

An Overview of Post-Fertilization Parental Care in Gobiidae

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Abstract

Parental care increases offspring survival but is typically costly to the parent providing it. Understanding diversity in parental care across animals is a timely topic in evolutionary ecology. Fishes are particularly well suited for studies aimed at understanding the diversity of parental care because parental care in fishes is highly variable across species. In most fish species, no care is provided. When parental care is provided, it is often paternal, although biparental and maternal care occur in some fish species as well. Parental care in fishes ranges from simple guarding of eggs in a territory to prolonged care of young after hatching. Within fishes, gobies are thought to exhibit diverse parental care. In the current manuscript, we begin to synthesize our knowledge of patterns of parental care in gobies by providing a review of the parental care strategies that are exhibited by gobiid species. Our review reveals that parental care in gobies most often includes guarding, fanning, and cleaning, although some species engage in other types of care such as larval release, the production of antimicrobial substances, and the construction of post-mating mounds. Care in gobies is most often paternal, but maternal and biparental care have been documented in some species.

Keywords: paternal care; biparental care; nest guarding; egg fanning; egg cleaning; removal; larval release



Academic Editor: Michael Wink

Received: 7 May 2025

Revised: 10 June 2025

Accepted: 18 June 2025

Published: 24 June 2025

Citation: Trujillo-García, M.; Ceballos-Vázquez, B.P.; Guevara-Fiore, P.; Klug, H. An Overview of Post-Fertilization Parental Care in Gobiidae. *Diversity* **2025**, *17*, 446. <https://doi.org/10.3390/d17070446>

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1. Introduction

The Gobiidae family (gobies) comprises over 1300 described species distributed across marine, brackish, and freshwater environments, making it one of the most speciose families of teleost fishes [1–3]. Gobies are typically small-bodied (<10–30 cm), benthic, and exhibit remarkable ecological and behavioral diversity. Following Balon’s reproductive guild classification, gobies are categorized as Guardians→Nest spawners [4,5], which implies eggs’ deposition in protected sites and parental defense until hatching. Many species of gobies lay eggs on fixed substrates—such as shells, coral, sand, polychaeta tubes, or artificial nests like PVC pipes—and provide post-fertilization parental care, most often performed by males [6].

Parental care in fishes has been studied through the lens of evolutionary trade-offs between current and future reproduction, mating opportunities, and offspring survival (e.g., [7–11]). Theoretical frameworks proposed by Trivers [12] and Clutton-Brock [13] have laid the groundwork for understanding sex-specific investment and the costs and benefits

of care across taxa. Yet despite gobies' exceptional diversity and widespread paternal care, no comprehensive synthesis has addressed how these behaviors vary across the group or what evolutionary and ecological factors are behind this diversity. While parental care has been well-documented in a number of individual goby species [14–20], a broader comparative analysis is lacking.

In this review, we aim to (i) synthesize what is currently known about post-fertilization parental care in gobies, (ii) explore patterns of the form and type of care across species, and (iii) discuss the evolutionary and ecological drivers that might explain this diversity.

Defining Parental Care

Historically, parental care has been defined in multiple ways. Parental care has been most broadly defined as any parental trait that is likely to increase offspring fitness and that likely originated and/or is currently maintained for this function [13,21,22]. Others have defined parental care more narrowly. For instance, Klug et al. [23] defined parental care as parental behavior that occurs post-fertilization (or after the production of daughter cells if reproduction is asexual), is directed at offspring, and appears likely to increase offspring lifetime reproductive success. Similarly, Clutton-Brock [13] noted that parental care has a broad and narrow sense. The broad sense includes preparation of a nest or burrow, the provisioning of eggs with a higher amount of yolk, care of eggs or offspring, and provisioning of offspring after nutritional independence. The narrow sense is only related to the care of eggs or offspring post-fertilization (or following the production of daughter cells in asexually reproducing organisms), whereas the broad sense also encompasses behaviors that occur pre-mating. In the current manuscript, we focus on parental care of offspring that occurs post-fertilization (following Klug et al. [23] and the narrow-sense definition by Clutton-Brock [13]).

2. Methods

We identified patterns of post-fertilization parental care in gobies by reviewing the relevant literature found through ScienceDirect and Google Scholar. These searches were performed between February 2024 and January 2025. We specifically used the following key words in our searches: “parental care”, “Gobiidae”, “male care”, “parental duties”, “female care”, “male only care”, “care”, “reproduction”, “reproductive behavior”, “behavior”, and each genera within the Gobiidae family, following the taxonomic classification found in *The Biology of Gobies* [6]. Since our goal was to obtain as much information as possible on parental care in Gobiidae, additional relevant sources were identified from the bibliography of articles that resulted from our ScienceDirect and Google Scholar searches. We included relevant papers from any year (i.e., we did not restrict our review to papers published during a particular timeframe), and we included studies that documented behavior under either captive or natural conditions. In this review, we only include species in which post-fertilization parental care has been documented and for which there were data available on the type of parental care provided and the sex of the caregiver. Thus, our review of parental care in gobies focuses on a sample of gobies that provide parental care and that have a published description of parental care traits by males and/or females. Notably, for most gobiid species, no details of parental care are available, and reliable information on mating systems is also limited. In particular, existing studies vary widely in how mating systems are defined and assessed—ranging from classifications based on single reproductive events to broader temporal scales such as breeding seasons or even lifetime patterns—making cross-species comparisons challenging. As such, we focus our review on parental care rather than mating systems more generally.

