



Parental fish change their cannibalistic behaviour in response to the cost-to-benefit ratio of parental care

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Partial filial cannibalism, the act of cannibalizing some offspring, has been explained as a response to the high energetic cost of care. I tested this hypothesis by manipulating the cost-to-benefit ratio of care in the scissortail sergeant, *Abudefduf sexfasciatus*, a tropical damselfish with male care. Background egg mortality was lower than the incidence of cannibalism, confirming that males did not just dispose of dead eggs. Investment in the current brood affected future investment, because males forced to skip a brood cycle put more effort into courtship during the following cycle and obtained larger broods than did unmanipulated males. Any factor influencing the cost-to-benefit ratio of parental care should also affect the incidence of cannibalism. I reduced the cost of care by supplementary feeding and reduced the benefit of care by simulating a decrease in paternity certainty through simulated intrusions by non-nesting males. Supplementary feeding significantly reduced partial filial cannibalism by parental males, a result compatible with the hypothesis that eggs are consumed to cover the energetic costs of parental care. Cannibalism decreased regardless of whether males were fed with conspecific eggs or crabmeat. Cannibalism was only reduced but not fully eliminated by supplementary feeding, and residual levels of cannibalism after feeding were similar to the background rate of egg mortality. Simulated intrusions by non-nesting males led to an increase in filial cannibalism and a decrease in parental effort.

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Filial cannibalism, the act of eating one's own offspring, is found in many taxa (Polis 1981), and it is especially common in fish (Manica 2002c). Filial cannibalism was long interpreted as an abnormal behaviour (Calhoun 1966; Lorenz 1966; Neel 1970; Dolhinow 1977; Ripley 1980). Rohwer (1978) suggested, however, that parents can use offspring as an alternative source of food to increase their current and future reproductive success. According to this adaptive explanation, filial cannibalism should be interpreted as one of the options available to guarding parents, and it is a common behaviour in connection with care of the offspring. The prediction follows that any factor influencing the costs and benefits of parental care should also affect the incidence of cannibalism.

Many factors can affect the costs and benefits of parental care. In teleosts, parental care consists mostly of defending the offspring from potential predators that are not a threat to the adult (Smith & Wootton 1995). This energetically demanding activity often limits foraging

opportunities (Smith & Wootton 1995), leading to a high energetic cost, which is at the heart of the evolutionary explanation of filial cannibalism proposed by Rohwer (1978). The energetic costs should be lower for males in good physical condition, and supplementary feeding should reduce the energetic cost of care and thus the incidence of filial cannibalism (Rohwer 1978; Sargent 1992). The benefit of parental care is proportional to the relatedness to the offspring being cared for (Owens 1993). Sneaking, defined as opportunistic males interfering with a spawning pair in the attempt to fertilize some of the eggs, can reduce certainty of paternity (i.e. perceived relatedness to offspring), and it is a relatively common behaviour in many species of fish (Taborsky 1994). Given that broods of low relatedness are of low value to the father, filial cannibalism is expected to increase with decreasing certainty of paternity (Svensson et al. 1998).

Supplementary feeding could decrease the incidence of cannibalism by decreasing the cost of care (Rohwer 1978; Sargent 1992), but evidence for this relationship is controversial (Sargent 1997). Hoelzer (1992) showed in a field study that, if Cortez damselfish, *Stegastes rectifraenum*, were fed with conspecific eggs, they cannibalized their brood less but still ate some of their own eggs. Kvarnemo

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et al. (1998) obtained similar results by feeding gobies, *Pomatoschistus microps*, with either conspecific eggs or mussel meat. Supplementary feeding reduced but did not eliminate filial cannibalism. However, several laboratory experiments have failed to show a decrease in filial cannibalism in males that received supplementary feeding (e.g. Belles-Isles & Fitzgerald 1991; Kvarnemo 1997; Lindström & Sargent 1997).

