Evolution of Female Egg Care in Haremic Triggerfish Minecanthus aculeatus

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Abstract

Paternal care is predominant among teleost fishes with external fertilization. This study describes maternal care in a haremic coral-reef fish and discusses the possible factors leading to its evolution. Both sexes of the triggerfish *Rhinecanthus aculeatus* (Balistidae) maintained territories; some individuals for more than 8 years. Each male's territory overlapped 2–3 female territories. Pair-spawning occurred around sunrise. Only females cared for the demersal eggs until hatching, which occurred just after sunset on the day of the spawning. No predation was observed on eggs under the maternal care, but experimental removal of parental females decreased the hatching rate to nearly zero. Egg-guarding females foraged as frequently as males, but less than half of non-spawning days. Spawning occurred only in the periods of about 1 wk around the new or full moon, and individual females spawned up to three times in each period. Thus, the maternal care did not significantly affect the duration of the females' spawning intervals, while males would suffer mate loss if they performed parental care. In this situation, maternal care should be the evolutionarily stable strategy. Evolutionary transition from no care to maternal care and then to biparental care is suggested in the Balistidae.

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Introduction

Maternal care of offspring is predominant among mammals, biparental care in birds, while paternal care is predominant among teleost fishes (BLUMER 1982; CLUTTON-BROCK 1991). The predominance of paternal care in teleosts has been explained from various viewpoints, e.g. external fertilization, certainty of paternity, rate of gamete production, male territoriality, guarding of multiple clutches, and indeterminate growth (TRIVERS 1972; BAYLIS 1981; GROSS & SHINE 1981; GROSS & SARGENT 1985; KUWAMURA 1987; SARGENT & GROSS 1993). Although uncommon, maternal care occurs in some teleosts with external fertilization. GROSS & SARGENT (1985) proposed the evolutionary transitions (cyclical dynamics) of parental care in fishes: from no care to male alone care, then to biparental care, and subsequently to female alone care, and then to no care again. The evolution of maternal care from biparental care has been documented in the Cichlidae (KEENLEYSIDE 1991; KUWAMURA 1997).

Conversely, a transition in the reverse direction, i.e. from no care to female care, has

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been suggested in the Salmonidae (GROSS & SARGENT 1985). Female salmonids establish territories within which they bury eggs, and this may have given rise to female nest guarding, which lasts until death, in *Oncorhynchus*. This seems a peculiar case in a semelparous fish, but other conditions for the evolution of maternal care from no care have also been suggested. A female-biased sex ratio may favor the evolution of maternal care, as predicted by a game theory model (YAMAMURA & TSUJI 1993). In particular, haremic mating systems associated with female territoriality will favor the evolution of maternal care from no care, even in non-semelparous fishes, because of the high cost (i.e. mate loss) of parental care in males (KUWAMURA 1987).

Maternal care is very rare among coral reef fishes with external fertilization (BARLOW 1981; THRESHER 1984), but is known in several species of haremic triggerfish (Balistidae: FRICKE 1980; THRESHER 1984; ISHIHARA & KUWAMURA 1996). Females guard and care for the demersal eggs until hatching, which usually occurs the first night after being laid in the early morning. This short duration of parental care is suggested to be related to the evolution of maternal care (FRICKE 1980; THRESHER 1984). This paper discusses the evolutionary factors of maternal care in the haremic triggerfish.

The subject species, *Rhinecanthus aculeatus*, is the most common triggerfish of subtidal reef flats and shallow lagoons along the Indo-Pacific coasts (MYERS 1989). Males and females of this species establish territories within which they forage for small benthic invertebrates such as crustaceans and sea-urchins (KUWAMURA 1991). Each male territory overlaps one to five female territories, suggesting an haremic mating system, but mating behavior has not been reported. Here, I describe stability of territories, spawning and parental behaviors, and sexual difference in feeding frequencies. I also discuss possible factors leading to the evolution of maternal care in this species, and propose a hypothesis for the evolutionary transitions of parental-care patterns in the Balistidae.