For each species meeting our inclusion criteria, we identified the following information: (1) whether the species is found primarily in freshwater, marine, or brackish environments, (2) details of the spawning site (i.e., nest type) in the study/studies, (3) clutch size, (4) egg size, (5) the form of parental care (uniparental versus biparental), (6) the type of parental care by sex, and (7) the duration of care. Types of parental care were described primarily following the seminal work by Blumer [24,25] that categorized parental care in bony fishes (Table 1). We also included more recently identified types of parental care in gobies, including larval release, post-mating construction of mounds, and the production of antimicrobial substances. A detailed description of the types of parental care considered is provided in Table 1. In Table 2, we report data for all species that met our inclusion criteria. We graphically illustrate the frequency of each type of parental care in Figure 1, where percentages were obtained considering the sum of all total traits observed in Table 2. To illustrate linkages between the sex of the caregiver, type of care provided, and nest type, we used a Sankey diagram where the nodes are sex of caregiver (i.e., form of care), type of care, and nest type (Figure 2). In Figure 2, line thickness reflects the number of species, and the numerical values reflect the number of interactions between each node. For example, a male can guard in a dug nest, guard in a natural cavity, guard in an artificial nest, guard in an open cavity, fan in a dug nest, etc. As such, this diagram illustrates how frequently each sex engages in each type of care in the various types of nests across species.

Table 1. A description of post-fertilization parental care traits identified in Gobiidae. Types of care were primarily categorized following Blumer [24,25], with additional traits specific to gobies included. Each type of care was defined by its functional role in enhancing offspring survival.

Type of Care	Description	References
Protection/guarding	Displays toward and/or directed at conspecifics or heterospecifics, presumably to drive potential predators away from eggs and/or the nest. Parents blocking the nest entrance in a vigilant posture. Parents bite or sometimes throw sand towards possible predators. This behavior is assumed to increase offspring survival by reducing predation on offspring.	[20,24–26]
Fanning/aeration of eggs	Parent creates a flow of water over eggs by rhythmically moving their pectoral fins, pelvic fins, caudal fin, or tail over the egg mass. This behavior is assumed to eliminate sedimentation from eggs and/or to increase oxygenation of eggs.	[24,25,27–29]
Cleaning	Taking eggs from the nest into mouth and manipulating the eggs without consuming them. Actions such as touching the eggs with fins were also considered as cleaning. Cleaning is assumed to increase egg survival or quality by improving the health and viability of eggs through preventative mechanisms.	[24,25]

Table 1. Cont.

Type of Care	Description	References
Egg/organism removal	Dead, sick, or non-viable eggs are removed from the egg mass with the mouth to prevent further spread of egg diseases. Parents can remove other organisms present in the nest such as gastropods. This type of behavior may be accompanied by inspection of eggs that may serve to detect non-viable eggs. Removal behavior is assumed to increase remaining egg survival and quality by improving the health and viability of eggs following infection or the presence of other living organisms that could harm the eggs.	[20,24,25,30]
Larval release *	Parents help fully developed larvae to hatch and leave the nest. This behavior is assumed to increase offspring survival by increasing hatching success and allowing larvae to be placed in a location that increases survival (e.g., a location away from potential predators).	[20,31]
Production of antimicrobial substances *	Parents produce substances that inhibit the proliferation of pathogens such as bacteria or fungi that can cause disease among eggs. Production of antimicrobial substances is assumed to increase egg survival or quality by improving the health and viability of eggs.	[32,33]
Construction of elevated mound	Using substrates to create a mound after closing the entrance of the burrow. This behavior is assumed to increase offspring survival by influencing oxygenation inside the burrow.	[24,25,34]

* This type of care was not formally described by Blumer.

