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Parental care and reproductive behavior of the clown goby, *Microgobius gulosus*, with observations on predator interactions

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Synopsis

I describe reproductive behavior and mating system of the clown goby from field observations. Clown gobies exhibit a loosely haremic mating system. Pairs construct burrows at the base of cattails, the roots of which provide structural support and a spawning substrate. Larger males monopolize multiple burrows, each with an individual female. After spawning, males camouflage burrow entrances with sand and females brood developing young for 4 days. Males continue to guard the covered nests in 50% of observed brooding periods. Burrows are also used as shelter from predators. Both sexes confront intruders but only males exhibit a distinct color response to juvenile blue crabs, *Callinectes sapidus*, the most significant predator. The male color response appeared to mimic the color of adult blue crabs, a known predator of juvenile crabs, perhaps acting as a deterrent. The presence of the predatory blue crab may require one parent to perform deterrent displays, promoting female care in this mating system.

Introduction

Parental investment theory predicts that in fishes, males will be the providers of parental care (Perrone & Zaret 1979). Empirical evidence supports this prediction; paternal egg care is the predominant mode of care in fishes (Gross & Sargent 1985). William's Principle states that paternal care should be selected for when: (1) paternity is ascertained through external fertilization (Williams 1975), (2) males, by virtue of their larger size, are able to monopolize a defensible resource such as nesting sites or a food source (Williams 1975), and (3) males are able to guard the eggs of more than one female simultaneously, facilitating polygamy (Wittenberger 1979).

The occurrence of maternal care in fishes presents an interesting puzzle to behavioral ecology. This is especially true for the Gobiidae, a widely distributed, speciose family of small benthic fishes (Moyle & Cech 1999), whose members have been widely reported as exhibiting paternal care (Breder & Rosen 1966). Reports of female contribution to parental care in gobies are limited to two cases. MacGintie (1939) reported that the blind goby, *Typhlogobius californiensis*, exhibit biparental care. Takegaki (2000) indicated that females of *Amblygobius phalaena* remain associated with the nest while males brood eggs, contributing to the deterrence of predators. By contrast, my preliminary personal observations on the estuarine clown goby, *Microgobius gulosus*, indicated that this species may exhibit maternal care of young. I undertook this study to describe the reproductive behavior of *M. gulosus*, and test these hypotheses regarding factors that may promote this mating system.

The genus *Microgobius* comprises 14 species of 7-spined gobies distributed throughout the western Atlantic and eastern Pacific oceans of America (Böhlke & Robins 1968, Birdsong 1981). Detailed behavioral information does not exist for the family, because most species are uncommon or unavailable in sufficient numbers for study (reviewed in Birdsong 1981). *M. gulosus* is an exception, occurring in dense populations in accessible areas (Provancha & Hall 1991, personal observation). Generally, clown gobies occur in shallow, protected, estuarine waters, occasionally vegetated, with substrata ranging from muck to beach sand, along the southeastern and south-central United States coasts (Ginsburg 1934, Tagatz 1968, Gilmore et al. 1981). Birdsong (1981) indicated that clown gobies form short tunnels, 25–50 cm long, with an opening at each end, in fine sediment. Provancha & Hall (1991) observed that central Florida populations along the Atlantic coast cease spawning in late fall. They calculated an annual mortality rate of 95%, indicating that few individuals live beyond age II. They also observed that these populations have low fecundity with large eggs, compared to those of other gobiids in the region.

Clown gobies are sexually dimorphic (Baird 1965). Males are larger and more colorful than females. They have three conspicuously elongated dorsal spines on the anterior dorsal fin and a greatly enlarged mouth. Females have better defined blotching than males. In addition, the pelvic fins of females exhibit a black, hyaline, distal margin. With the exception of gonads, no internal sexual dimorphism is known.

Methods

Study site

I tagged and observed members of a population of *M. gulosus* using mask and snorkel over 1 year for a total of 322 h of observations. My study site was a large pond southwest of Fort Pickens, Gulf Islands National Seashore, Pensacola, Florida (30°19′33″N, 87°17′46″W). The pond, measuring approximately 400 by 120 m and having a maximum depth of 8 m, is situated on a barrier island. It is normally separated from the Gulf of Mexico by approximately 180 m of sparsely vegetated sand. During episodic events such as tropical depressions, hurricanes, and storm surges, introduction of larvae, juveniles, and adults of species dwelling in the near-shore habitat of the Gulf of Mexico may occur.

The shoreline vegetation was dominated by narrow-leaved cattail, *Typha angustifolia*, and black needlerush, *Juncus roemerianus*. The substratum ranged from sand to soft silt and mud. Several areas of shallow sand banks (up to 1 m deep) near the shoreline, provided clown goby spawning sites that were accessible for observation. These areas ranged in size from narrow tracts of shoreline to 50 m^2 patches of varying shapes.

I tagged 62 female and 61 male gobies between August 1997 and July 1998. I measured standard length to the nearest millimeter, using calipers. Rather than tagging all fish at the beginning of the study season, a more practical approach was to tag three or four pairs at a time, and observe them closely over shorter periods of time. This allowed me to focus on pairs that were particularly active. Furthermore, the complex and quickly changing associations between subjects and their territories, the cryptic nature of females during the refractory periods (determined from preliminary observations from May to August, 1997), and the heterogeneous nature of the environment, resulted in some fish eventually being lost. Therefore, it was necessary to introduce newly tagged subjects throughout the study.

I caught gobies with a hand-net. Placing a hand-net over the main burrow entrance, and inserting a finger into the alternate entrance, caused the goby to exit into the net. I took individuals to a floating field station, and immobilized them on a dry tissue with the ventral side down. I marked fish subcutaneously with injections of undiluted latex paint of different colors using a 26-gauge hypodermic needle (Lotrich & Meredith 1974). I returned gobies to their burrows, which were marked with numbered survey flags.

Behavior and reproduction

To facilitate the description of the clown goby's behavior, I identified several behavioral units (modal action patterns [MAPs], Barlow 1977). I made these observations ad lib over approximately

65 h between June and September 1997, prior to the beginning of focal sampling. I noted all observations underwater on plastic slates in shorthand, using a digital watch to record the duration of behavioral units.