The benefit of parental care to the male depends on the relatedness of the offspring being cared for (reviewed in Owens 1993). Paternity has an important effect on parental effort in birds, both in comparative studies (e.g. Møller & Birkhead 1993; Møller & Cuervo 2000) and in those within species (e.g. Dixon et al. 1994). Although sneaking is relatively common in fish, and some species have developed specialized sneaker morphs (reviewed in Taborsky 1994), there is little evidence that fish modify their parental effort as a response to certainty of paternity. Bluegill sunfish, *Lepomis macrochirus*, males dynamically adjust parental care in response to perceived paternity in the field (Neff & Gross 2001; Neff 2003). In a laboratory experiment, Svensson et al. (1998) confined common goby males each in a tank with another much smaller male, which often acted as a sneaker. Control males were left alone in an empty tank. There was no effect on either fanning or defence against a simulated predator, the other two measures of parental expenditure. Besides the potential effect on parental effort, sneaking should also increase the incidence of partial filial cannibalism, because the relative cost of eating eggs decreases with decreasing certainty of paternity (Svensson et al. 1998). Svensson et al. also found no difference between the number of eggs eaten by treatment and control males.

Using field manipulations, I investigated the effect of the cost-to-benefit ratio of parental care in the scissortail sergeant, *Abudefduf sexfasciatus*, a tropical damselfish with paternal care. First, I measured the background rate of cannibalism in unmanipulated nests, as well as the natural rate of mortality in unattended nests, to estimate what proportion of cannibalism could be explained as 'nest cleaning'. I then evaluated the energetic consequences of care by forcing males to miss a brood cycle and measuring reproductive success as well as cannibalism during the following brood cycle. In another experiment, I reduced the cost of care by providing supplementary feeding with conspecific eggs. I then tested whether supplementary feeding with a source of food other than conspecific eggs would lead to the same decrease in filial cannibalism as observed with eggs. Finally, I decreased the benefit of care by decreasing certainty of paternity through simulated intrusions by nonterritorial males.

METHODS

Field Site and General Methodology

I investigated a population of scissortail sergeant on a patch reef south of Pulau Balak Balak, Malaysia (7°08'N, 117°08'E), and carried out all observations and manipulations by SCUBA diving. Males become territorial when mating and protect the eggs against potential predators.

Territories are clustered in discrete groups that can include over 30 nests (Manica 2002a). I monitored nine groups (range 4–26 males each). Males undergo brood cycling, i.e. the alternation of 1–3 days of mating ('mating phase') with 4–5 days of parental care ('parental phase'; Manica 2002a). Females school all the time and enter males' territories only to lay eggs, leaving immediately afterwards.

Eggs are laid in a uniform monolayer on dead substrate (rock and coral), and egg age could be estimated by colour (Manica 2002a). The area covered by eggs was traced on transparent plastic sheets with crayons. I took tracings twice a day, within 2 h of dawn and dusk, scanned them on to a personal computer and estimated the size of the brood ($\pm 1 \text{ cm}^2$). I also recorded the area covered by differently aged eggs, as estimated by colour. During over 900 h of observations, filial cannibalism was the only important source of mortality in the nest. Potential egg predators, such as the pinstripe wrasse, *Halichoeres melanurus*, and small gobies were almost always chased away by guarding males, and even when successful, predators removed only a few eggs at a time, an amount that would not affect the area of the tracing. Invertebrates were never seen to prey successfully on the eggs. Predator exclusion experiments on the same reef (Manica 2002b) also showed no decrease in egg mortality.

Background Egg Cannibalism and Mortality

To estimate the background rate of cannibalism in unmanipulated nests, I measured brood size and filial cannibalism in 30 nests by taking egg tracings twice a day until hatching during March 2000. To estimate baseline egg mortality during the same month, I covered 30 other nests with a fine plastic mesh net (6.25 mm²) for the duration of the brooding phase to investigate the basal mortality rate caused by disease, unfertilized eggs and misdevelopment. All the eggs had been laid on the columns of a dead *Goniopora* sp. colony, and each nest could span several columns. Each individual column was removed, enclosed in a net and hung at 6-m depth (the same as in the original colony) in a 15-m-deep channel. The channel experienced currents ranging from 0.5 to 1.5 knots, which ensured maximum oxygenation to the eggs. The nets were cleaned five times a day to minimize fouling and maximize aeration to the eggs. I estimated brood size and filial cannibalism by taking egg tracings twice a day until hatching.

Consequences of Parental Care

To evaluate the effect of parental care on future reproductive success, I prevented 35 reproducing males from obtaining eggs in March 2000. Starting from the day that the males started cleaning the nesting area, a diver chased away females that approached the nest. Whenever a female was successful at laying a few eggs, these were immediately removed. In April 2000, I selected 35 control males. Each control had a nest adjacent to one of the treatment males. Brood size and cannibalism were

monitored in all pairs of nests for two brood cycles following the manipulation. Of the 35 pairs, both males bred successfully throughout the investigation in 32 pairs and were included in the analysis.