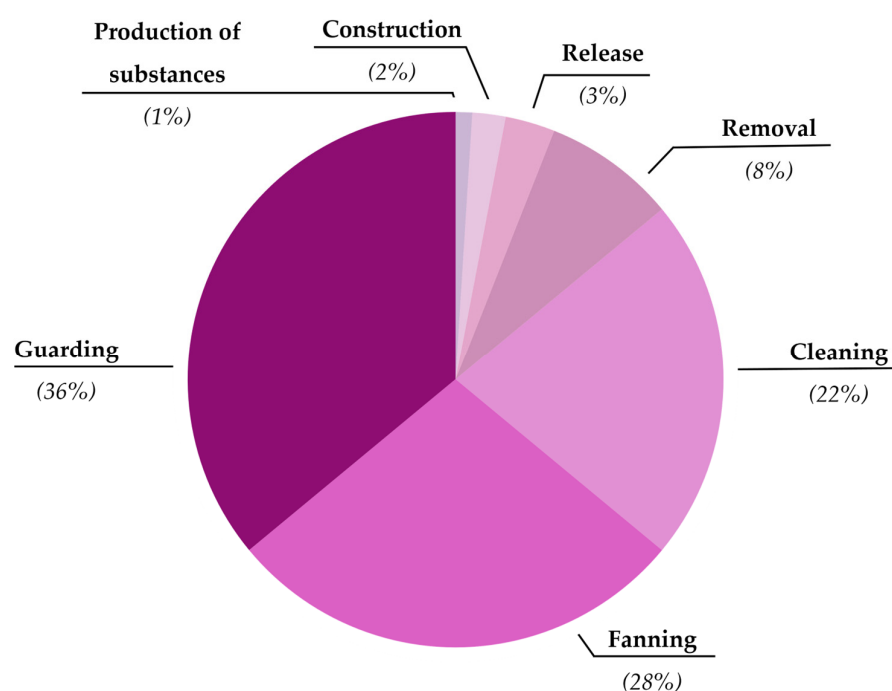


Figure 1. The types of post-fertilization parental care found in Gobiidae. Percentages were obtained considering the sum of all total traits observed in Table 2. For more detailed information about each type of care, see Table 1.

Table 2. Post-fertilization parental care in a sample of Gobiidae. The primary environment is indicated as follows: ★ = Freshwater, ★ = Brackish, and * = Marine. Details of the type of care are provided, where **G** = Guarding/Protection, **F** = Fanning/Aeration, **R** = Removal of Dead or Diseased Eggs or Other Living Organisms, **C** = Cleaning, **L** = Larvae Release, **O** = Production of Antimicrobial Substances, and **M** = Construction of Elevated Mound. ♂ = Male. ♀ = Female. We additionally note the form of care, clutch and egg size, care duration, and the spawning site utilized in the studies considered. Note that a single species may exhibit multiple types of parental care.

Species	Spawning Site	Clutch Size (Number of Eggs)	Egg Size (mm)	Form of Care	Type Of Care Performed By Each Sex							Care Duration (days)	References
					G	F	C	R	L	O	M		
<i>Amblygobius phalaena</i> *	Males construct a burrow under coral pavement	11,022–95,858	1.64	Uniparental ₁	♂ or ♀	♂ or ♀	♂ or ♀ ²					3–4	[35–37]
<i>Bathygobius fuscus</i> ★★*	Holes or cracks in the rocks or empty shells of bivalves	72,467		Uniparental	♂	♂						4–5	[38–42]
<i>Bathygobius soporator</i> ★★*	Shells (underside)	15,000–18,000 per female	2.25–2.42	Uniparental	♂	♂	♂					5	[14,43,44]
<i>Chlamydogobius eremius</i> ★	Under rocks crevices			Uniparental	♂	♂	♂						[45–49]
<i>Crystallogobius linearis</i> *	Empty tubes of polychaetes			Uniparental	♂								[50]
<i>Elacatinus colini</i> *	Inner sponge lumen; PVC pipes	168		Uniparental	♂			♂	♂			6.8	[31,51]
<i>Elacatinus evelynae</i> *	Cracks or holes between/in live coral or dead coral debris	200–250	1.1–3.3	Potentially Biparental ³	♂	♂						5–6	[52–56]
<i>Elacatinus figaro</i> *	Underside of shells ⁴	430–1020	1.81	Uniparental	♂	♂						6.8	[57,58]
<i>Elacatinus oceanops</i> *	Small shell of <i>Tridacna</i> with concave surface downwards	300–450	2.3–3.3	Uniparental	♂								[56,59,60]
<i>Elacatinus puncticulatus</i> *	PVC pipes ⁴	277–418	1.71–2.64	Uniparental	♂	♂	♂	♂	♂			6–8	[20]
<i>Eucyclogobius newberryi</i> ★*	Burrows constructed in sand or mud by males; PVC pipes	100–1000	5–6	Uniparental	♂					?	⁵	9–11	[61–64]

Table 2. Cont.

Species	Spawning Site	Clutch Size (Number of Eggs)	Egg Size (mm)	Form of Care	Type Of Care Performed By Each Sex							Care Duration (days)	References
					G	F	C	R	L	O	M		
<i>Eviota abax</i> *	PVC pipes ⁴			Uniparental	♂	♂	♂					5	[65,66]
<i>Eviota prasina</i> *	Holes or crack in substrate			Uniparental	♂	♂		♂				4–5	[30,67]
<i>Gobius cobitis</i> ★★	Under rocks with flattened lower side	3000–24,000	3.44–4.3	Uniparental	♂	♂	♂ ⁶						[15,16,68, 69]
<i>Gobius cruentatus</i> *	In the lower side of a horizontal rock ⁴	21,296	1.90–2.10	Uniparental		♂	♂ ⁶						[70]
<i>Gobius ophiocephalus</i> ★★	Males excavate cavity in soft bottom of seagrass meadows			Uniparental	♂	♂	♂			♂			[32,71–73]
<i>Gobius niger</i> ★★	Excavation of small cavities under rocks or artificial nests or shells			Uniparental	♂	♂							[74–76]
<i>Gymnogobius isaza</i> ★	Under a stone or a large rock	5000		Biparental ⁷	♂ & ♀ ⁸	♂ & ♀	♂ & ♀ ⁶					10–21	[77–79]
<i>Knipowitschia panizzae</i> ★★	Empty shells of bivalves, preferably <i>Cerastoderma lamarcki</i> ; the male excavates under the shell and covers it with sand			Uniparental	♂							7	[80–82]
<i>Lythrypnus dalli</i> *	PVC pipes; ⁴ natural nesting sites can include empty abalone shells, under the surface of rocks, or small crevices	319–2333	1.88	Uniparental	♂	♂	♂ ⁶						[83–86]
<i>Lythrypnus pulchellus</i> *	PVC pipes ⁴			Uniparental	♂								[87]

Table 2. *Cont.*[illegible]

Table 2. Cont.

