Ann. Zool. Fennici 45: 55–65 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 28 February 2008

Partial filial cannibalism enhances initial body condition and size in paternal care fish with strong male–male competition

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Received 14 Aug. 2006, revised version received 12 Nov. 2007, accepted 19 Dec. 2007

Gomagano, D. & Kohda, M. 2008: Partial filial cannibalism enhances initial body condition and size in paternal care fish with strong male–male competition. — *Ann. Zool. Fennici* 45: 55–65.

Partial filial cannibalism by parental males in fish has been regarded as an adaptive behaviour that compensates for the toll that parental care exacts on their body condition, which is supported by empirical evidence. Here we report that parental males of a nest breeding fish enhance their initial body condition and sustain growth through partial filial cannibalism. Males of the long-snout clingfish (*Diademichthys lineatus*) use scarcely available empty shells as nests, which limit the number of breeding males. Males continuously breed up to 4 months, during which they hardly leave the nests. Soon after breeding starts, all care-giving males exclusively and frequently consume some of their own eggs. In contrast to previous reports on fish cannibalism, almost all care-giving males grew and enhanced their initial body condition from the early days of care, where males with larger and better-conditioned bodies cannibalised more eggs. Male–male fights for nests were frequently observed: males with larger and more robust bodies won and sometimes took over breeding nests, and it is likely that defeated males could not breed unless they occupy a nest again. These observations indicate that in this fish, partial filial cannibalism produces cannibals of large and robust bodies, and may be advantageous to care-giving males in defending nests against rival males. We suggest that the ability to defend a nest will ensure a longer care-period, and thus, a higher reproductive output. This is the first documented evidence that filial cannibalism enhances the initial body condition of cannibals.

Introduction

Filial cannibalism, the consumption of one's own offspring, by males is not rare in paternal care fishes (reviewed in Dominey & Blumer 1984, Manica 2002). Cannibals consume either all or a part of their broods, i.e., whole or partial filial cannibalism. In either case, filial cannibalism entails losses in current reproduction, but is considered to be an adaptive behaviour that may provide benefits in current or future reproduction, thus outweighing its costs (e.g., Rohwer 1978, Dominey & Blumer 1984, Sargent 1992, Hoelzer 1995, Manica 2002).

During paternal care, males usually suffer from a decrease in foraging opportunities (Mag-

This article has been scientifically edited by Johan Kotze

nhagen 1986, DeMartini 1987, Petersen 1990) and an increase in energy demands (Lindström & Hellström 1993), during which their body condition often deteriorates (e.g., Marconato *et al*. 1993, Kraak 1996, Skolbekken & Utne-Palm 2001). Lower body condition may reduce the survival of care-giving males through increased susceptibility to disease, starvation, or both (Marconato & Bisazza 1988, Chellappa *et al*. 1989, Okuda & Yanagisawa 1996). Therefore, filial cannibalism, especially partial filial cannibalism, is generally seen as benefiting care-giving males by enhancing their survival and enabling them to complete current parental care and/or future reproduction (e.g., Rohwer 1978, FitzGerald 1992, Sargent 1992, Marconato *et al*. 1993, Kraak 1996, Manica 2002). This energy-based hypothesis is supported by many studies demonstrating frequent cannibalism by males in poor physical or nutritional condition (partial filial cannibalism: e.g., Marconato *et al*. 1993, Kvarnemo *et al*. 1998, Neff 2003, Takahashi & Kohda 2004, Okuda *et al*. 2004, whole filial cannibalism: e.g., Okuda & Yanagisawa 1996), but is not always observed (e.g., Belles-Isles & FitzGerald 1991, Lindström & Sargent 1997, Klug & Mary 2005).

Energy-based hypotheses (Rohwer 1978, Sargent 1992) predict that partial filial cannibalism may moderate the deterioration of body condition. However, only a few studies have examined the energetic effect of partial filial cannibalism on body condition. Limited numbers of laboratory studies indicate that filial cannibalism moderates the decline in body condition when males have no opportunity to forage for other food (Lindström & Sargent 1997, Lindström 1998). Because parental males usually have restricted foraging opportunities in natural conditions, partial filial cannibalism is expected to have only a small energetic effect that will not halt the decrease in body condition (Smith 1992). In fact, many empirical studies indicate that the body condition of males usually begins to decline after paternal care starts, even when partial filial cannibalism occurs (e.g., Chellappa *et al*. 1989, Marconato *et al*. 1993, Kraak 1996, Gonçalves & Almada 1997).