Focal observations (10 min) were conducted to monitor parental behaviour during the two brood cycles following the manipulation. I recorded the following activities during each focal observation: guarding time (time spent within 10 cm of the eggs), number of nips to eggs, number of attacks on other fish and number of intrusions by other fish within a 1-m radius around the nest. I took one to three sets of focal observations for each group throughout the parental phase, and used the average of all the observations for each male in the analysis. During the mating phase of these two brood cycles, I also monitored the frequency of courtship displays during 10-min focal observations of each male. Focal observations were ended when a female entered the nest. Only data from observations at least 5 min long were used in the analysis.

Reducing the Cost of Care by Supplementary Feeding

Between March and May 2000, I randomly chose 35 pairs of reproducing males. Nests within each pair were separated by one unmanipulated nest, which acted as a behavioural 'buffer'. Starting from the day that the males began to clean a nesting area, the treatment male of each pair was fed three times a day with conspecific eggs. I collected the eggs from nearby nests using a plastic paint scraper and offered them to the treatment males, with a 30-ml pipette. Males were fed to satiation with eggs of the same age as their brood, even though males show no preference for egg age (Manica 2003). The control males were presented with an empty pipette for a similar period. All nests were unmanipulated during the following two reproductive cycles. Throughout the mating and parental phases, the area covered by eggs was traced twice a day. I took behavioural observations as before during the manipulated brood cycle and the first brood cycle following supplementary feeding. In 29 of 35 pairs, both males bred successfully throughout the investigation and were included in the analysis.

Supplementary Feeding with Eggs and Crabmeat

In September 1999, I tested the effect of supplementary feeding on current reproductive success. Fifteen groups of four males were randomly selected. All nests within each group were close to each other but were always separated by one unmanipulated nest. Starting from the day that the males began to clean a nesting area, the fish received supplementary food in the form of conspecific eggs or a mixture of two parts crabmeat and one part bread; the bread, besides being a source of carbohydrates, helped to make a firm paste that made handling easier. A full factorial design was used in each group of fish, with two factors (egg diet and crabmeat diet), each with two levels (fed or not fed). Thus, each fish in a group received either no supplementary feeding (control) or supplementary

feeding with either conspecific eggs, crabmeat mixture or equal amounts of both conspecific eggs and crabmeat mixture. I collected the eggs from nearby nests with a plastic paint scraper. Males were fed to satiation with a 30-ml pipette twice a day, and control males were presented with an empty pipette for a similar period. Tracings of the eggs were taken throughout the mating and the parental phase.

Decreasing the Benefit of Care by Simulated Sneaking

The effect of sneaking on parental effort and filial cannibalism was tested in August 2000. I haphazardly selected 15 pairs of nesting males during each brood cycle. The nests within each pair were separated by one unmanipulated nest. During each day of mating at the beginning of the brood cycle, each treatment male was exposed to simulated intrusions by conspecifics. I captured a non-nesting male with a net and stored it in a transparent plastic bag (confinement of fish in clear plastic bags is common practice to test aggressive responses; e.g. Colgan & Gross 1977; Gross & MacMillan 1981). The plastic bag was tied to a 2-m pole with a 1.5-m-long fishing line and was weighted with a 50-g lead sinker. When the treatment male was observed spawning, the male in the plastic bag was introduced into the nest for 5–10 s. This exposure was long enough to elicit a vigorous response from the nesting male and, because it was longer than most observed intrusions by males, I expected it to simulate a successful sneak. The nesting male was then allowed to settle down for at least 5 min before the intrusion was repeated. The water in the bag was changed every 15 min. I performed two treatment sessions during each of the 2 days of the mating phase, one from 0645 to 0915 hours (five intrusions per male) and one from 1015 to 1230 hours (three intrusions per male). A different, freshly captured male was used during each session. Control males were exposed to a female pinstripe wrasse, a local egg predator.

I took tracings of the eggs twice a day to estimate brood size and monitor filial cannibalism. I also measured brood size in another 15 unmanipulated nests, each adjacent to a treatment–control pair, to assess the effect of repeated interruptions during spawning. Parental effort was monitored during 10-min focal observations. I randomly took one focal observation of each male between 0700 and 1100 hours during each of the first 3 days of the parental phase. Two treatment males and one control male fully cannibalized their broods. Only pairs in which both males hatched their brood ($N = 27$ pairs) were used in the analysis.