Species	Spawning Site	Clutch Size (Number of Eggs)	Egg Size (mm)	Form of Care	Type Of Care Performed By Each Sex							Care Duration (days)	References
					G	F	C	R	L	O	M		
<i>Signigobius biocellatus</i> *	Both parents construct several burrows			Biparental		♂ & ♀ ¹²	♂ & ♀				♀ ¹⁰		[63,114]
<i>Trimma taylori</i> *	PVC pipes ⁴	190–1233		Biparental	♂ ¹³ & ♀ ¹³			♂					[115]
<i>Typhlogobius californiensis</i> *	Burrow in the sand	5040	2.7–2.85	Biparental	♂ & ♀	♂ & ♀			♂ & ♀ ¹⁴			10–12	[116]
<i>Valenciennea longipinnis</i> *	Excavate burrows under coral pavement and rubble; after spawning, female closes the entrance and constructs a conspicuous mound	128,873	1.1	Biparental		♂	♂				♀	3–5	[34,117,118]
<i>Valenciennea strigata</i> *	A mating pair construct burrows under coral pavement and rubble; after spawning, female deposits coral rubble and algae over the burrow entrance			Biparental ¹⁵							♀ ¹⁶	1–4	[119,120]

¹ Female care has been observed only when the male is removed from the nest. ² The male takes the eggs into his mouth and then returns them. ³ Female contribution is reported but the nature of such contribution is unclear or not mentioned. ⁴ In captive conditions. ⁵ Body mucus was found, and it has been suggested that this mucus supports the burrow, but it might also play a part in antimicrobial substances. ⁶ Behavioral units such as rubbing or touching the eggs with fins were considered cleaning behavior even when there was no clear declaration of a cleaning function. ⁷ Females exhibited little parental care. ⁸ Both males and females attacked female intruders and this was considered protection. ⁹ Female takes care of progeny during development of eggs. ¹⁰ Males or females cover the nest entrance but there is no evidence for the construction of a mound. ¹¹ Because of the presence of eggs when the male is present in the nest vs. absent, parental care has been suggested via protection. ¹² Fanning was related to water exchange of the burrow. Both parents performed amplitude slow tail beats at the entrance with their heads pointing outwards. ¹³ Males guarded the eggs inside the nest while females hovered near the nest and chased away intruders. ¹⁴ Both parents' movements seem to help larvae to hatch. ¹⁵ The male cares for the eggs inside the burrow but parental activities are not mentioned. ¹⁶ Females place coral rubble and algae over the burrow entrance when the male is inside as in *V. longipinnis* and this is considered female contribution to parental care.

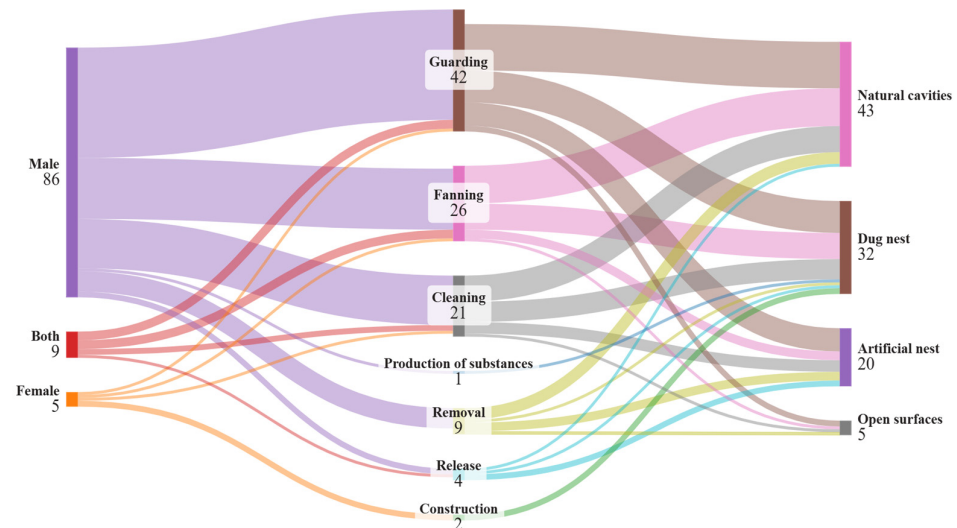


Figure 2. A Sankey diagram representing interactions between the number of species displaying each parental care type in relation to the sex of the caregiver and nesting type for thirty-six species of gobies. The left nodes indicate the sex of the caregiver displaying each type of care. The middle nodes indicate the type of care performed in relation to the nest type. A *dug nest* refers to a burrow or a small cavity constructed in the substrate, which can include the use of material to cover the surface of the nest. An *artificial nest* refers to a non-natural nesting site (e.g., PVC pipe). *Natural cavities* are spaces between rocks, crevices, or lumen of sponges that do not involve significant modification of substrates. *Open surfaces* refer to spawning on algae or plant stems. Line thickness indicates the number of species for each interaction (male—guarding, male—fanning, etc. or guarding—dug nest, fanning—dug nest, etc.). Color is used to identify the lines connecting different nodes. Note: many species perform multiple types of care and spawn in different nest types, such that the numerical values of the nodes do not equal the number of species considered. For definitions of parental care types, see Table 1. See Table 2 for additional information on species-specific data. The image was made with <https://sankeymatic.com/build/> accessed on 8 June 2025.