To standardize data collection and interpretation, I based behavioral terminology and recording methods on guidelines set by Martin & Bateson (1993). Once I had identified behavioral units, I used focal animal sampling with continuous recording to quantify behaviors and characterize behavior patterns. I collected samples ad lib from 2 April to 1 September 1998, during daylight (06:00–20:00 h). I directed my sampling at gobies exhibiting pair establishment, burrow construction, courtship, spawning, termination of parental care, and post-reproductive behaviors. Either one or a pair of gobies was the focus of observations during a particular sample period. I also recorded behavior of non-focal individuals (such as blue crabs, *Callinectes sapidus*, and non-resident conspecifics) when they interacted with the focal animals. In the case of blue crabs, I estimated the crab's size (carapace width) visually to the nearest 1.0 cm. In the case of conspecific intruders, I described their behavior by the same guidelines as those for focal animals. I noted the sex and size of the intruder relative to the focal animal (i.e., smaller, larger). I used a digital watch to record the duration of behavioral sequences, and the duration of the entire observation period. In the interest of evaluating whether it was appropriate to include all focal samples, even if they were only 15 min in duration, I performed a Kruskal–Wallis non-parametric test (Zar 1996) on samples that were 30 min or longer. I compared the frequencies of behaviors in the first 15 min and the last 15 min of the observation period. This test found no significant difference in frequency of behaviors between the two periods, indicating that it was appropriate to use focal animal samples that were 15 min or longer. I standardized frequencies of behavior action patterns and reported them as number of units per 30 min.

In addition to focal sampling, I noted relatively rare but important events with the use of scan sampling. I censused the entire group of tagged individuals one or more times per day and noted their behavior at those instances. I tabulated exceptional observations of behaviors, such as pair establishment and dissolution, new burrow acquisition and construction, spawning, and termination of parental care, as total number of occurrences. I identified the beginning of the paired interval at the time of tagging so actual cohabitation periods may have been longer. In addition, I conducted scan sampling at nighttime to determine the nocturnal behavior of clown gobies. I made these scans from 21:00 to 23:00 h, from 23:00 to 01:00 h, and from 01:00 to 03:00 h, each on a different day within a 2-week interval. Moonlight was sufficient for the majority of observations but I used a flashlight occasionally.

I surveyed the site daily from 1 August to 15 September 1997, and from 2 April to 1 September 1998, weekly from 16 September to 15 November 1997, and from 2 March to 1 April 1998, and biweekly from 16 November to 1 March 1998. During scan sampling I scored females as ovigerous, intermediate or spent. It was possible to determine if females had recently spawned because their abdomens, which were distended before spawning, appeared concave. Examination of two females in each category confirmed a correlation between vitellogenic maturation and abdomen shape.

I used a fiber-optic surgical laparoscope (Surgical Image Laboratories) to inspect clown goby burrows throughout the study. The instrument was 30 cm in length and 1 cm in diameter and was equipped with an eye-piece (5× magnification) and a light-source inlet. Light was provided by holding an underwater flashlight (UKE Minipocket Light, 1.13 W) over the inlet.

I inserted the laparoscope directly into burrows, at different stages of the reproductive cycle, to determine: (a) burrow structure; (b) presence and sex of the parent providing parental care; (c) arrangement of embryos within the nest; (d) stage of developing young within the burrow; and (e) progress of hatching at termination of parental care. In cases where the shape of the burrow prohibited the use of the laparoscope, I determined the above categories by manual inspection or excavation of the nest. I also made detailed descriptions of embryo arrangement on collected clutches using light microscopy (magnification 6–50×).

I measured depth of the burrow, from the surface, and noted the amount of vegetation surrounding the burrow, and the type of supporting structures (e.g., plant roots, logs). Sample sizes vary for these measurements because not all burrows were measured for the same variables and sample groups are not mutually exclusive.

Results

Glossary of behavioral units

Here I outline some of the most frequently observed clown goby MAPs or behavioral units. Unless otherwise specified, each behavior was displayed by both sexes.

Fin display: The fish extended its dorsal, caudal and anal fins maximally, while supported on its pelvic disk. The signaling fish adopted a parallel, anti-parallel, or perpendicular position to its recipient.

Fin display with throat expansion and throat darkening: In addition to fin display, males lowered their brachiostegals and expanded their throats, which intensified in color to a grayish black. The body remained pale.

Fin display with body darkening: Fin display was accompanied by darkening of the entire body to a brown or charcoal gray color. This behavior was only observed in males.

Gape: In intraspecific aggressive displays the fish held its mouth open wide, sometimes such that the jaws almost formed a straight line, for approximately one second. Each fish, facing its opponent, or just slightly off-center, took turns gaping. The fishes' bodies were angled laterally at approximately 90° to the head, in the opposite direction of their opponent's body (Figure 1).

Gape push: Both fish held the gape and the jaws came into contact. One fish used its mouth to push the other downward into the substratum.

Jaw locking: The fish seized each other's jaws, one grasping the lower jaw of the opponent, the other grasping the upper jaw. Three males with dislocated jaws were seen functioning normally (i.e., courting females, defending territories, spawning) throughout the study.

Parallel swim: Both fish swam in the same direction, remaining approximately 5 cm apart, while maintaining fin display.