A few authors have suggested that the potential future benefits of partial filial cannibalism include sexual selection and survival (Hoelzer 1995, Lindström 1998). Empirical studies, however, have failed to document examples other than that of compensation of deteriorated body conditions of cannibals, i.e. examples of investment beyond survivorship. Sexual selection theory predicts that when resources, e.g., nest sites, are essential to male reproduction but are scarce, resource monopolization by males should be crucial for their reproductive success (Andersson 1994). Thus, in species with strong male–male competition, sexual selection favours males with large and robust bodies and/or effective weapons that will be advantageous in combats (e.g., Dugatkin & FitzGerald 1997). If filial cannibalism can induce enlarged and robust bodies of individuals, and these traits are crucially important for male fighting and for occupying resources for breeding, filial cannibalism can be advantageous for males of species with severe male–male competition (e.g., Hoelzer 1995, Lindström 1998, Manica 2002).

We studied the long-snout clingfish (*Diademichthys lineatus*), a nest brooder with exclusive paternal care. Males use enclosed nests, e.g. empty bivalve shells, which are scarce, and they may be faced with severe male–male competition for nests (Sakashita 1992). Thus, large body size and robustness of males are predicted to be critical for obtaining resources. Our preliminary observations suggest that shell nests used by a care-giving male were often targeted and were occasionally taken over by non-nesting males, and that some care-giving males did not show a decline in body conditions in spite of no foraging outside the nest during long care-giving periods. These observations lead us to propose a hypothesis that care-giving males of this clingfish cannibalise their own eggs that induce their growth and/or enhance their initial body condition, which is advantageous in severe male–male fights. Thus, this fish provides an excellent opportunity to study filial cannibalism in terms of sexual selection. Here we examine the following predictions: (1) care-giving males of *D. lineatus* will frequently eat only their own vital eggs during care; (2) these cannibalistic males will grow and enhance their initial somatic condition; (3) males cannot sustain their body condition if they experience starvation (or if they do not cannibalise eggs), and (4) small and/or low conditioned males (i.e. disadvantageous in male fight) will grow and enhance their condition faster than large and good condition males to reduce the risk of nest takeover. Finally, (5) large size and/or robustness will be essential for male–male fights, and small and low conditioned nesting males are prone to nest takeovers. We will discuss the evolution of filial cannibalism by caring males of this fish in terms of sexual selection.

Material and methods

Study subject

The long-snout clingfish is a small fish that inhabits shallow waters in reefs of the Indo–West Pacific (Masuda *et al*. 1988). The fish exhibits sexual dimorphism in size and snout shape (Briggs 1955, Sakashita 1992). Adult males are 50–70 mm in total length (TL) and have thick snouts, whereas adult females are 45–60 mm in TL and have slender snouts. Anatomical examination revealed that variation in male snout width reflects the volume of muscle attaching to the mandible (D. Gomagano pers. obs.). Non-care-giving adult fish spend a large amount of time foraging, and feed primarily on shrimp eggs, sea urchin (*Diadema* spp.) tube feet, and bivalve mantles (Sakashita 1992, D. Gomagano pers. obs.). We made preliminary field observations as follows. In the breeding season (May–October), males use empty bivalve shells exclusively as a spawning substrate, which are apparently limited in number in comparison with fish numbers as in other populations of the same species (Sakashita 1992). One female repeatedly lays a clutch of 200–250 eggs in a single layer inside nests at intervals of several days. Males continuously fan the eggs, which hatch in 10–15 days. Care-giving males usually receive additional daily spawn, and paternal care of multiple clutches by a single male continues for more than one, and up to six months without intermission. Aggression between nesting males and non-nesting males is frequently observed, and non-nesting males attempt to take over the brooding nests at times. Care is occasionally terminated due to the takeover of nests by conspecific males or due to egg predation by aggregations of carnivorous snails (*Ergalatax* spp.: D. Gomagano pers. obs.).