3. Results

We identified relevant data on post-fertilization parental care for 36 gobiid species (Figure 1 and Table 2). The types of care in gobies consist of behaviors such as protection/guarding, fanning, cleaning, egg/organism removal, larval release, and post-mating construction of mounds. Parental care also included a non-behavioral trait: the production of antimicrobial substances. These traits vary in complexity and energetic cost and represent both direct and indirect types of offspring care. Note that care types are tallied as individual instances across species, and a single species may exhibit multiple types of parental care. As noted above, definitions of each care type can be found in Table 1. Across species, paternal care was by far the most commonly reported form, although biparental care occurs in a minority of goby species (Figure 1 and Table 2). In the following sections, we discuss the behavioral and non-behavioral types of parental care observed in gobies.

3.1. Behavioral Parental Care in Gobies

Among the 36 goby species included in this review, we identified six distinct types of behavioral parental care. Protection/guarding was the most frequently reported type of care (Figures 1 and 3a). Specifically, 31 of the 36 species exhibit protection/guarding behavior (Table 2), and guarding by the male was performed in dug nests, natural cavities, artificial nests, or open surfaces (Figure 2). Protection/guarding can also be performed by both parents together and the female alone (Figure 2). In the remaining five species, protection/guarding cannot be ruled out—and is perhaps even likely given that one or more parents remain at the nesting site—but was not noted in the references that we located.

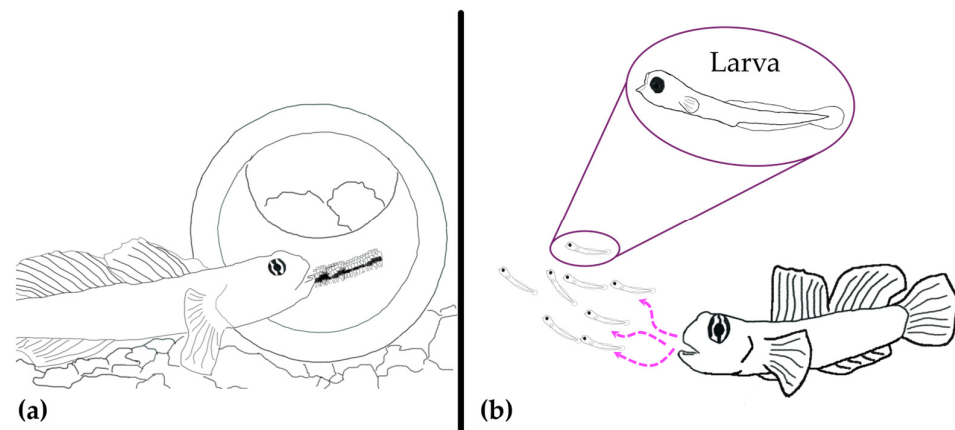


Figure 3. A schematic representation of some behavioral types of post-fertilization care found in Gobiidae. (a) Parent blocking nest entrance (protection/guarding). (b) Parent releasing larvae. Dotted pink arrows indicate movement of larvae released from parent's mouth. For further information about each type of care, see Table 1. The illustrations were created by M.T.-G. The goby image is inspired by Figure 1 of [27].

Fanning/aeration was the second most commonly reported type of parental care behavior in the goby species that we considered (Figure 1). This behavior was documented in 24 of the 36 species (Table 2) and was performed by the male in a dug nest, a natural cavity, an artificial nest, and/or an open surface (Figure 2).

Cleaning and egg/organism removal (see [24,25]; Table 1) were the third and fourth most commonly reported types of care in gobies, respectively (Figure 1). Of the thirty-six species considered in the present study, nineteen species engaged in cleaning and seven engaged in removal behavior (Table 2). Cleaning was performed by the male, both parents, or the female in dug nests, natural cavities, artificial nests, and/or an open surface, while removal was always performed by the male alone (Figure 2).

Larval release is relatively rarely documented (Figures 1 and 3b). This behavior was documented in just three goby species and was performed by the male (Belize sponge goby, *Elacatinus colini*, and the redhead goby, *E. puncticulatus*) or both parents (blind goby, *Typhlogobius californiensis*) (Table 2). This type of care was observed in species nesting in dug nests, natural cavities, or artificial nests, performed by the male or both parents together (Figure 2), and involves active facilitation of larval emergence (Figure 3b).

Post-mating mound construction was the rarest type of behavioral care reported in our study (Figure 1) and was only reported in two species of the genus *Valenciennaea* (Table 2). Post-mating mound construction in these two species occurs after spawning and is known to improve water exchange around eggs. It is performed only by females in dug nests (i.e., burrows; Figure 2). Other species such as the sand goby (*Pomatoschistus minutus*) are known to prepare mounds prior to mating and likely modify their mounds after mating but were not included here since our focus was exclusively on post-fertilization parental care.