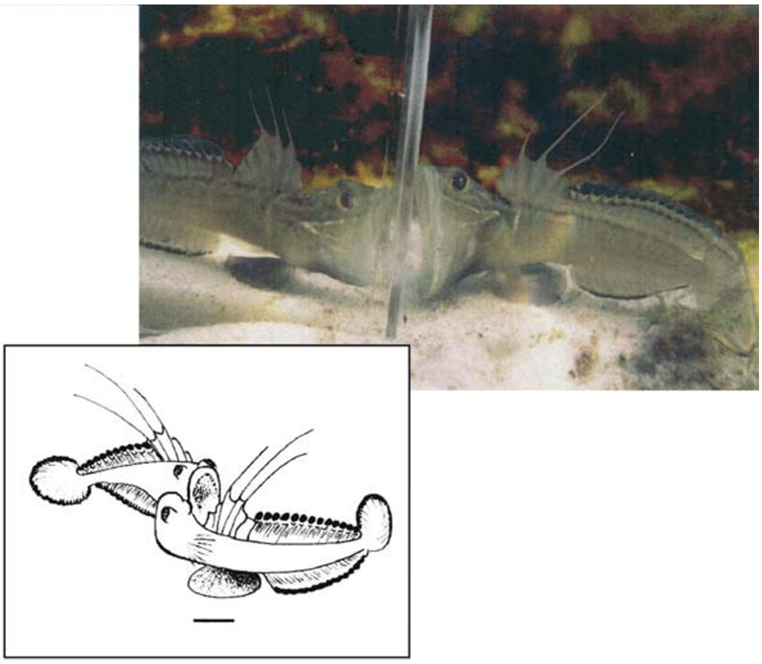

Figure 1. Gaping contest between two males. In gaping contests males (shown here) or females positioned themselves face to face while extending their jaws maximally. One fish was contained in a plexiglas box to facilitate photography. Body posture relative to the opponent such that the greatest surface area is presented (line drawing). Scale bar = 10 mm.

Charge: The fish made a rapid, accelerated approach toward another fish.

Tail-sweep: The fish quickly swung the posterior half of the body back and forth while close to the substratum causing sand to be brushed away.

Sand-spit: Fish exited the burrow carrying sand or debris in its mouth from inside the burrow and expelled it.

Abdomen display: Female arched her body laterally, forming a crescent or sigmoid shape, with the abdomen directed at the male. While performing abdomen display, the female turned her pelvic disk such that it framed the abdominal region like a fan, facing in the direction of the male (Figure 2). The surface of the disk was white or yellowish white, matching the brightness of the female's abdomen. Since the disk and the abdomen were similarly colored, they blended in together, visually to the observer. The border on the edge of the disk functioned to redefine the boundaries of the abdomen, making the area appear larger than it was. The dark blotching on the rest of the female's body contrasted with the white abdomen, heightening the optical effect.

Mouth: The female swam to the male, sometimes rapidly, for a short distance, then gently pushed him with her open mouth, contacting him on the flanks and just behind the pectoral fins.

Side-to-side: The male swung his body from side to side rigidly, with fins erect and mouth slightly open. The substratum was not disturbed.

Head-down-swim: The fish swam a short distance, with fins erect. In males, the pelvic disk often became a charcoal or black color.

Gentle undulate: The fish swung its body from side to side, with fins partly erect, while pivoting on the pelvic disk. This was done without disturbing the substratum.

Description of nest-site preparation and burrow structure

In loose sand, nests were excavated under the roots of aquatic plants, primarily cattails, such that the

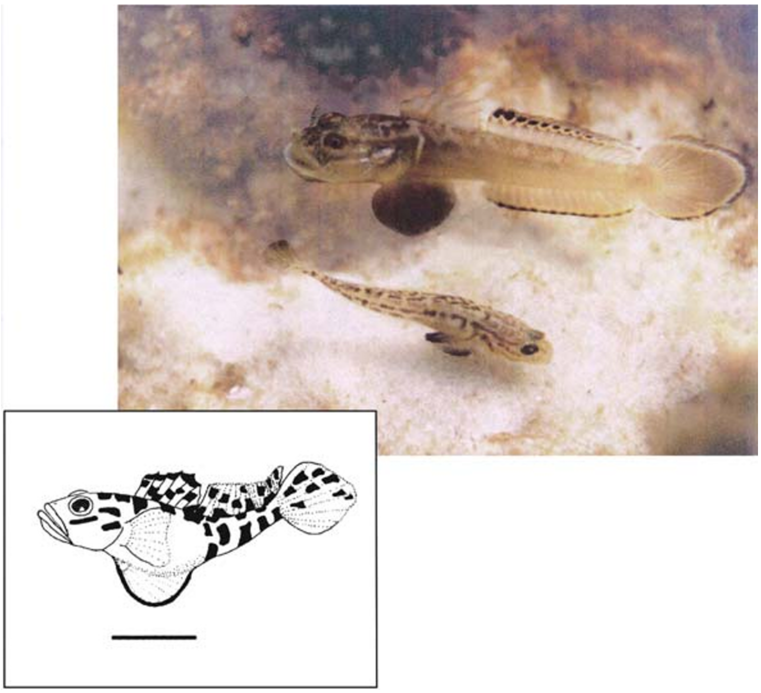

Figure 2. Abdominal display. Female (lower fish) performs abdominal display to male by curving her abdomen towards him and turning her pelvic disk to frame the abdomen. Line drawing shows male's perspective of female abdominal display: the white abdomen combined with the while pelvic disk creates an optical illusion, extending the perceived surface are of the abdomen. The dark edge of the disk accentuates the abdomen's new border. Scale bar = 10 mm.

fine rootlets of the plant lined the ceiling and occasionally the entire tunnel. Mean burrow length was 12.1 cm ± 2.4 (mean ± SD, range 5–15 cm, n = 21), and diameter, along the length of the tunnel varied between 1.5 and 2.0 cm. The mean water depth of burrows which I studied was 53.5 cm (±12.8, min 35, n = 34), but this varied slightly with the changing water level (unpublished data). Mean spacing of burrow entrances was 39 cm apart (±22 SD, range 9–100, n = 39).

At the time that this study commenced, many burrows were in existence and were inhabited by gobies. On 7 July 1997, the surge from tropical storm Danny deposited sand on a significant portion of the nesting area, affording an opportunity to observe one male's assessment of a cattail base for burrow construction. The male spent approximately 1 min swimming around a cattail stump, then began excavating a burrow by diving into the sand at the base of the stump, headfirst, while performing tail-sweep. A tunnel of approximately 5 cm was completed within 3 min. At this point, the male abandoned the construction and moved to another area. Manual inspection of the tunnel and the cattail stump revealed that its roots were deeper than 15 cm from the surface of the substratum, suggesting that construction was abandoned because they were too deep. Other stumps in the area, that had harbored burrows before the sand storm, also remained unoccupied. In another instance, a pair was observed constructing a burrow together. In the initial stages of construction, the male and female took turns plunging into the sand headfirst, while performing vigorous tail-sweep, and exited immediately after the plunge. Once the tunnel was excavated the pair took turns at tail-sweep and sand-spit, one entering as the other exited. They occasionally paused in the burrow between digging bouts, which lasted approximately 2–4 s. Over a period of 9 min, the male and female performed 53 and 35 bouts of cleaning, respectively.