Methods

Underwater observations were conducted using snorkel and scuba on the fringing reef of Sesoko Island (26°38′N, 127°52′E), Okinawa, southern Japan. A study area of 60 × 70 m was mapped on a reef flat with a depth of about 2 m at mean sea level (for the map around the study area, see KUWAMURA 1991). In Jul. 1984, 29 territorial adults were identified based on individual variations in the pattern of short black lines on the caudal peduncle (for coloration, see MYERS 1989). Their total length (TL) was estimated to the nearest 1–2 cm underwater, and their sex determined (nine males and 20 females) based on reproductive behavior.

The whole study area was surveyed every day from 16 Jul. to 3 Aug., 1984, recording the positions of the identified fish and their egg masses. I conducted 10-min observations two to five times for each individual, and recorded the swimming routes, feeding sites and frequencies, and interactions with other fishes. Although territorial attacks did not occur frequently (once in 1–2 h; KUWAMURA 1991), the outermost range of the swimming routes, which was exclusive to each fish, was regarded as an individual's territory. For feeding frequencies I counted the number of picks at the bottom and the sea-urchin, excluding the number of picks to break the sea-urchin's test. The average feeding frequency in 10 min for each fish was used for the analyses.

The census of the identified fish and their egg masses for 1–4 wk was repeated in Sep. and Oct. 1984, Mar., Jul. and Aug. 1985, May and Nov. 1986, Jan. and Aug. 1987, Jul. and Aug. 1988, Aug. 1990, and Aug. and Sep. 1992. When I found unknown individuals establishing territories in the study area, I recorded their patterns of black lines on the caudal peduncle. I calculated survival rates of the identified fish and also the spawning frequencies of each individual. To confirm the stability of the territory arrangement, 10-min observations of swimming routes and feeding sites were conducted at least once for each fish in each period. A map of the territories in Jul.–Aug. 1988 has been given elsewhere (KUWAMURA 1991). One female (171 mm TL) in Aug.

1984 and one male (215 mm) in Aug. 1985 were removed, by angling with hook and bait underwater, and change of the territory owners recorded thereafter.

Because new egg masses were found in the early morning, I attempted to observe courtship and spawning behavior of a focal fish continuously for about 1 h around sunrise, four times in Jul. and Sep. 1984, 10 times in Jul. and Aug. 1985, and four times in Aug. 1988. The behavior of parental fish (female) was observed for 10 min, and the duration of fanning (aeration), number of attacks and identity of the attacked species, feeding sites and frequencies, and the presence (visiting) of the partner male and his behavior recorded. A 10-min observation was carried out two to six times for each female, except for five females that were very cautious in the presence of the observer (i.e. aggressive or fleeing) when eggs were present; the average values in 10 min for each individual were used for the analyses. Because the egg masses had always disappeared by the next morning after being laid, the behavior of the parental fish was observed continuously for about 1 h around sunset, five times in Jul. and Sep. 1984, three times in Jul. 1985, and three times in Aug. 1988. Hatching was confirmed by occasional use of a light during the observation.

To examine the effect of parental care on survival and hatching of eggs, two parental females were removed from their nests in the morning, 3–4 h after spawning, in Aug. and Sep. 1992. Fishes visiting the nest and their behavior for 40 min after the removal were recorded. About 1 h before sunset of the removal day, I collected the nest substrate (sand, coral rubble and filamentous algae) from an area 15 cm in diameter on the bottom surface, using a scoop and a plastic bag. After that, the removed females were returned to their territories. Substrate was also collected from another nest that was normally guarded by the female parent, as a control. The collected materials were kept in a bowl with sea-water, and the numbers of hatched larvae and unhatched eggs were counted 3–4 h after sunset. The water and materials in the bowl were stirred and the water transferred into a bottle. One-tenth of the bottle water was then filtered through a plankton net and the numbers of eggs and larvae counted using a binocular microscope. The numbers in the bottle were estimated by multiplying the resulting figure by 10. This procedure was repeated two more times for each clutch, adding new water into the bowl, and finally counting the number of eggs still attached to the nest materials. The total number of eggs and larvae was estimated by combining the respective estimates. In addition, the length of 10 eggs and 10 newly hatched larvae collected from a clutch in the morning and evening, respectively, in Jul. 1984 was measured.