Data collection

We observed and sampled care-giving males offshore at Hunakoshi in the Uwa Sea, Shikoku Island, Japan (33°03´N, 132°26´E), during May–August 1999 by SCUBA diving. During the study period the water temperature ranged from 20.0–25.5 °C. The study area consisted of a rocky substrate at 7–10 m water depth, where empty bivalve shells for nests were scarce. We made artificial nests using empty shells of *Chlamys nobilis* (Pectinidae), approximately 9 cm in diameter. Two shell halves were closed with a rubber band, leaving interstices of several millimetres between the shell edges. A small oval entrance hole was made, through which we could observe care-giving males. In late May, we set 20 nests at various points on the rocky substrate, with the shortest distance between nests more than 10 m. Males soon began to nest in the shells. No fish other than *D. lineatus* used the nests.

To examine the stomach contents and changes in the physical condition and size of care-giving males during the brooding period, we captured males at the end of three breeding periods (≤ 4, ca. 20 and ca. 40 days of care). When clutches were not discovered at the onset of breeding, the first day of breeding was easily approximated by the coloration of egg clutches associated with development. When fish were captured, we photographed the eggs in the nests using an underwater camera (Nikonos-V, Nikon). A total of 16 males were sampled for the within-four-day breeding period study. Their TL (± 0.1 mm) and snout widths (± 0.05 mm) were measured underwater with callipers.

To obtain samples for periods of longer care, additional males were captured within four days of the start of breeding. Males were measured in the manner described above before individually marking them with injections of elastomeric coloured paint (Northwest Marine Technology) under the skin. The males were immediately returned to their nests and began fanning the eggs as they did before capture. Thereafter, we observed whether the marked males were caring for the egg clutches in the nest at four to eight days intervals. Of the marked males, 25 continued parental care in the same nests 20 days after marking, and all were again measured underwater. Fourteen of the 25 males were sampled randomly, and the 11 remaining males were returned to their nests. All of these 11 males continued to breed for another 20 days and were sampled 40 days after marking. Thus, of the total of 41 studied males, 16 were measured once (≤ 4 days), 14 were measured twice (≤ 4 and 20 days), and 11 were measured three times (≤ 4, 20, and 40 days), although measurements at ≤ 4 days were missed in two males sampled at 20 days and in three males sampled at 40 days. The 16 shell-nests of which males were sampled at ≤ 4 days were reset at the same sites after cleaning inside the nests. Observational periods of subject males of each breeding period of ≤ 4, 20 and 40 days overlapped considerably.

Neither TL nor the relative snout width (RSW = snout width/TL × 10^2) of males at the start of brooding was different among males caring for ≤ 4 days (TL, mean ± SD = 60.6 ± 3.9 mm, RSW = 9.9 ± 0.6, $n = 16$), 20 days (TL = 61.8 ± 3.4 mm, $n = 12$, RSW = 10.2 ± 0.4, $n = 10$) and 40 days (TL = 62.0 ± 3.0 mm, RSW = 10.3 ± 0.7, $n = 8$, ANOVA: TL, $F_{2,33} = 0.48$, $p = 0.5$; RSW, $F_{2,31} = 2.11$, $p = 0.14$).

All sampled males were weighed (± 0.01 g) on land soon after capture, and were preserved in a 10% formalin solution. To examine the physical condition of males, condition factor K was calculated (K = wet body mass/TL^3 × 10^6). The liver and gonads were weighed (± 0.01 g), and the liver index (LI = liver mass/TL^3 × 10^6) and gonad index (GI = gonad mass/TL^3 × 10^6) were calculated. RSW was strongly correlated with K ($r = 0.69$, $p < 0.0001$, $n = 41$). Thus, we used RSW as an indicator of change in body condition for males that were repeatedly measured. No intestinal fat was found in the abdominal cavity of any males. We examined the stomach contents of the samples under a binocular microscope and counted the number of *D. lineatus* eggs, which have a specific adhesive pedestal and are easily distinguished from the eggs of other fish. Most of the undigested eggs seemed to have been alive when they were cannibalised.