Among established pairs, burrow maintenance was performed either by the male, the male and the female, or the female alone. Once paired, both fish participated in burrow alteration and maintenance. Males and females were seen to enter and exit burrows regularly throughout observation periods, performing sand-spit and tail-sweep (Table 1). Females spent a mean of 8.07 min 30 min^{-1} engaged in burrow maintenance. This was significantly greater ($\alpha = 0.05$) than the 3.49 min spent by males (Mann–Whitney $U = 809$, $p = 0.0032$).

Table 1. Frequency and duration (mean, standard deviation, minimum, maximum) of modal action patterns pertaining to burrow maintenance by *Microgobius gulosus*, calculated from focal animal samples (n = sample size).

Description of behavior	Mean frequency in 30 min	SD	Min	Max	N
Female enters burrow. If the female was already in the burrow at the beginning of the observation period this was scored as one	5.98	6.29	0.00	25.00	45
Male enters burrow head-first. Because males (unlike females) occasionally backed into burrows and performed gentle undulation, only head first entrance was scored in this category	3.61	4.39	0.00	18.00	53
Female performs tail-sweep	0.16	0.67	0.00	4.00	45
Male performs tail-sweep	0.94	1.88	0.00	8.00	53
Female performs sand-spit	0.60	2.17	0.00	12.00	45
Male performs sand spit	0.94	2.31	0.00	10.00	53
Duration that female remained in burrow or performed maintenance activities affecting the structure of the burrow nest or immediate area around entrance	8.07	10.39	0.00	30.00	45
Duration that male remained in burrow or performed maintenance activities affecting the structure of the burrow nest or immediate area around entrance	3.49	8.04	0.00	30.00	53

Burrow maintenance was ongoing throughout all phases of reproduction and gobies altered their burrows' structure in conjunction with different reproductive stages. The burrows of unpaired males had wide-open entrances and a relatively uniform diameter throughout the length of the tunnel. The rootlets lining the ceiling of these burrows were pressed close to the ceiling and were littered with sand and detritus. As pairs neared spawning, females pulled the rootlets lining the ceiling down to the floor and cleared them of detritus, and in three cases, I observed that burrows became narrower towards the exterior.

Paired and interpaired intervals

Clown gobies co-inhabited burrows for extended periods, before spawning. For example, I observed one pair together for 17 days prior to spawning, and the female had previously co-inhabited a burrow with a neighboring male for 10 days. Males engaged in courtship with multiple mates throughout the co-habitation period, and alternated back and forth between partners many times during the day. For example, one male was seen associating with four burrows, two of which had females. Males often associated with two burrows (n = 21) even if they were single (n = 8).

Courtship was initiated either by females (n = 2) or males (n = 2). In a typical bout, the female swam toward the male on his territory and performed abdominal display. The male responded with fin display and throat darkening, accompanied by head-down-swim. The female followed him; staying within several centimeters of his posterior, while they traveled together for approximately 10–30 cm. She performed mouth and repeated abdominal display, and the male responded with fin display and side-to-side. He used head-down-swim to lead the female to a burrow and the pair continued with varying combinations of the above sequence of courtship MAPs.

Throughout the paired interval, gobies maintained an active repertoire of communication. Mouthing, abdominal display, fin display, and other behavioral units that were used in initiation of courtship, continued to be part of paired-interval courtship displays. Courtship bouts among established pairs were initiated more frequently by females (Table 2; Mann–Whitney $U = 732.5$, $p = 0.0808$, $\alpha = 0.10$). For example, during two focal samples, females initiated 24 and 22 bouts of courtship, respectively, while their mates only initiated 3 and 2 bouts, respectively.

Females that were distended, as well as those whose abdomens appeared flat, used abdominal display whenever entering a new male's territory or reentering their mate's territory, and even when males were the ones reentering the territory. Females that were exiting the burrow (and thereby were re-entering the males' field of view) also mouthed males.

Table 2. Frequency and duration (mean, standard deviation, minimum, maximum) of modal action patterns of *Microgobius gulosus*, pertaining to pair-bond reinforcement efforts during the paired interval, calculated from focal animal samples (n = sample size).

Description of modal action pattern	Mean frequency in 30 min	SD	Min	Max	N
Pair-bond reinforcement effort (PBRE): Female mouths male	5.51	8.58	0.00	36.00	35
PBRE: Male performs fin display, side/side, head down swim	4.40	5.02	0.00	20.00	35
PBRE: Female performs abdominal display	3.38	6.69	0.000	39.00	35
All male initiations of PBRE	1.96	2.75	0.00	14.00	35
All female initiations of PBRE	4.26	6.12	0.00	24.00	35
Male leaves focal female to engage in courtship with another female	0.34	2.03	0.00	12.00	35
Female leaves focal male to engage in courtship with another male	0.03	0.17	0.00	1.00	35
PBRE: Male performs head-down-swim	0.743	1.704	0.000	7.000	35
Duration of all PBREs measured in seconds, for males and females combined	0.60	0.78	0.00	3.33	35
Duration that female kept her body in C shape while perching with male, measured in seconds	0.50	2.55	0.00	15.00	35

Courtship displays and nest preparation were interspersed among long periods of perching in front of or near the burrow entrance, or among bouts of nest maintenance and agonistic interactions. In nine of the paired interval focal samples, zero time was spent on courtship activities. Even in the sample where the pair was most actively engaged in courtship, only a total of 3.3 min of the 30 min sample was actually spent on courtship maneuvers.

For males, the minimum time elapsed between successive spawning events (*interpair interval*) was <z1 day, because males were seen courting a new mate even as the first was engaged in egg-laying. Interpair interval for females could not be determined, because it would have been possible to miss the first pairing for a female after she had spawned.

Occasionally pairs covered burrows at dusk. Nighttime surveys indicated that gobies did not enter the burrows at night; they rested motionless on the sand near the entrance. At sunrise, pairs that had covered their burrows, without having spawned, opened them and cleaned them using sand-spit and tail-sweep.