Results

Territories and Mortality

In Jul. 1984, nine males and 20 females were holding territories in the study area. Female territories were 10–15 m diameter and contiguous with each other. Each male territory overlapped two or three female territories (n = 7 and 2 males, respectively). Males (20–23 cm TL) were always larger than the females (17–20 cm) of their harems. None of these identified fish moved to other territories, and six of eight males (75%) and six of 19 females (32%), excluding the one male and one female removed (see below), remained in their territories for 8 yr until Sep. 1992. The survival rate of males was significantly higher than that of females (Fisher's exact probability test, $p = 0.049$).

When a male was removed from his territory, which was situated near the edge of the study area, a similar-sized, unknown male invaded the territory on the next day, and thereafter monopolized the harem of two females until 1992. When I removed a female from another harem of two females, a slightly smaller unknown female invaded within 7 wk, during which no observation was made, and remained there until 1992. When territorial males disappeared (n = 2), a new male took over the territory in one case, and a neighboring male just out of the study area expanded his territory in the other case. When females disappeared (n = 13), a new female took over the territory in 11 cases, and a neighboring female of the same harem expanded her territory in two cases.

Thus, the fish maintained territories for several years, and the territory arrangement was rather stable even if the owners changed. Moreover, the territories were maintained not only in the reproductive season (Jul. to Sep.; water temperature = 26–31°C), but also in the non-reproductive season (Oct. to May, 18–27°C).

Spawning Sites, Behavior and Cycles

Females spawned adhesive demersal eggs on the bottom within their territories. The egg mass was 5–15 cm in diameter. Eggs were usually attached to sand and coral rubble or filamentous algae (e.g. *Gelidiella* sp.) on the rock floor, but were sometimes (15% of 164 nests examined) attached to calcareous red algae such as *Galaxaura fasciculata* and *Dignea simplex*.

Spawning occurred in the early morning between 05.48 and 06.34 h, i.e. from 16 min before sunrise to 39 min after that (n = 11). Courtship and spawning behavior were as follows. The female began to clean the nest by picking sand or algae with her mouth from 26 to 43 min before spawning. The male began nuzzling the caudal peduncle of the female from 7 to 27 min before spawning. The male and female then settled on the nest, side by side with abdomens touching, and released gametes. During the courtship and spawning other males were never seen to approach the pair to sneak fertilizations. After spawning, the female remained at the nest to take care of the eggs, while the male left to visit another female or to forage.

Spawning occurred only during the periods of about 1 wk around the new moon or the full moon; i.e. from 1–2 d before to 4–6 d after (Table 1). Within each period, each female spawned 0–3 times (mean ± SD = 1.31 ± 0.35, n = 20 female territories, averaged for five spawning periods of different years; the data of different females were pooled for each territory, if the owner changed). When females spawned more than once during a

Table 1: Spawning cycle (daily number of spawning females) of *Rhinecanthus aculeatus* in relation to the moon age

	Moon age (days)														
Observation period	23 8							0 15							7 22
July–Aug. 1984	0	0	0	0	0	0	7	1	4	9	0	1	6	0	–
July 1985	–	–	–	–	0	3	5	0	3	6	8	0	2	–	–
Aug. 1985	–	–	–	–	–	–	–	–	–	–	–	2	2	0	0
(cont.)	0	0	0	0	*	*	*	*	0	0	6	9	0	*	*
(cont.)	*	*	0	0	0	2	3	5	4	–	–	–	–	–	–
Aug. 1987	–	–	–	–	–	–	3	0	2	7	0	1	0	–	–
July–Aug. 1988	–	–	0	–	0	–	–	5	7	1	5	1	0	0	0
(cont.)	0	0	*	0	0	2	4	2	0	0	1	0	5	0	0
Aug.–Sept. 1992	–	–	–	–	–	7	1	2	3	2	8	7	0	2	0
(cont.)	0	0	0	0	0	0	1	3	0	*	*	*	0	7	0