It is important to note that the apparent rarity of some care behaviors may reflect observational biases or limited reporting, rather than true biological absence. As parental care is not well described in most goby species, less conspicuous or infrequent traits—such as larval release or mound building—may be underrepresented in the literature.

3.2. Parental Care Is Not Just Behavior: Non-Behavioral Parental Care in Gobies

In addition to behavioral types of care, some gobies exhibit non-behavioral mechanisms following mating that enhance offspring survival. One such mechanism is the production of antimicrobial substances, which may reduce the risk of fungal or bacterial infection on developing eggs (see Table 1). This type of care is rarely reported in gobies

and in this study was found to be performed by the male (Figure 2). Of the 36 species considered in this study, only 1 (grass goby, *Gobius ophioccephalus*) is known to produce antimicrobial substances. In this species, the male produces antimicrobial substances for eggs that are laid in a dug nest (Table 2).

3.3. Form of Parental Care

Uniparental paternal care was the most prevalent pattern observed in our review. Specifically, 27 species exhibited paternal care, while 8 species were reported to display biparental care (Table 2). Only one species showed flexibility in parental care in which females care for offspring if the male is removed from the nest, suggesting context-dependent flexibility in caregiving roles (*Amblygobius phalaena*, Table 2). No species in the reviewed sample were found to provide exclusive maternal care.

These results confirm that paternal care is the dominant form of post-fertilization care in gobies. Flexibility in which sex provides care has been rarely documented; however, it is unclear whether such flexibility in care is truly rare versus not well studied. Additionally, males were found to exhibit almost all types of care described in this review—including guarding, fanning, cleaning, and egg/organism removal (Figure 2). The sole exception was post-mating mound construction, a behavior that was performed only by females of the genus *Valenciennea*. In some species, female contribution to care was not described/specified (Table 2). In some species with biparental care, females were also found to perform protection, fanning, and cleaning to help their mates care for the eggs (Table 2). Therefore, the apparent rigidity in sex roles should be interpreted cautiously until more comprehensive behavioral data become available. Moreover, the extent of plasticity in caregiving roles remains poorly understood and may be underestimated due to observational limitations or a lack of experimental manipulation.

4. Discussion

In the present paper, we summarized patterns of post-fertilization parental care in gobies integrating classic classifications of parental behavior by Blumer [24,25] with more recent observations. Our findings confirm that protection/guarding is the most commonly reported type of care in gobiid species, and this behavior is likely related to the fact that goby eggs are attached to a substrate. Because eggs are attached to a substrate, they are susceptible to predators and defensible by parents. Protection is potentially the most important parental behavior in gobies because predation can lead to complete clutch death. For example, when parents are removed from the nest, predators consumed all eggs in the redhead goby, *Paragobiodon echinocephalus* [92], and in the sand goby, *Pomatoschistus minutus* [102]. Our finding that protection/guarding is the most common type of care in gobies is also consistent with previous work that has noted that this type of care is the most common type of care in fishes in general [25,121]. The absence of guarding in some gobies could be linked to one of three possibilities: (1) the parental care description in those species is incomplete, (2) the nesting site is a closed structure, as observed in some species that construct burrows and close the entrance (e.g., *Signigobius biocellatus* and *Valenciennea longipinnis*; see Table 2), such that it is not necessary for parents to protect the nest entrance against possible predators, and (3) mate guarding may incidentally benefit offspring by deterring potential predators (for example, mate guarding (i.e., a behavior in which one sex, typically the male, guards his mate to presumably prevent remating) exists in species such as the blind goby, *Typhlogobius californiensis* [116], the whitebarred goby, *Amblygobius phalaena* [35], isaza, *Gymnogobius isaza* [77], and the sharknose goby, *Elacatinus evelynae* [52], and could parallelly drive away potential predators, thus reducing or eliminating the need for direct guarding of eggs).

The second most common type of parental care observed in the gobies considered in our review was fanning. As with guarding, fanning is possible because eggs are clumped together and adhere to the substrate. Fanning is thought to increase water flow and oxygenate eggs [122] and it usually increases when oxygen concentration is low (e.g., [28, 123]). Eggs also have an increase in oxygenation requirements as they develop [124], and parents increase fanning behavior as eggs are closer to hatching in some species including the Padanian goby, *Padogobius bonelli* [17], the long-finned goby *Valenciennea longipinnis* [28], and the redhead goby, *Elacatinus puncticulatus* [20]. Some authors have also reported a positive correlation between fanning activity and hatching success, such as in the greenbubble dwarfgoby, *Eviota prasina* [67].

Cleaning and egg/organism removal are also relatively common (Table 2). In gobies, cleaning generally involves touching the eggs with fins or rubbing the body against the eggs and is assumed to remove debris and reduce microbial risk. Removal behaviors, such as taking inviable eggs into the parent's mouth, have been documented in the Arno goby, *Padogobius nigricans* [18], the redhead goby, *Elacatinus puncticulatus* (Figure 4), and the common goby, *Pomatoschistus microps* [125]. In some cases, this removal behavior is linked with filial cannibalism of eggs (e.g., see non-viable offspring and brood hygiene hypothesis in [126]), and filial cannibalism can in some cases serve as a type of parental care in fishes (see [127]).