Spawning

During spawning, courtship display behaviors continued at low frequencies. Initiations of pair-bond reinforcement were still greater for females (mean = 1.00 times 30 min^{-1} ± 1.15 SD, range 0.00–2.00, n = 4), than for males (mean = 0.50 ± 0.58 SD, range 0.00–2.00, n = 4). Females occasionally exited the burrow for 1–3 s at a time and mouthed the male. On two of these occasions, an egg was seen protruding from the female's ovipositor (n = 2). Toward the end of spawning, females rarely exited and males placed the posterior of their body into the burrow, while gently undulating for several seconds at a time. Observations with the laparoscope indicated a white filmy substance coating the rootlets. Once all of the eggs were laid, the female cleared sand and detritus from the burrow by repeatedly entering it for 1 s at a time, and exiting with sand-spit. This lasted approximately 1 h (n = 11).

One spawning event, observed continuously from initiation to completion, took approximately 6 h from the time the female's ovipositor became extended to the time she was spent and began performing repeated sand-spit. During three focal samples conducted throughout this event the male left the spawning female to court another female, at a burrow 35 cm away, a mean of 2.6 times 30 min^{-1} (±1.2 SD, range 1.6–4.0). He spent a mean of 7.1 min (±6.0 SD, range 2.8–14) of his time at the second burrow. I did not observe any females courting other males or visiting other burrows during spawning.

For females, the number of days between two consecutive spawning events, beginning on the day the male was seen covering the burrow entrance, ranged from 18 to 49 days (mean = 32 ± 13 SD, n = 4). Males chased females away from the nest immediately after brooding. Females became secretive in behavior and cryptic in appearance during the early segment of the refractory period.

Parental care and duration of embryonic development

After spawning, males covered burrows from different angles, sweeping sand, algae, and detritus over the entrance. This created a camouflage that was indistinguishable from the surroundings. I disturbed covered burrows of 13 pairs. In nine cases males re-covered burrows within 30 min. In one, a spent female exited and performed tail-sweep into the burrow, covering the entrance alone within 30 min. Males did not return to the other three burrows.

Following nest covering, males usually moved to a burrow approximately 50 cm from the young-containing nest. Of 36 spawning events recorded, 18 (50%) had males that continued guarding the young-containing nests. Males responded to nest disturbances, such as blue crabs or my probing for eggs, with fin display and occasionally by biting. They immediately covered and camouflaged the burrows once the disturbance ceased.

Developing young were brooded by females. Of 10 such nests examined, nine also contained a spent female. One nest did not contain a parent, and it is possible that the brooding female exited unobserved during, the examination of the nest, or that a predator ate her. There was no evidence to suggest that females leave the nest during an undisturbed brooding period. In one case, uncovering the entrance caused a spent female to exit through an alternate opening. The male chased her back to the burrow and covered the entrance using tail-sweep. In another case where the male was not present, the female covered the burrow alone after disturbance. In two cases where the burrow structure was partly damaged (by me, and by a blue crab), the male chased the female away and ate the young.

The *brooding interval* began when the male covered the entrance of the burrow, and ended when young hatched and departed. Hatching was assumed when previously covered burrows were found open, without evidence of disturbance by predators, or when either the male or the female were seen cleaning out the nest. For each of three pairs observed, the brooding interval lasted four days at temperatures ranging from 28 to 32°C.

The eggs of two females were counted for this investigation. One female, (3.1 cm SL) contained 340 eggs (July 1997). The second female (≈3.5 cm SL, August 1997) was found brooding 442 embryos.

Arrangement of embryos in the nest

I determined the arrangement and position of embryos in the nest from 12 field observations and one aquarium spawning. In all cases, eggs were entangled among the fine rootlets of cattails, which protruded into the burrow. Each egg was attached to a thread (≈10 mm long), which was attached to another thread that connected several eggs. This thread was then connected to another thread that connected all the eggs on a particular rootlet together (Figure 3).

Using the laparoscope, the presence of embryos and I confirmed their developmental stage in four nests without disrupting the brooding cycle. In the nest that was observed for two consecutive days

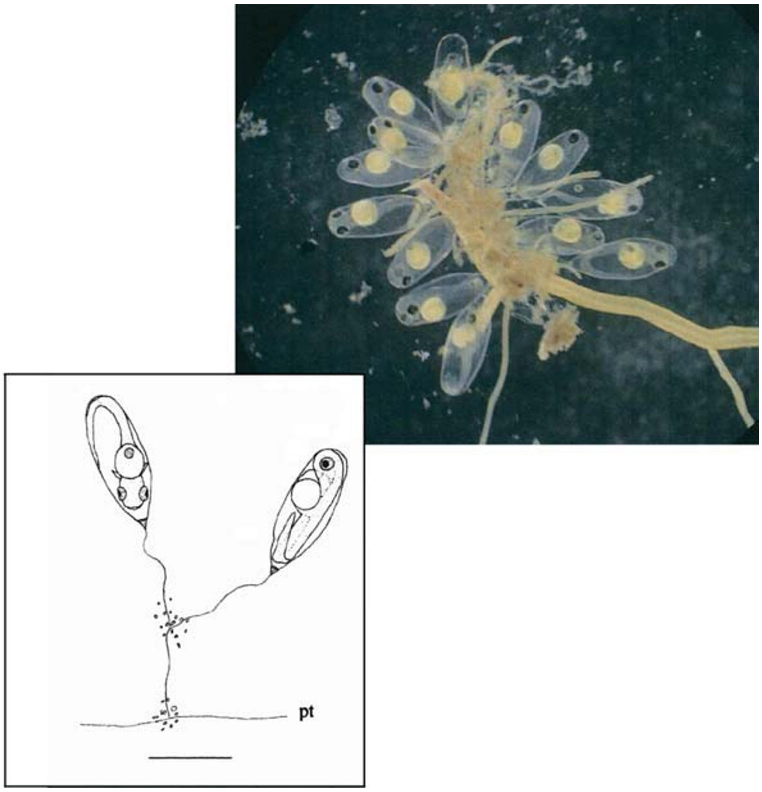

Figure 3. Arrangement of developing embryos on *Typha angustifolia* rootlet. Embryos depicted in photograph are entangled on the rootlet by primary threads. Line drawing depicts attachment of embryos to individual threads, which attach to the primary thread (pt). Age of embryos estimated at 3 days post spawning. Scale bar = 5 mm.