Non-nesting males often visited nests with males and sometimes tried to enter the nests, but were prevented by nesting males in most cases. When we observed the nests 4 days after sampling the owner males, new males had often occupied the re-set nests. To evaluate the effects of body size and physical condition on nest occupancy in clingfish males, we compared the TL and RSW of consecutive owners of the same nests in cases where we had removed the previous owners. Furthermore, if nest takeover occurs, newly occupying males are expected to be stronger. We observed only two incidents of nest takeover during the study period. To evaluate the effects of body size and condition, we also used fish data from nest takeovers observed in the breeding season in 1999 at another study area near the present study area where we observed fish behaviour on a daily basis. In the present study area, replacement of nest holders occasionally occurred, but we could not discriminate nest takeover from nest replacement after the disappearance of previous nest holders because of infrequent sampling (i.e. every 4 to 8 days). Breeding conditions were likely not to be different between the two study areas: e.g., similar sized fish used the same artificial nests at which similar sized clutches were deposited (D. Gomagano unpubl. data). In the present study, we occasionally observed aggressive interactions between nest owners inside the nests and visiting males that tried to enter the nests.

To examine the effects of starvation on the body size and body condition of males, we conducted a starvation experiment. Sixteen males collected near the study area were maintained in newly constructed bivalve nests without eggs. The nests were set in aerated aquaria (30 × 18 × 25 cm), with a water temperature of 26–28 °C. A mesh net covering the entrance of the nest prevented the male from leaving the shell. We measured TL (± 0.1 mm), snout width (± 0.05 mm), and body mass (± 0.01 g) of the males at the beginning of the experiment and after 10 days, when all the fish were still active. K and RSW were also calculated.

Statistical analyses

Parametric tests were used except when departures from normality or lack of homogeneity of variances required non-parametric tests. To examine the relationship between the number of eggs cannibalised and the male's physical characteristics or the number of eggs in the nest, we first used Pearson's correlation coefficient. Because some correlations were significant, we then used a partial correlation coefficient to control for some variables while examining the relationship between another variable and the number of eggs cannibalised.

Results

Body condition and growth

When breeding nests were observed, males were always inside the nests and vigorously fanning the eggs. The number of eggs in the nests increased significantly with time of care (≤ 4 days: mean ± SD = 1043.5 ± 874.6, $n = 16$; 20 days: 3729.5 ± 1191.5, $n = 14$; 40 days: 4772.0 ± 1138.2, $n = 11$; ANOVA: $F_{2,38} = 45.71$, $p < 0.0001$; *post hoc* sequential Bonferroni test: all pair-wise comparisons were significant). Males sampled at 20 and 40 days of care showed significantly higher TL, RSW, K and GI than did males sampled at ≤ 4 days, but the LI was not significantly different among the three care periods (ANOVA with *post hoc* sequential Bonferroni test: TL, $F_{2,38} = 5.85$, $p = 0.006$; RSW, $F_{2,38} = 23.10$, $p < 0.0001$; K, $F_{2,38} = 7.79$, $p = 0.002$; GI, $F_{2,38} = 17.46$, $p < 0.0001$; LI, $F_{2,38} = 0.29$, $p = 0.75$, Fig. 1). No significant differences were found in these physical characteristics between males sampled at 20 and at 40 days of care.

In males examined for changes in body size and RSW, TL significantly increased as the days of care increased (≤ 4 *vs*. 20 days, paired t-test: $t_{19} = 6.04$, $p < 0.0001$; 20 *vs*. 40 days, paired t-test: $t_7 = 2.91$, $p = 0.023$, Fig. 2a). RSW increased significantly during the first 20 care days (Wilcoxon signed rank test: $T = 0$, $n = 18$, $p = 0.003$), but not during the next 20 days (20 *vs*. 40 days, paired t-test: $t_7 = 0.95$, $p = 0.37$, Fig. 2b). Smaller males grew faster than larger ones during the first 20 care days (regression analysis; $r^2 = 0.38$, $n = 20$, $p = 0.002$, Fig. 3a), but did not maintain the lead in the next 20 days ($r^2 = 0.11$, $n = 8$, $p = 0.413$). Similarly, the snout width of males with smaller RSW increased more than that of males with larger RSW during the first 20 care days ($r^2 = 0.60$, $n = 18$, $p < 0.0001$, Fig. 3b), but not during the next 20 days ($r^2 = 0.46$, $n = 8$, $p = 0.064$).