Moon age: 0, new moon; 15, full moon;
–, no survey;
* no survey due to heavy waves caused by typhoon.

period (37% of 92 periods of all females pooled), the intervals were 1–6 d (mode and median = 3 d, n = 38 intervals).

The spawning sites were not fixed but distributed over the female territory (Fig. 1a). In each male territory, two to three females of the harem spawned on the same day on 22.5% (± 15.2 SD) of the male's spawning day (10.9 ± 2.8 d SD, n = 9 male territories, total of five spawning periods). The total number of spawnings (in the five periods) of each male varied from 9 to 22 (13.4 ± 4.0 SD, n = 9); the two males that had a harem of three females showed higher values than the others (Mann–Whitney U-test, z = 2.06, p = 0.04).

Female Egg Care

The maternal care continued only for a short period, about 12–14 h. Hatching occurred just after the sunset of the spawning day, and females entered their shelter hole within their territory at 18.49–19.50 hours (i.e. 18–30 min after sunset, n = 11).

A parental female positioned herself just above the egg mass and, in a head-down position, fanned the eggs with her pectoral fins. Parental females allocated about 30% of their time to fanning (187 ± 110 s SD in 10 min, n = 15 females). Females often (11.7 ± 5.4 times SD in 10 min) interrupted fanning and left the nest to conduct attacks or feeding. Females attacked almost all fish approaching or passing the nest (0–8 times in 10 min), and no predation upon eggs occurred during the observations. The attacked fishes belonged to 45 species of 18 families, such as Labridae, Mullidae, Nemipteridae, Acanthuridae and Chaetodontidae, most of which were benthos feeders. When a starfish *Nardoa tuberculata*, a gastropod *Strombus luhuanus* or a shrimp *Alpheus* sp. entered the nest, the parental female removed them by mouth.

Parental females foraged only within a few meters around the nest, while they foraged over almost all their territories on non-spawning days (Fig. 1b, c). The feeding frequencies of females on spawning days (14.8 ± 5.3 times SD in 10 min, n = 15 females) were much lower than on non-spawning days (41.4 ± 9.6; Wilcoxon matched-pairs signed-ranks test, z = 3.35, p = 0.0008), but did not differ significantly from those of males (Mann–Whitney

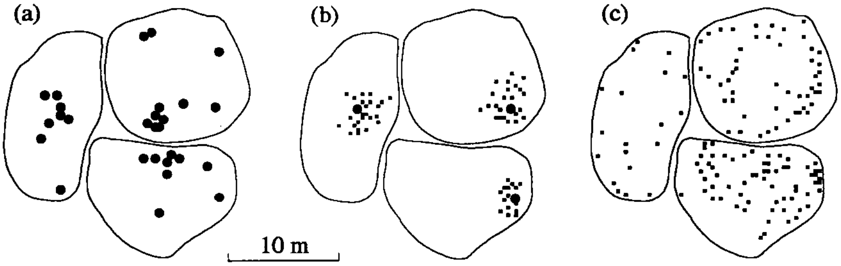

Fig. 1: Examples of spawning and feeding sites of female *Rhinecanthus aculeatus*. The three female territories illustrated were covered by one male's territory. a. Spawning sites of each female are given by solid circles (data for 5 yr). b. Feeding sites (dots) of each female during a 10-min observation on a spawning day; the spawning site is given by a solid circle. c. Feeding sites (dots) of each female during a 10-min observation on a non-spawning day

U-test, z = 1.79, p = 0.07; Fig. 2). The feeding frequencies of males did not differ between non-spawning days (18.4 ± 4.2, n = 9 males) and spawning days (18.3 ± 5.0; Wilcoxon matched-pairs signed-ranks test, z = 0.18, p = 0.86).