(see previous section) developing young were suspended from rootlets lining the ceiling, beginning approximately 5 cm into the burrow and extending to the back of the 11 cm tunnel. On the third day, the burrow entrance was open, indicating that parental care had been terminated. In another nest, the embryo cluster began only 2 cm from the nest entrance and was primarily situated on the side rather than at the top of the burrow. Individual embryos encased in chorionic membranes measured 2 mm in length and 0.7 mm in width (n = 5).

Termination of parental care and post-reproductive behavior

In June, 1998, I found a nest containing embryos in the process of hatching with the aid of the female. I observed a cluster of embryos against the side of the tunnel about 2 cm from the opening. I removed and placed a portion of the clutch from the nest into a cup and some young hatched immediately. My actions of removing young damaged part of the nest entrance and attracted predators. The spent female entered and exited the burrow with mouthfuls of sand repeatedly, and lunged at predators (primarily rainwater killifish, *Lucania parva* and sheepshead minnow *Cyprinodon variegatus*). The male positioned himself in front of the nest whenever a blue crab approached. Otherwise he ignored intruders. The number of embryos in the nest progressively decreased as, presumably, they hatched. After 4 h (08:00 p.m., twilight), I could not see any more embryos in the burrow. The female slowed down the frequency of sand-spit and the male was at an alternate burrow 25 cm away.

In general, spent, post-brooding females were chased from male dominated territories (n = 22). I observed non-ovigerous females on unvegetated substratum adjacent to male territories and at vacant burrows. They did not defend these areas and were easily displaced.

Notes on behavior of young

Anecdotal observations were made on young whenever they were encountered. Schools of several hundred young occupied the water column adjacent to the vegetated shoreline inhabited by adults (August 24–30, 1997). I caught two individuals, measured them (0.9 cm) and observed them by light microscopy. They lacked secondary sexual characteristics but had fully developed fins and eyes that were placed in the same position as those of adults. I observed juveniles (≈2 cm, n = 10) using tiny burrows or perching on open sand between patches of vegetation.

Agonistic interactions with conspecifics

Both males and females engaged in agonistic interactions (Table 3). Mild agonistic interactions typically occurred when a smaller male or a female intruder entered the territory of a male. The interaction consisted of the exchange of a few gapes until the intruder left or was chased off the territory.

More intense fights evolved when an equally sized or larger male intruded onto a resident's territory. The resident male approached the intruding male and performed fin display with throat-darkening. Males then faced each other and performed parallel swim, followed by a gaping contest. The antagonists gaped at each other repeatedly with fin display and throat-darkening. Jaw locking also occurred.

Agonistic interactions among females were similar to those of males. Fights began when one female approached another's burrow. I also saw females engaged in jaw locking while rolling horizontally on the substratum. Once the spawning season ended, unpaired, non-distended females were commonly seen fighting and guarding territories around burrows.

Paired males chased non-resident females intruding on their territories (observed in 8 of 52 focal samples). Yet, males allowed rejected females to occupy adjacent burrows if no females resided there. By contrast, females engaged in courtship with any male that approached, and were never observed to respond aggressively to males during the breeding season. For example, one distended female of a courting pair was chased from the burrow by a sheepshead minnow, *Cyprinodon variegatus*. She settled in another area where two males began courting her simultaneously and responded to both equally with abdominal display. I caught and relocated her at the original burrow, where she immediately resumed courtship with the original male.

Table 3. Frequency and duration of agonistic interactions for *Microgobius gulosus* and intruders, calculated from focal animal samples.

Focal sample resident engaged in agonistic interaction	Intruder type	Mean frequency in 30 min (ranked higest to lowest)	SD	Min	Max	Mean proportion of 30 min sample (rank in brackets)		SD	Min	Max	N
Male	Cs	0.95	1.24	0.00	5.00	0.69	(1)	1.59	0.00	8.00	52
	Lr	0.40	1.30	0.00	8.00	0.06	(5)	0.22	0.00	1.07	52
	O	0.37	1.21	0.00	8.00	0.05	(6)	0.13	0.00	0.53	52
	Cml	0.28	0.63	0.00	3.00	0.21	(3)	0.74	0.00	4.50	52
	Cms	0.25	0.67	0.00	4.00	0.16	(4)	0.60	0.00	3.20	52
	Fgg	0.25	0.65	0.00	3.00	0.37	(2)	2.10	0.00	15.00	52
	Cf	0.21	0.66	0.00	4.00	0.03	(7)	0.10	0.00	0.50	52
	Tot	2.70	3.04	0.00	14.00	1.57		2.60	0.00	15.00	52
Female	Lr	0.33	1.02	0.00	6.00	0.08	(3)	0.34	0.00	2.07	45
	Cs	0.27	0.81	0.00	3.00	0.11	(2)	0.50	0.00	3.33	45
	Cf	0.11	0.38	0.00	2.00	0.03	(4)	0.12	0.00	0.53	45
	Fgg	0.07	0.25	0.00	1.00	0.34	(1)	0.08	0.00	0.5	45
	O	0.04	0.21	0.00	1.00	0.01	(5)	0.06	0.00	0.33	45
	Cml	0.02	0.15	0.00	1.00	0.01	(5)	0.05	0.00	0.33	45
	Cms	0.00	0.00	0.00	0.00	0.00	(6)	0.00	0.00	0.00	45
	Tot	0.84	1.58	0.00	8.00	0.59		2.29	0.00	15.03	45

Cm – Larger or equal sized conspecific male; Lr – *Lagodon rhomboides*; Cms – Smaller conspecific male; Fgg – *Fundulus grandis grandis*; Cf – Conspecific female; O – Other species; Cs – *Callinectes sapidus*; Tot – All intruders.

Interactions with blue crabs

Agonistic interactions with males and blue crabs were the most prevalent and the longest in duration. For females they were the second most prevalent and second longest in duration. They occurred in 26 and 5 focal samples on males (n = 52) and females (n = 45), respectively.