Fish TL tended to decrease over the 10 day starvation period, although this was statistically insignificant (before and after the experiment, 58.2 ± 2.0 mm and 58.0 ± 2.2 mm, respectively; paired t-test: $t_{15} = 2.04$, $p = 0.060$). Body mass declined significantly (before, 1.16 ± 0.14 g; after, 1.02 ± 0.12 g; paired t-test: $t_{15} = 12.1$, $p < 0.0001$). Consequently, K and RSW decreased during the starvation period (K: before, 5.88 ± 0.30; after, 5.20 ± 0.22; paired t-test: $t_{15} = 17.80$, $p < 0.0001$; RSW: before, 9.98 ± 0.62; after, 9.31 ± 0.57; paired t-test: $t_{15} = 15.26$, $p < 0.0001$).

Filial cannibalism

Only clingfish eggs were found in the stomachs of parental males ($n = 41$). Only three males sampled at ≤ 4 care days had empty stomachs (7.3% of all care-giving males; Table 1). The frequency of cannibals did not vary significantly among males during the three care periods (Table 1). The number of eggs cannibalised by males sampled at ≤ 4 care days tended to be less than that by males sampled at 20 and 40 care days (Table 1). The proportion of eggs cannibalised to eggs in nest was not significantly different among males for the three care periods (Table 1).

Correlations between the amount of cannibalised eggs and K or RSW were positive in the three care durations, and were highly significant when data were pooled (Table 2). The number of cannibalised eggs was weakly positively correlated with the number of nest eggs and GI, but not with TL or LI (Table 2). K and RSW correlated positively with number of eggs in the nest (K: $r = 0.36$, $p = 0.02$; RSW: $r = 0.62$, $p < 0.0001$, $n = 41$) and with GI (K: $r = 0.41$, $p = 0.007$; RSW: $r = 0.58$, $p < 0.0001$, $n = 41$).

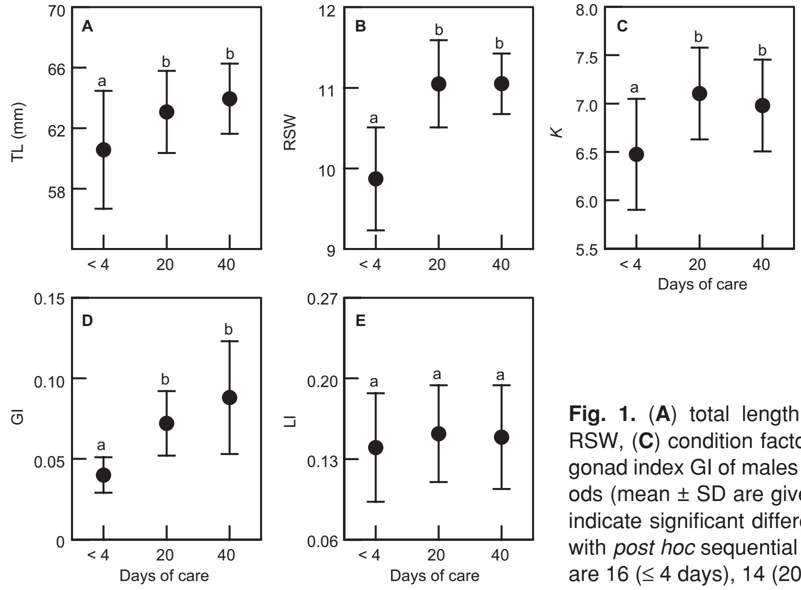

Fig. 1. (**A**) total length TL, (**B**) relative snout width RSW, (**C**) condition factor *K*, (**D**) liver index LI, and (**E**) gonad index GI of males of the three care-duration periods (mean ± SD are given). Different lowercase letters indicate significant differences among groups (ANOVA with *post hoc* sequential Bonferroni test). Sample sizes are 16 (≤ 4 days), 14 (20 days), and 11 (40 days).

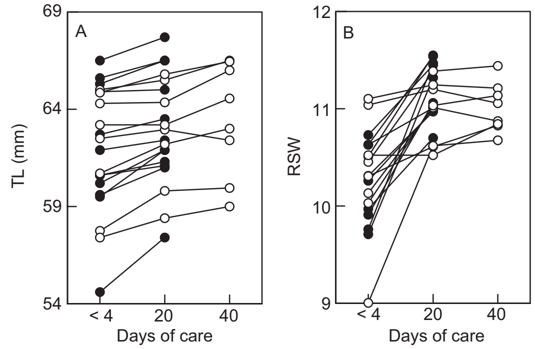

Fig. 2. Change in (**A**) total length TL, and (**B**) relative snout width RSW of individual males with paternal care days. Dots: 20 care days [$n = 12$ in **A**, $n = 10$ in **B**]; circles: 40 care days ($n = 8$).