Statistical Analysis

Statistical analysis was performed using Genstat 6.1 (Lawes Agricultural Trust, Rothamsted, U.K.). I initially analysed all the data with generalized linear mixed models (GLMM), which allow investigation of repeated measures by fitting random factors (Schall 1991). Fish identity

(when present) and experimental group or pair (i.e. males with nests close to each other) were entered as random factors. Random factors never gave a nonsignificant result, so I subsequently fitted generalized linear models (GLM) to all data (Crawley 2002). GLMMs and GLMs gave qualitatively similar results, and I present only GLMs here. The number of cannibalized eggs is related to total brood size, so cannibalism was analysed with a binomial error structure with total brood size as binomial denominator, using William's correction for overdispersion. I used a similar approach for time spent close to the nest and the number of intruders that were attacked during a focal observation. Behavioural counts, such as nips and courtship bouts, were fitted with a Poisson error structure, using a quasi-Poisson error structure if the data were overdispersed (Crawley 2002).

RESULTS

Background Egg Cannibalism and Mortality

Nests attended by parental males lost a mean \pm SE of $13.69 \pm 0.10\%$ of their eggs to filial cannibalism, even though the baseline rate of egg mortality in netted nests was significantly lower ($7.51 \pm 0.78\%$; GLM with William's correction: $\chi^2_1 = 23.49$, $P < 0.001$). There was no difference in brood size between the two treatments (ANOVA: $F_{1,58} = 1.65$, $P = 0.205$).

Consequences of Parental Care

Males forced to skip one brood cycle tended to have larger broods than did controls (ANOVA: $F_{1,124} = 3.62$, $P = 0.059$), but this difference was large only during the first cycle following the manipulation (766.4 ± 24.6 versus 683.9 ± 19.6 cm² of eggs; interaction between treatment and cycle' $F_{1,124} = 4.63$, $P = 0.033$). During this cycle, males that had to skip one brood cycle performed more courtship bouts than did control males (11.03 ± 0.59 versus 9.00 ± 0.53 cm² of eggs; GLM with William's correction: $\chi^2_1 = 6.60$, $P = 0.010$). There was no difference between the incidence of filial cannibalism by males forced to skip one brood cycle and by control males ($\chi^2_1 = 0.18$, $P = 0.674$). There was no effect of skipping one brood cycle on any of the parental behaviours ($P > 0.2$ for all variables).

Reducing the Cost of Care by Supplementary Feeding

No overall effect of supplementary feeding on brood size was detected (ANOVA: $F_{1,168} = 0.17$, $P = 0.679$), but there was a significant interaction between feeding and brood cycle ($F_{2,168} = 4.16$, $P = 0.017$). This interaction was mostly because fed males obtained slightly larger broods than did control males during the first brood following the manipulations ($t_{168} = 2.53$, $P = 0.012$; Fig. 1). Feeding led to a decrease in filial cannibalism (GLM with William's correction: $\chi^2_1 = 14.21$, $P < 0.001$), but the percentage of

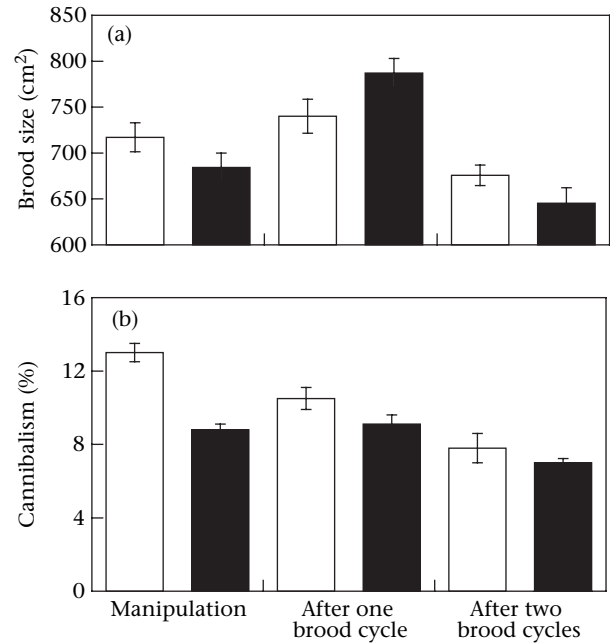


Figure 1. Mean \pm SE (a) brood size and (b) partial filial cannibalism during supplementary feeding and during the following two brood cycles. Treatment males were fed with conspecific eggs (■) and control males were presented with an empty pipette (□).