One-way analysis of variance on ranked data revealed statistically significant differences in the amount of time males dedicated among the intruder groups tested ($F_{6,364} = 2.56$, $p = 0.0193$). Duncan multiple range test (post hoc) analysis (Zar 1996) revealed that time males spent defending burrows from crabs was significantly different ($\alpha = 0.05$) from time spent defending against other intruders. No statistically significant differences were found between females and interactions with different groups of intruders.

A combination of focal samples and scan sampling yielded 91 instances of clown goby-blue crab interactions throughout the study: 72 with males and 19 with females. In this study, crabs were observed making contact with, and altering the structure of, 20 burrows. Nine of these were completely destroyed. Spawning was in progress in six of these burrows and hatching was in progress in one.

Clown gobies responded to crabs in one of three ways: fin display, fin display with body darkening (dark fin display), and avoidance. Responses observed were as follows: in 47 instances (65%) males performed dark fin display, in 14 (19%) males performed fin display but darkening was not noted, in 11 instances (15%) males avoided crabs. In 19 instances (100%), females avoided crabs by swimming away. One of the females hid in the burrow while her mate performed dark fin display. Crabs responded to male displays by avoiding the territory, or if already there, by eventually leaving. Occasionally crabs backed away with outstretched claws – a behavior they often exhibited toward each other. Juvenile (smaller) crabs avoided adult (larger) crabs altogether.

The crabs that were the most likely to pose a threat to burrows and embryos were those ranging from 2.5 to 6.0 cm (carapace width). These individuals were brown in carapace color. Larger crabs (>7.0 cm) had bluish carapaces with red claws and orange tips at swimerette joints (Figure 4). The smaller crabs were frequently seen eating razor clams, which they found by probing several centimeters below the substratum. They often foraged into goby burrows as they explored the substratum. Crabs excavated nests by wedging the side of their carapace into the sand and dragging sand away with their claws. I observed one crab doing this for 15 min. The male goby of this spawning-in-progress maintained dark fin display and bit the crab twice. Crabs also probed into the burrows with their back legs and one crab consumed eggs that it scooped from the entrance of the nest. Crabs that were larger than 7.0 cm carapace width were usually only traversing goby territories and did not stop to forage.

Interactions with other predators

I noted interactions between gobies and several other species. Agonistic interactions with pinfish (fast moving, opportunistic feeders) were relatively frequent for both males and females; yet, mean durations occupied only a small proportion of focal samples. They occurred in eight and seven focal samples on males ($n = 52$) and females ($n = 45$), respectively. During an attack by pinfish (>8 cm), gobies took shelter in the closest burrow. Males performed fin display to smaller pinfish (<6 cm) but did not exhibit a color change.

The Gulf killifish initiated infrequent but sustained interactions. Rainwater killifish, though abundant, were rarely seen to interact with gobies, except during the observation on young release. During young release, 11 *L. parva* were counted within 15 cm of the nest entrance, which they repeatedly tried to enter.

Other species, including mosquitofish, *Gambusia affinis*, southern flounder, *Paralichthys lethostigma*, sheepshead minnow, sailfin molly, *Poecilia latipinna*, and red drum, *Sciaenops ocellata*, occasionally elicited weak lunges or fin displays from gobies. One southern flounder was seen trying to engulf a goby.

Two other gobiids were observed within the pond: the darter goby, *Gobionellus boleosoma*, and the much larger (≈15 cm), frillfin goby, *Bathygobius soporator*. Frillfin gobies were only seen seven times throughout the study and were not observed to interact with clown gobies. Darter gobies were relatively abundant during 1997, and engaged clown gobies in interesting displays, where the male of each species used his own ritualized display against the opponent. Male clown gobies performed fin display and parallel swim to the darter goby, while the darter goby maintained a fin display and darted, incrementally, forward, in a parallel orientation, alongside the opponent.

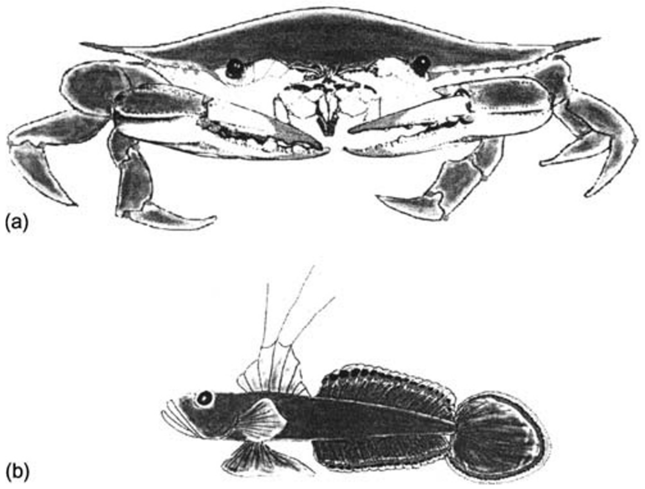

Figure 4. (a) Adult blue crab coloration, and (b) male clown goby display to blue crab.

Feeding and non-breeding season activities

Feeding activities

Gobies were occasionally seen to pick at the substratum, or consume particles out of the water column. Feeding behavior was observed in 12 of 52 samples for males and 9 of 45 samples for females. Females fed a mean of 0.67 times 30 min^{-1} ± 2.31 and males fed a mean of 0.33 times 30 min^{-1} ± 0.70. Feeding events never exceeded three per sample with the exception of two females (sample nos. 22 and 55), who fed 10 and 12 times, respectively, the first exclusively by consuming particles out of the water column, and the second, by picking at the substratum.

Non-breeding season activities

By early October, most gobies occurred as singly at burrows, exhibited cryptic non-breeding colors. By early November, few fish were visible on the substratum but many were discovered occurring singly in burrows. At the end of December no gobies were observed on the substratum, but adults continued to occupy burrows (n = 5). They continued to occupy burrows throughout the winter. Gobies emerged from burrows near the end of February 1998 (16°C), and were abundant by March 1st (18°C). Scan sampling conducted on March 5th (17°C), revealed many paired and unpaired individuals with breeding colors and females with distended abdomens.