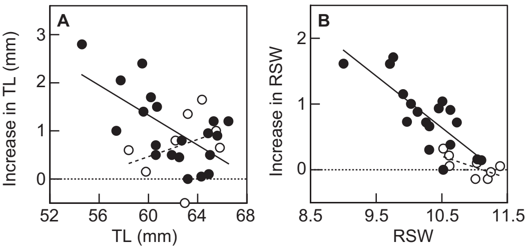

Fig. 3. Increase in (**A**) size, and (**B**) relative snout width RSW of care-giving males as a function of initial size. Dots: first 20 days; circles: following 20 days. Linear regressions: $y = -0.16x + 10.6$ for the first 20 days for **A**; $y = -0.79x + 8.89$ for the following 20 days for **B**.

Male competition for nests

New males that started to breed in nests by 4 days after the artificial removal of the former males had smaller RSW (10.2 ± 0.5 SD, $n = 12$) than the previous owners (10.8 ± 0.7, $n = 12$; paired t-test: $t_{11} = 3.11$, $p = 0.01$). However, the size of the previous owners (62.1 mm ± 1.9 in TL, $n = 12$) was not significantly larger than the newcomers (61.3 ± 2.0, $n = 12$, paired t-test: $t_{11} = 1.66$, $p = 0.12$).

Non-nesting males, most of which appeared smaller than nesting males, frequently visited nests. In most cases, the non-nesting males gave up entering nests without notable interactions with the owner males, or were repelled by threats from the owner males at the nest entrance. In a total of 21 nest takeovers, the invading males had significantly higher RSW (9.8 ± 0.7) than did the original nesters (9.2 ± 0.9; paired t-test: $t_{20} = 3.0$, $p = 0.007$), and the TL of the invaders was significantly greater (59.8 ± 2.2 mm) than that of the nesting males (58.5 ± 2.6; paired t-test: $t_{20} = 2.43$, $p = 0.025$). In two direct observations of nest takeovers, the nesting males rushed out of the nest with bite marks on their bodies after the invasion by non-nesting males, and did not reenter. We often observed non-nesting males with similar marks, sometimes with serious wounds, probably caused by male fighting. Such serious wounds were never observed on females.

Discussion

Filial cannibalism and body condition

Our study shows that *Diademichthy lineatus* males frequently consumed only their own living eggs during care. Care-giving males rarely left their nests, and were always observed vigorously fanning the eggs. The care-giving males of some other fish that spawn in closed structures also intensively fan their eggs and rarely leave their nests (e.g., fantail darter: Knapp & Sargent 1989; Mediterranean blenny: Kraak & Groothuis 1994). Eggs in enclosed nests may require continuous care for normal development, and this intensive care may prevent *D. lineatus* males from foraging outside the nest. In addition, our observations of nest takeovers and attempted invasions by non-nesting males suggest a risk of nest takeover. Thus, outside foraging would reduce the defensibility of nests against rival males. For example, nesting males of the peacock blenny minimize excursions from their nests in locations where non-nesting males attempt to intrude into brooding nests (Gonçalves & Almada 1997). Thus, the risk of foraging outside their nests may lead *D. lineatus* nesting males to consume their own eggs exclusively.

In paternal care fish species, the body and liver masses of care-giving males usually decrease within one month after the reproductive season or parental care begins because of the energetic cost of parental care (Marconato *et al.* 1993, Kraak 1996, Okuda & Yanagisawa 1996, Gonçalves & Almada 1997, Takahashi & Yanagisawa 1999, Okuda 2001). However, *D. lineatus* did not

Table 1. Frequency of cannibals, number of eggs in stomachs of care-giving males, and rate of egg cannibalism (mean ± SD) for three durations of care. Sample sizes are in parentheses.

	Care duration			Statistical test
	≤ 4 days (16)	20 days (14)	40 days (11)	
Cannibal males (%)	81.3	100	100	Fisher's exact test[c]: $p = 0.053$
No. of eggs in a stomach[a]	7.00 ± 7.06	13.07 ± 7.03	13.46 ± 6.49	ANOVA: $F_{2,38} = 3.99$, $p = 0.03$
Cannibalised eggs (%)[b]	1.04 ± 1.43	0.39 ± 0.23	0.32 ± 0.22	Kruskal-Wallis test: $H = 2.44$, $p = 0.30$

[a] All differences between care periods were non significant in post-hoc pair-wise comparison with the sequential Bonferroni test (Rice 1989).