eggs eaten by fed males was not significantly different from the background mortality estimated during that brood cycle in the experiment above ($\chi^2_1 = 1.88$, $P = 0.170$). Total brood size ($F_{2,168} = 21.70$, $P < 0.001$) and cannibalism ($\chi^2_2 = 13.72$, $P < 0.001$) both varied significantly during the three brood cycles (Fig. 1).

Fed males made more jump signals than did control males during the cycle after the manipulation ($F_{1,112} = 5.00$, $P = 0.027$). During the parental phase, fed males spent more time in the nest ($F_{1,112} = 5.41$, $P = 0.020$; Table 1) and attacked a higher proportion of intruders ($\chi^2_1 = 6.35$, $P = 0.012$) compared to control males. Fed males also showed a nonsignificant tendency to give more nips to the eggs ($F_{1,112} = 2.96$, $P = 0.088$). All the variables showed significant differences between the two seasons ($P < 0.04$ for all variables).

Supplementary Feeding with Conspecific Eggs and Crabmeat

Supplementary feeding with either diet did not affect brood size (ANOVA: eggs: $F_{1,56} = 0.03$; $P = 0.867$; crab: $F_{1,56} = 0.58$; $P = 0.451$; Fig. 2a), but it significantly decreased the incidence of partial filial cannibalism (GLM with William's correction: eggs: $\chi^2_1 = 5.75$, $P = 0.016$; crab: $\chi^2_1 = 5.13$, $P = 0.023$; Fig. 2b). The interaction between the egg diet and the crab diet had a significant effect on the incidence of filial cannibalism (GLM with William's correction: eggs: $\chi^2_1 = 6.65$, $P = 0.010$), because there was no additive effect of the two diets (i.e. the decrease in filial cannibalism caused by supplementary feeding with both eggs and crabmeat was not equal to the sum of the decrease caused by feeding with just eggs and just crabmeat). There was no significant difference

Table 1. Parental effort following a feeding experiment

	Supplementary feeding	One cycle later
% Time guarding		
Control	74.8±2.3	71.4±2.5
Fed	79.0±2.4	78.7±2.7
% Intruders attacked		
Control	56.8±3.9	74.0±2.1
Fed	66.0±3.4	63.5±2.2
Number of nips		
Control	6.4±0.5	7.9±0.8
Fed	7.7±0.6	9.2±0.9
Number of jumps		
Control	11.4±1.1	9.3±0.4
Fed	9.2±0.9	10.4±0.5

Mean ± SE percentage of time spent guarding the nest, percentage of intruders attacked by the nesting male, number of nips to eggs and number of jump signals during a 10-min focal sample. Observations were made during the brood cycle when males received supplementary feeding and during the following cycle. $N=29$ males.

between the number of eggs cannibalized by fish fed with conspecific eggs and fish fed with crabmeat ($\chi^2_1 = 0.02$, $P = 0.881$; Fig. 2b). Brood size was not correlated with the number of cannibalized eggs in controls (Pearson correlation: $r_{13} = -0.144$, $P > 0.60$), but this correlation was significant when considering all three feeding regimes ($r_{43} = 0.435$, $P = 0.003$. Considering each diet individually, to give a comparable sample size to the