Discussion

The *M. gulosus* in this study exhibited maternal care of young and appeared to mate polygamously. The guarding of young is considered a divisible resource, meaning that a unit of parental energy may be given to one offspring or to many. Thus, a fish may be able to guard large clutches (composed of eggs from multiple females) as easily as small ones (Williams 1975). In polygamous gobiid mating systems, males usually guard the developing young of several females in *one* nest (Hesthagen 1977, Kvarnemo et al. 1998). Clown goby males simultaneously courted multiple females, at different nests, and females brooded eggs, suggesting that in this species, males may achieve polygamy by fertilizing the eggs of multiple females, each at a separate nest.

Burrows observed in this study were a limited and defensible resource. Suitable burrow support was restricted to availability of cattails. In addition, not all cattails were acceptable for burrow construction. Acceptable plants had to have root systems that were at an appropriate depth in the substratum to provide a ceiling for the burrow and a substratum for egg deposition. Therefore, suitable cattails and consequently the burrows constructed beneath them were a limited resource.

Given that the first two conditions of William's Principle are met (external fertilization and a limited defensible resource), female care may be selected in this mating system because the third condition, the ability of males to achieve polygamy by guarding multiple clutches in a single burrow, is constrained. I hypothesize that female care is selected for by significant predation pressure from egg predator, *Callinectes sapidus*, requiring males to guard burrows.

Young that require continual maintenance through fanning and cleaning may prohibit the parent engaged in these duties from being able to effectively guard the nest from predators. This could lead to the requirement for a second parent to brood eggs, in this case the female, while males undertake predator defense. In at least 50% of clown goby spawns, males continued to guard burrows throughout the brooding interval, suggesting that the actual mode of parental care is biparental. Although such a mating system has not previously been described for gobies, a similar pattern exists in *Lamprologus ocellatus*, a shell-dwelling cichlid. This species relies on snail shells for nesting space and shelter and both juveniles and adults are subject to intense predation (Walter & Trillmich 1994). Males monopolize the shells and females compete for access to them, becoming part of a harem. The combination of limited nesting space and significant predation may also be operative in promoting harems in the clown goby mating system.

In response to juvenile blue crabs, clown goby males exhibited a darkening of their body color, which combined with their blue and red fin borders, mimicked the coloration of adult blue crabs (Figure 4). Cannibalism among crabs is well-documented (Hines & Ruiz 1995, Ryer et al. 1997) and juvenile blue crabs avoided adult crabs. This leads to the hypothesis that clown goby males are mimicking adult blue crabs in order to encourage juvenile crabs to avoid the territory.

Typically, mimicry systems involve three components: (a) the model, which is the class being imitated; (b) the mimic, the species that looks and acts like another species or object by resembling the model; and (c) the dupe, which is the deceived predator or prey (Barrows 1995). In this case the male clown goby (the mimic), mimics the adult blue crab (the model), in order to deter the juvenile blue crab (the dupe).

Males covered burrows immediately after spawning, possibly acting to deflect the attention of predators away from young-containing nests. When crabs found an open burrow that contained young (while spawning was in progress), they spent more time investigating it than an empty burrow. This may have been due to chemical cues (Finelli et al. 2000) which indicated that young were present. Therefore, olfactory cues may lead crabs to egg containing nests, and covering of the burrow may aid in reducing such cues. Visually masking the presence of nests may also reduce their conspicuousness to predators, as well as to other clown gobies, thereby reducing the energy expenditure required to defend them.

Parental care incurs a cost for the care-providing parent, and the sex more likely to evolve care is the one with the lower relative costs to future fertility, because it will receive the higher relative benefits from care (Sargent & Gross 1993). Clown goby males would potentially miss additional spawning by providing care to young because the male interspawn interval is potentially zero. For females, the brooding period is only a relatively short segment, approximately 12%, of the mean interspawn interval. This cost may also be offset by the benefit females gain from the guarding (predator defense) behavior of males. Since males provided antipredator protection to young, females, by undertaking the task of parental care, were receiving protection and shelter by default. By remaining with the young after spawning, they were, in effect, extending the duration of those benefits.

The benefit females gained, as a result of males' guarding activities may account for their interest in gaining access to male protected territories beyond reproduction, and the willingness of females to contribute to nest construction and maintenance. Among pairs, females engaged in burrow maintenance more than twice as long as males. Burrow maintenance by females may, in turn, liberate additional time for males to guard the territory.

In intraspecific interaction, female clown gobies exhibited intense intrasexual aggression. Swenson (1997) also found aggressive females in tidewater gobies, a species where males construct energetically expensive nests. Tidewater goby females however, exhibited strong mate guarding, as well as mate choice, as evidenced by aggression toward non-resident males. This is expected, because tidewater goby males provide care of young. By contrast clown goby females readily courted with, and accepted, any male that approached the burrow. This suggests that in clown gobies, female aggression is intended to secure access to burrows, not particular mates.

Males, by contrast, were always selective regarding which females were allowed on the territory and assisted their mates in excluding nonresident females. Males chased females even more frequently than females chased one another. Therefore, males ultimately determined which female resided at their burrow, suggesting that males not only exhibit habitat selection, but also strong mate selection.

Females initiated pair-bond reinforcement signaling more often than males did, suggesting that in order for females to retain access to the territory they had to perpetually affirm their status as mates. Reavis (1997) reported that females of *Valenciennea strigata*, a monogamous species, formed a crescent of dark pigments on their abdomen, which resembled a gravid condition, which functioned to enhance continuation of pair bonds. The abdominal display by clown goby females may also function to enhance pair bonds and, more specifically, to allow females extended access to burrows prior to spawning by exaggerating their ripeness and thereby their readiness to spawn.

Examples of plasticity in parental care are found within many species of fish (Neff & Gross 2001). Plasticity is likely to be present in the clown goby mating system as well. I only observed males to guard nests in 50% of cases, and I observed one case where the female covered the burrow without the help of a male. This suggests that females have the ability to continue brood care without males. Thus, it is possible that nest guarding by male clown gobies is facultative and, thus, a plastic behavior.

In conclusion, I found that clown gobies exhibit a unique and possibly versatile mating system, worthy of further study. The occurrence of such an 'exception to the rule' (Williams 1975) provides and an opportunity to test theories on parental care (Sargent & Gross 1993), sex role reversal (Vincent 1992), and how mating systems are shaped by predators and other environmental constraints. Future study of the clown goby should help broaden our understanding of these concepts and of the evolution of mating systems in general.

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