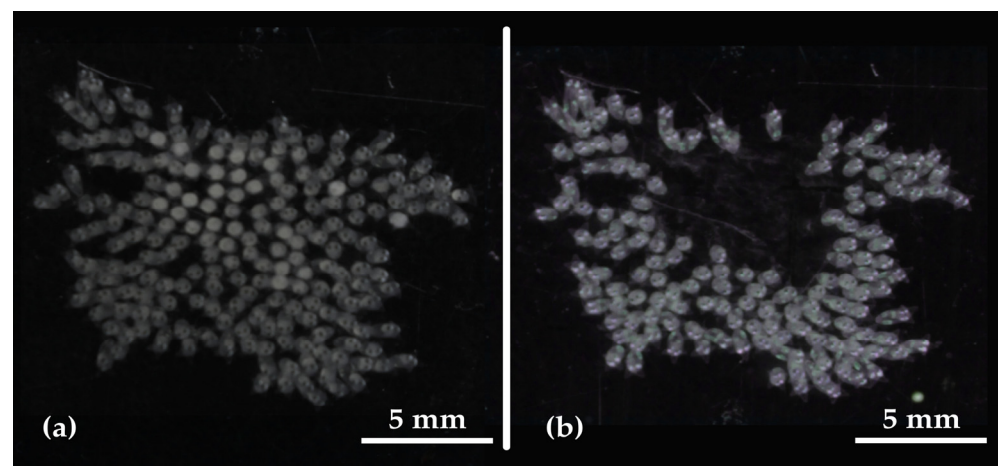


Figure 4. Cannibalism of dead eggs in redhead goby, *Elacatinus puncticulatus*. (a) A clutch of five days age, where the developing eggs possess black eye spots and dead eggs are light brownish in color and lack pigmented eye spots. (b) A day after (day six), the male parent has consumed the dead or non-developing eggs, as can be observed by the lack of eggs in the upper center of the clutch. Photos taken by M.T.-G.

The aforementioned parental care behaviors occur prior to offspring hatching. Once larvae are ready to hatch, a very small number of goby species help their offspring hatch and leave the nest. The finding of larval release in gobies is consistent with research in some non-gobiid species, including *Cyclopterus lumpus* (Family Cyclopteridae) [128], *Omobranchus anolius* (Family Bleniidae) [129], *Tripterygion tripteronotus* (Family Tripterygiidae) [130], and some species of mudskippers (Family Oxudercidae) [131]. The mechanism of gobies helping larvae leave the nest is similar to that observed in *Tripterygion tripteronotus*, *Omobranchus anolius* and in some mudskippers where parents take larvae into their mouth and then spit them out. In gobies, this pattern was reported for two species of the genus *Elacatinus* (*E. colini* [31] and *E. puncticulatus* [20]) (Table 2). In *E. puncticulatus*, it has been hypothesized that males release larvae according to the proximity of the female to minimize filial cannibalism by the female on larvae [20] since females have been reported to cannibalize larvae [132].

MacGinitie [116] suggested that parents of *Typhlogobius californiensis* could also help their larvae hatch. Additionally, parents taking larvae into their mouth could have additional advantages. Thomson and Bennett [129] suggested that in *Omobranchus anoliis*, parents taking larvae into their mouth could eliminate an irregular layer that covers larvae after hatching, and they suggested that by doing so, parents increase offspring survival. It is possible that this type of care is more common than previously thought since most studies of parental care in gobies do not follow offspring post hatching, and we suggest that future research on parental care in gobies should seek to identify if and when larval release occurs more broadly.

Some gobies construct structures to increase egg survival after mating. After spawning, females of the genus *Valenciennae* have been observed to create a mound while the male is taking care of eggs inside a burrow. In *V. longipinnis*, this mound structure has a role in water exchange inside the burrow, which influences the development of eggs and complements the care provided by the male inside the burrow [34]. Notably, this is one of the few parental behaviors observed to be performed exclusively by females, suggesting potential sex-specific contributions in some biparental systems. This appears to be a relatively rare type of parental care in gobies though.

Beyond behavioral traits, some gobies exhibit non-behavioral types of care (as suggested by the parental care definition in [22]), such as the production of antimicrobial substances. In our review, we found that one goby is known to produce substances with antimicrobial activity (Table 2). This finding is consistent with research in non-gobiid species, including blennies such as the peacock blenny, *Salaria pavo*, and the redlip blenny, *Ophioblennius atlanticus*, where males produce mucus enriched with antimicrobial substances [133]. For instance, in *Salaria pavo*, these lysozyme-like compounds inhibit the growth of Gram-positive and -negative bacteria, and offspring of parental males deprived of structures that produce these compounds had lower survival compared with offspring from males with anal glands that could produce antimicrobial substances [33]. Similarly, in three-spined sticklebacks, *Gasterosteus aculeatus*, glue produced by the urinary bladder decreased the growth of the fish pathogen *Pseudomonas fluorescens* and a fungal infection commonly seen in laboratory studies [134]. Additionally, eggs exposed to this glue hatched at a higher rate compared to those that were not exposed to the glue [134]. In the fringed darter, *Etheostoma crossopeterum*, epidermal mucus showed an inhibitory effect on infections of eggs [135]. In gobies, the production of substances with antimicrobial properties seems to be related to the presence of seminal vesicles or sperm duct glands; these structures are present in males of most goby species [6,136]. These glands are a pair of leaf-like structures that grow out from the sperm duct and are organized in chambers [6]. Diverse functions have been proposed for these structures such as the promotion of sperm viability, enhancing the contact of sperm with the eggs, cementing of nest walls, the production of sperm trails, and the production of egg-protective substances [136–139]. In the grass goby, *Gobius ophiocephalus*, Giacomello et al. [32] found that secretion of material from sperm duct glands inhibits the proliferation of Gram-positive and -negative bacteria. Additionally, as noted above with respect to parental care behaviors, the absence of evidence for the production of antimicrobial substances in most species might reflect a lack of observation and targeted study rather than true biological absence. Because these substances are not directly observable through behavioral observation alone, they are likely underreported in the literature. This highlights a broader challenge in documenting non-behavioral types of care, which may require physiological or biochemical analysis to detect. Given the potential adaptive significance of these traits, especially in environments prone to microbial proliferation, further investigation is needed to assess their prevalence and functional role in gobies.