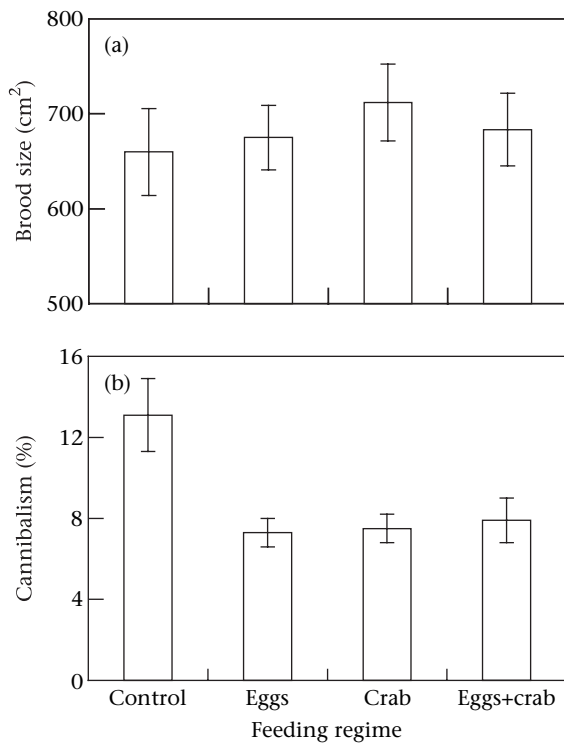


Figure 2. Mean ± SE (a) brood size and (b) partial filial cannibalism in male scissortail sergeants provided with different supplementary feeding regimes ($N=15$ for each regime).

nonfed males, led to several nonsignificant trends: eggs: $r_{13} = 0.47$, $P = 0.079$; crab: $r_{13} = 0.468$, $P = 0.078$; eggs + crab: $r_{13} = 0.44$, $P = 0.101$).

Decreasing the Benefit of Care by Simulated Sneaking

Simulated intrusions by non-nesting conspecifics and egg predators had no effect on brood size (ANOVA: $F_{2,33} = 1.13$, $P = 0.334$; Fig. 3a). However, simulated intrusions did affect cannibalism; males that experienced intrusions by non-nesting conspecifics ate more eggs than did males in the control or egg-predator groups (GLM with William's correction: $\chi^2_1 = 3.93$, $P = 0.20$; Fig. 3b). Males subject to intrusions by conspecifics tended to attack fewer intruders than did males challenged with a wrasse ($58.6 \pm 3.7\%$ and $70.4 \pm 2.6\%$, respectively; $\chi^2_1 = 6.74$, $P = 0.009$). Simulated intrusions had no effect on the time spent guarding ($68.7 \pm 2.6\%$ and $73.4 \pm 2.5\%$, respectively; $\chi^2_1 = 1.64$, $P = 0.200$) or the number of nips to eggs (3.6 ± 0.6 and 2.8 ± 0.4 , respectively; $\chi^2_1 = 1.15$, $P = 0.284$).

DISCUSSION

One assumption behind the theory of filial cannibalism is that parental care is expensive, and that an investment in

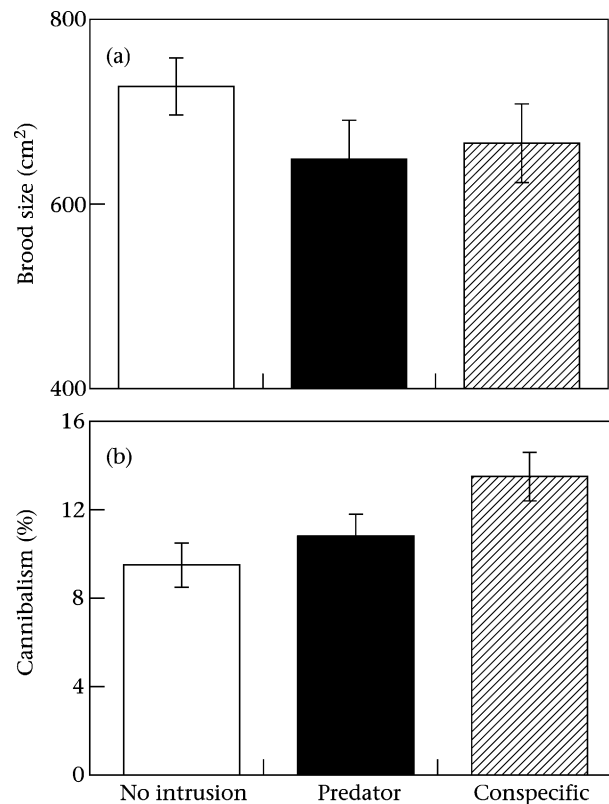


Figure 3. Mean ± SE (a) brood size and (b) partial filial cannibalism during simulated intrusions into the nest. Nesting males experienced either no intrusion (□) or intrusions from either a wrasse (a potential egg predator, ■) or a conspecific (▨).

current reproductive success implies a decrease in future reproductive success. Much evidence has been accumulated on the energetic cost of parental care (reviewed in Smith & Wootton 1995). However, there is little evidence that investment in current reproductive success has a negative effect on future reproductive success in fish (Sargent 1997). Balshine-Earn (1995) showed that early removal of a brood in the Galilee St Peter's fish, *Sarotherodon galilaeus*, a biparental mouthbrooder, led to a decrease in the interval between spawns in both sexes. Furthermore, females that cared for their broods had smaller second broods than did females whose broods had been removed. Male *A. sexfasciatus* showed a similar response when forced to skip a brood cycle; they put more effort into courtship during the following cycle and consequently obtained a larger brood.