[b] Number of eggs in stomach/(Number of eggs in stomach and nest) × 100.

[c] Frequencies of cannibals between ≤ 4 days care period and a class that combined the 20 days and 40 days care periods were compared.

Table 2. Pearson correlation coefficients between the number of cannibalised eggs and male characteristics. Sample sizes are in parentheses. $p < 0.05$ are all significant according to the sequential Bonferroni procedure (Rice 1989). Correlations are tested for pooled data of the three durations.

Variable	Care duration			Total (41)	p
	≤ 4 days (16)	20 days (14)	40 days (11)		
Number of eggs in the nest[a]	0.403	–0.017	–0.398	0.350	0.024
Total length (TL)	–0.105	–0.021	–0.172	0.101	NS
Condition factor (K)	0.438	0.400	0.396	0.488	0.001
Relative snout width (RSW)	0.547	0.284	0.376	0.566	< 0.0001
Liver index (LI)	0.220	0.080	0.192	0.115	NS
Gonad index (GI)	0.309	0.117	0.054	0.356	0.022

[a] Number of eggs in stomach and nest.

NS = $p > 0.45$.

exhibit physical deterioration, in spite of vigorous care of the eggs and no consumption of food other than their eggs. The liver index did not change during 40 days of care. The condition factor and relative snout width increased during the first 20 days, and were maintained at high levels afterwards, even up to 110 days after the start of care (three males: D. Gomagano unpubl. data). Furthermore, care-giving males exhibited growth in body size, and gonadal development. Starvation experiments confirmed that without food, males could not maintain good body conditions, and did not grow. Thus, *D. lineatus* males re-invest energy and nutrients from consumed eggs into fanning activity, production of sperm, and maintaining or improving body condition and size throughout the care period. These nutritional investments, when no other food is consumed, may explain the frequent egg cannibalism (93% of males overall) throughout the care period. The frequency of filial cannibalism of *D. lineatus* was much higher than that observed in many species in which the physical condition of males decreases rapidly after the start of care, or that have other opportunities for foraging, or both (7%–50% of males from stomach analysis; Belles-Isles & FitzGerald 1991, Marconato *et al.* 1993, Takahashi & Yanagisawa 1999, Vinyoles *et al.* 1999, Ito & Yanagisawa 2000, but 70% of males, Hoelzer 1988).

Previous studies have shown that paternal males in poor physical condition tended to cannibalise more eggs (e.g., Marconato *et al.* 1993, Kvarnemo *et al.* 1998, Neff 2003, Takahashi & Kohda 2004, Okuda *et al.* 2004). In contrast, *D. lineatus* males with higher body condition (higher *K* or RSW) consumed more eggs than males with low condition. In the former cases, poor physical condition is likely to cause more filial cannibalism, but it is difficult to determine the cause–effect relationship of this pattern in *D. lineatus*. Nevertheless, we propose some plausible factors facilitating frequent cannibalism in high condition males of *D. lineatus*. Males of high condition had more eggs in their nests, suggesting that egg abundance may encourage consumption (Ito & Yanagisawa 2000, Manica 2002, Okuda *et al.* 2004). Males of high condition possessed well-developed gonads, and cared for a larger number of eggs, in which males may have a higher energetic investment (sperm production: Taborsky 1998, Schärer & Robertson 1999, for parental activity: Coleman & Fischer 1991, Kraak & Videler 1991). These energetic demands may require an increase in egg consumption. Total energy required for metabolism and locomotion increases with body mass (i.e., muscle mass) in fish (Clarke & Johnston 1999). *D. lineatus* males of higher condition also have more developed muscle, and may need more energy for maintenance. However, we cannot confirm that these factors facilitate filial cannibalism in this fish, but can state that partial filial cannibalism not only maintained the initial liver index but also increased condition factor or relative snout width and body size during care.