Finally, our review confirms that uniparental paternal care is the predominant form of care in gobies (Table 2). The predominance of male parental care in gobies can be attributed to a convergence of ecological conditions and evolutionary incentives that consistently favor male over female investment. First, external fertilization combined with male territoriality allows for high paternity certainty, reducing the risk of misdirected effort—an essential precondition for male care to evolve [140–142]. Moreover, when males already defend nest sites to attract females, the incremental cost of remaining to care for eggs may be low relative to the fitness gains from enhancing egg survival, especially when additional mating opportunities are limited or unpredictable. Theoretical modeling by Whittingham et al. [141] suggests that when offspring survival increases sharply beyond a care threshold, selection will favor males that invest fully once paternity is assured. Furthermore, male care may also be maintained through sexual selection, as caring behaviors can function as honest signals of quality that attract additional females [104,143]. Together, these factors help explain the evolutionary stability of paternal care in gobies despite the absence of female-only care.

Interestingly, we found one goby species, *Amblygobius phalaena*, in which females provided care if the male was removed from the nest [36], suggesting that sex-role flexibility may exist in gobies but is rarely documented. The idea that parental care can be flexible regarding sex is rarely considered in fishes. It would be interesting to explore whether other species have the potential to be flexible in which sex provides care. Importantly, though, in some cases, details of female contribution to care are not described even when the authors reported that the female has a role in care, as observed for the sharknose goby, *Elacatinus evelynae* [53], and isaza, *Gymnogobius isaza* [77,79]. It is unclear why some goby species provide paternal versus biparental care, but some possible explanations for biparental versus uniparental care include the following: (1) high egg mortality, which may select for cooperative care leading to the evolutionary transitions from uniparental to biparental care [144]; (2) sex differences in energetic constraints, such as females needing to forage more frequently than males, as observed in *Valenciennea strigata* [119], which could decrease their ability to provide care; (3) stable pair bonds, which may facilitate biparental coordination by increasing the likelihood that females remain in close proximity to their mate while he is caring for eggs, as observed in the blind goby, *Typhlogobius californiensis* [116]. Additional studies are needed to fully understand sex-specific patterns of care in gobies. In the future, it will be particularly important to explore how the mating system is linked to parental care patterns in gobies.

Given the striking diversity of parental care in gobies, we suggest that future research should consider evolutionary transitions among types of care in a phylogenetic context. It would also be worthwhile to broaden the consideration of factors that are likely to influence parental care patterns in gobies. For example, details of egg characteristics (adhesion patterns, egg and clutch sizes, development time) and other life history characteristics such as the pace of life and adult mortality are likely to influence care.

5. Conclusions

In summary, parental care is relatively rare in fishes, but when it does occur, it is typically provided by males and frequently includes behaviors such as guarding, fanning, and cleaning. Our review suggests that parental care in gobies is similar to that of many other fish species. Gobies that exhibit parental care typically engage in protection/guarding, fanning and cleaning, and egg/organism removal, and care is most often paternal. Importantly, parental care is not described in most species of gobies, making it difficult to assess the full extent of variation across the family. To better understand the evolution of care in gobies, future research should prioritize the systematic documentation of both parental care

and mating systems across a broader range of taxa. Integrating these two aspects will be essential for uncovering potential co-evolutionary patterns and for identifying the ecological and social factors that shape care strategies in gobies. Moreover, integrating these data into a phylogenetic framework will be essential for uncovering evolutionary transitions in the form, type, and sex roles of parental care within this diverse group of fishes.

Author Contributions: Conceptualization, M.T.-G. and H.K.; methodology, M.T.-G. and H.K.; formal analysis, M.T.-G.; writing—original draft preparation, M.T.-G., H.K., B.P.C.-V. and P.G.-F.; writing—review and editing, M.T.-G., H.K., B.P.C.-V. and P.G.-F.; visualization, M.T.-G. and H.K.; supervision, H.K.; project administration, M.T.-G., H.K. and B.P.C.-V. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Data are contained within the article.

Acknowledgments: We thank the three anonymous reviewers for their feedback.

Conflicts of Interest: The authors declare no conflicts of interest.

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