Males were never seen fanning eggs, nor attacking fishes around the nest. They visited parental females 0–3 times in 10 min (median = 1, n = 15 females), usually leaving them soon. In a few cases (five out of 49 10-min observations of parental females) males continuously stayed within a few meters from the nest and were aggressive to the observer, as were some egg-guarding females.

When sunset approached, females increased the duration of fanning and began circling on the nest with their abdomens touching the egg mass, sometimes blowing on the nest probably to accelerate hatching. Larvae of 1.32–1.44 mm TL (n = 10) hatched from eggs 0.45–0.52 mm in diameter (n = 10). The larvae then became planktonic.

Removal of Parental Females

The egg-guarding females were removed from two nests (A and B). The partner male never visited nest A during the 40-min observation after the removal of the female. In this case, one of the two other females of the harem also guarded eggs on that day. A school of parrotfish associated with goatfish passed by the nest 2 min after the removal, but they did not pick at the nest. No predation upon the eggs occurred until 17 min after the removal, when a surgeonfish picked at the nest.

In the case of nest B, the other female of the harem had not spawned on that day. A rabbitfish picked at the nest 4 min after the removal of the female, and thereafter various fish such as wrasses, goatfish and sandperch gathered to pick at the nest. The male partner visited the nest 7 min after the removal. He began to attack the fish around the nest but was unable to defend the eggs effectively. A neighboring female also visited the nest and attacked the fish, including the male. Both the male and the female began to pick at the

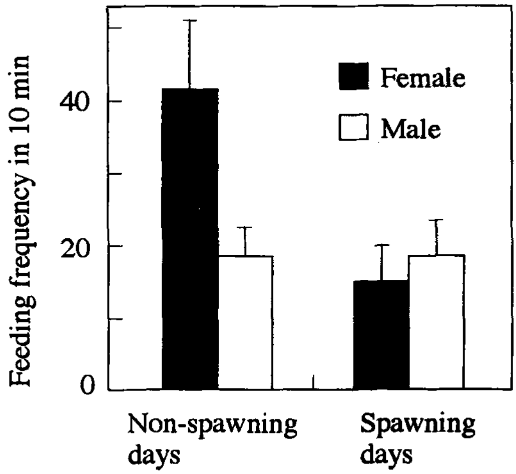

Fig. 2: Mean (± SD) feeding frequencies in 10 min for males and females on spawning and non-spawning days

nest (probably to eat the eggs) 26–27 min after the removal. They remained there, sometimes attacking other fishes, until the end of the observation (40 min after the removal).

The estimated numbers of larvae and unhatched eggs (counted 3–4 h after sunset) were 40 and 10, respectively, from nest A, and 930 and 830 from nest B. In contrast, from a control nest guarded by the female, about 55500 larvae hatched and no eggs remained unhatched. Thus, removal of parental females affected both the survival and development of the offspring, decreasing the hatching rate to 0.1–1.7% of the control. If we take account of the effect of maternal care before the removal (3–4 h after spawning), the expected survival (hatching) rate of eggs would be almost zero if they did not receive maternal care.

Discussion

The present study revealed that adult *R. aculeatus* maintained territories for more than 8 yr, reproducing repeatedly. Therefore, the evolutionary factors leading to maternal care in this species should be different from those of the semelparous salmon showing maternal care (GROSS & SARGENT 1985). The parent-removal experiment in triggerfish showed that parental care (fanning and guarding) is necessary for eggs to survive and hatch. However, one parent (female) appears to be enough for egg care, because no predation occurred of eggs under maternal care. Why should females, rather than males, take on this role? This may be determined by the difference in costs of parental care between the sexes, although it is often difficult to measure the costs precisely (CLUTTON-BROCK 1991).