It has often been argued that care-giving males exhibit partial filial cannibalism to compensate for their decrease in body condition, and increase their survivorship to complete current and/or future parental care (e.g., Rohwer 1978, FitzGerald 1992, Marconato *et al.* 1993, Kraak 1996, Manica 2002). The starvation experiments showed that the physical condition of *D. lineatus* males decreased, but all were still vigorous after 10 days. For this species, egg consumption appears to be enough to maintain their initial physical condition. Moreover, maintenance of the initial level of liver, improved somatic condition and growth during the care period indicate that partial filial cannibalism is not only linked to survivorship. Accordingly, improved male survivorship should not be necessarily the primary benefit associated with partial filial cannibalism. Instead, it is likely that the primarily benefit from improved body condition and size is in male–male competition, which is thought to be common in this species (*see* also Sakashita 1992). In a few species, partial filial cannibalism has been suggested to enhance the growth of the cannibals (cortez damselfish: Hoelzer 1992, sand goby: Lindström 1998). Large males of these species have an advantage in competing for suitable spawning substrates (Hoelzer 1990, Lindström 1988, 1992).

Body condition and male aggression

Like in other areas, at our study site the number of empty bivalves suitable for spawning nests was not adequate for *D. lineatus* males (Sakashita 1992). Our observations of nest occupation by non-nesting males soon after the removal of nest owners, incidents of nest takeover, and the presence of seriously wounded males suggest that strong male–male competition for nests occurs in this fish.

The snout width of original nest owner males was larger than that of new males that occupied the nest soon after experimental removal of the previous nest owners. In contrast, males that took over nests had significantly wider snouts and body lengths than the original nest owners. This suggests that wide snouts and large body sizes are likely to be advantageous to males competing for nests. The thick snout of males, a remarkable sexual dimorphic trait in *D. lineatus* (Sakashita 1992), is caused by the development of muscles attaching on the adductor mandible (D. Gomagano pers. obs.). The snout may function as a weapon in biting fights when males compete for nests, as in the case for the angel blenny (Hastings 1988, 1991). Angel blenny males in good physical condition have wider heads because of the volume of the mandible muscle. If nesting males with less-developed mandible muscles and smaller body sizes are more vulnerable to nest takeover, these males should greatly increase their muscles and body sizes. In fact, our results clearly indicated that parental males that were small in size and/or had small snouts greatly increased in both size and snout width, which may reduce their vulnerability to nest takeover.

To increase their initial body condition and size, cannibals need to sacrifice a large number of eggs (Smith 1992). In *D. lineatus*, females repeatedly spawn during a long reproductive season, and a limited number of nests continually receive spawn (D. Gomagano unpubl. data). Accordingly, once males occupy the nests, the owner males will obtain many egg clutches unless they lose the nests. Thus, the spawning success of a male is largely related to the duration of nesting (D. Gomagano unpubl. data). Frequent consumption of a portion of daily spawned clutches that induce a robust snout and large body size (i.e., high nest defensibility) will possibly mean that *D. lineatus* males could extend their breeding duration. Although the cost–benefit relation is not explicitly examined in our study, it is highly possible that the reproductive benefit of cannibalism stemming from a longer breeding season outweighs the cost of consuming eggs, and if so, partial cannibalism in this species is potentially an adaptive strategy. An explicit examination of the net costs and benefits of cannibalism should be evaluated in future studies.

In conclusion, care-giving males of *D. lineatus* exhibit unique patterns of partial filial cannibalism, which provide not only an energetic base for breeding, but also enhance increments in body size and physical condition. The enhancement of body conditions and increased body size may enable care-giving males to better defend the limited number of nests, and hence, probably results in a longer breeding period and higher reproductive output. This study provides the first evidence that partial filial cannibalism in paternal care fish species where male–male competition occurs can benefit cannibalistic males by enhancing their competitive ability in intra-sex combat as well as their survival.

Acknowledgments

We are grateful to T. Takeyama and S. Awata of the Laboratory of Animal Sociology, Osaka City University, Osaka, Japan, for valuable suggestions and advice, and to Y. Yanagisawa who permitted us to use the facilities of the UWA Marine Science Center, Ehime University, Matsuyama, Japan. We also thank members of the centre, especially the late A. Kamiharako, for support during our field works. This work was financially supported by an Osaka City Grant for Graduate Course Students to DG and by a Grant-in-Aid from the Japanese Ministry of Education, Science, Technology, Sports and Culture to MK.

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