et al., 2017) and tourism activities (Bessa & Gonçalves-de-Freitas, 2014) also impair nesting. By considering nesting as a key factor in fish reproduction and survival, we also assume that changes in the natural environment that affect this behaviour will directly affect the abundance and the presence of a fish species in a particular environment. As summarized in Figure 3, alterations in abiotic factors can negatively impact nesting, as some of them interfere in nest building and other types of reproductive behaviour. For example, temperature and oxygen level drive nesting site choices in *G. aculeatus* (Bakker & Mundwiler, 2021), and sexual selection is affected by light intensity in the same species (e.g. Hiermes et al., 2021). Stimuli that affect hormones and neural activities related to the physiological control of nesting (e.g. pollution by endocrine disruptors and distress) can also impact reproductive success. Therefore, nesting can be an indicator of the internal state of fish as well as the "health" quality of aquatic environments. Studies related to this subject, therefore, need more attention.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

This is a revision paper, therefore, data referred to herein are the cited articles.

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