In the haremic mating system of *R. aculeatus*, males that monopolized more females had greater reproductive success. Because the territories of the females in a harem did not overlap and females spawned only within their own territories, a male guarding the eggs of one female would be deprived of the other females in his harem by other males. Multiple (two to three) females of a harem spawned on the same day on about 23% of the male's spawning days, and an egg-guarding male would lose these additional matings. Moreover, egg-guarding males would also risk losing these mates thereafter, because a neighboring or unknown male soon took over the territory whose owner was removed or had disappeared. Thus, paternal care would considerably decrease the future reproductive success of the male.

Parental care may also cost females a delay in future egg production. The feeding frequencies of female *R. aculeatus* on spawning days were less than half of non-spawning days. This would make females suffer a delay in egg preparation for the next clutch, but of 1 d at most as maternal care is completed by the evening of the spawning day. However, this does not appear to affect significantly the duration of female spawning intervals. In fact, some females spawned two or three times with intervals of 1–6 d within a semi-lunar spawning period of about 1 wk, while others had no or only one spawning. This suggests that the spawning interval of each female may have been affected more by the amount of feeding during the semi-lunar non-spawning periods than by the maternal care itself.

Thus, the parental care in *R. aculeatus* appears to cost males much more than females. In this situation, maternal care should be the evolutionarily stable strategy, as a game theory model predicts (MAYNARD SMITH 1982).

Haremic mating systems with female territoriality and maternal egg care are also known in other balistids such as *Pseudobalistes fuscus* (FRICKE 1980), *Sufflamen verres* (THRE-

SHER 1984) and *S. chrysopterus* (ISHIHARA & KUWAMURA 1996). Males help females in egg guarding (but not fanning) in a few other balistids with different mating systems. In the planktivorous balistid *Odonus niger*, a male monopolizes a foraging group of more than 10 females, which spawn synchronously within a small area of about 5 m diameter (FRICKE 1980). In *Pseudobalistes flavimarginatus*, males migrate to a traditional mating ground to establish territories, where females visit to spawn (GLADSTONE 1994). In both species, females conduct fanning of their own eggs, and each male defends multiple clutches (and females) at the same time.

The possibility of guarding multiple clutches within a small territory has been suggested to be one of the main factors for the evolution of paternal care in teleosts (BAYLIS 1981; KUWAMURA 1987; YAMAMURA & TSUJI 1993). Why do females of *O. niger* and *P. flavimarginatus* not desert their eggs and mates? One parent alone may not be able to allocate enough time to fanning (aerating) each of the multiple clutches including tens of thousands of eggs in a mass. Females allocate most of their time to fanning a single clutch in *O. niger* and *P. fuscus* (FRICKE 1980), and about 30% of time in *S. chrysopterus* and *R. aculeatus* (ISHIHARA & KUWAMURA 1996; present study). Therefore, lone male care of multiple clutches would considerably decrease the survival and hatching rates of eggs. This will be confirmed by removal experiments of parental females in *O. niger* and *P. flavimarginatus*.

The different mating systems and patterns of parental care among these balistids appear to be related to the distribution of food and breeding sites, as predicted by the classical theory of animal mating systems (EMLEN & ORING 1977; REYNOLDS 1996). Both feeding sites and spawning sites are available within females' territories in the haremic species such as *R. aculeatus*. In contrast, breeding sites are limited or separated from feeding sites in *O. niger* and *P. flavimarginatus* (FRICKE 1980; GLADSTONE 1994). Thus, the parental sex (maternal or biparental) may change with the mating system according to the patterns of resource use, though it is not known which is the ancestral mating system. If fanning is necessary for the development and survival of the demersal eggs of the balistids, as discussed above, it is unlikely that paternal care of multiple clutches has evolved from no care. Instead, the evolutionary transitions in the Balistidae appear to have been from no care to maternal care and then to biparental care, although reverse transitions have been suggested to be common among teleost fishes (GROSS & SARGENT 1985).

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