Supplementary feeding in *A. sexfasciatus* led to a significant decrease in the number of eggs cannibalized by parental males in both manipulative experiments, a result predicted by Rohwer's (1978) theory and analogous to the findings by Hoelzer (1992) and Kvarnemo et al. (1998). As in the studies by Hoelzer and Kvarnemo et al., supplementary feeding in this study decreased cannibalism but did not eliminate it. The residual level of cannibalism after supplementary feeding was similar to the level of egg mortality experienced in the nests that were protected by a fine mesh, suggesting that fed males consumed only nonviable eggs (e.g. infertile or diseased eggs). Further evidence for this conclusion came from the positive correlation between brood size and the number of cannibalized eggs found only in fed but not in control males. The mouth-brooding cichlid *Pseudocrenilabrus multicolor* is also able selectively to consume unfertilized eggs (Mrowka 1987). Therefore, partial filial cannibalism in *A. sexfasciatus* may be both a response to the energetic demands of parental care and a form of cleaning behaviour. During the second brood cycle following supplementary feeding, the number of eggs cannibalized by both fed and control males was relatively small and similar to the basal mortality rate measured during the feeding manipulation. One explanation for this result is that natural food availability was so high that males were well fed and did not need to cannibalize eggs to maintain their physical condition.

An alternative explanation for the decrease in partial filial cannibalism with supplementary feeding is that egg mortality in nests tended by starved males is higher because they are unable to provide adequate fanning (Kvarnemo et al. 1998). For example, parental convict cichlids, *Cichlasoma nigrofasciatum*, reduced fanning rates when kept on a reduced diet (Townshend & Wootton 1985). This explanation is unlikely to apply to the scissortail sergeant. Fanning in this species was minimal or even absent (A. Manica, personal observation) and I therefore did not measure it. Egg mortality in unattended nests was, on average, equal to the mortality found in nests of fed males and much lower than in those of starved males. Unless oxygenation in the unattended nests kept in midwater was much better than in the natural nests, this result contradicts the hypothesis that fanning by fed males increases egg survival.

There was no difference between the incidence of partial filial cannibalism in males fed with the two different diets, conspecific eggs and crabmeat. The nutrient value of crabmeat should be relatively similar to that of zooplankton (except for the lower chitin content), the main food source for *A. sexfasciatus* (Lieske & Myers 1996; A. Manica, personal observation). This finding is not consistent with the hypothesis that eggs might contain rare nutrients unavailable to males (Belles-Isles & Fitzgerald 1991; Fitzgerald 1991). Kvarnemo et al. (1998) also found that mussel meat is an acceptable substitute for eggs in the common goby. However, even fed males cannibalized a few eggs, so I cannot exclude the possibility that eggs could act as a high-quality source of nutrients that are not commonly available in the male's diet.

Sargent (1992) argued that partial filial cannibalism is an investment in both present and future reproductive success. However, the evidence in the literature for an effect on future reproductive success is limited. Hoelzer (1992) showed that fed garibaldi damsel fish, *Hypsypops rubicundus*, spent more time on the mating grounds, but showed no significant increase in reproductive success. Lindström & Sargent (1997) found that egg eaters in the fantail darter, *Etheostoma flabellare*, maintained better fat reserves than did noncannibals, and fatter males would be expected to have a higher probability of survival. My experiment demonstrated an increase in brood size during the brood cycle following supplementary feeding. Previously fed males performed more invitation swims than did controls, thus putting more effort into courtship. Female preference for males in good physical condition is also compatible with the increase in mating success by previously fed males, but I did not test this possibility.

Fish subjected to simulated intrusions by conspecifics changed their parental effort, demonstrating their ability to perceive the relatively low certainty of paternity following from repeated intrusions by foreign males. A decrease in parental effort with low certainty of paternity has been reported in several studies of birds (e.g. Dixon et al. 1994; Sheldon & Ellegren 1998), but this is only the second example in fish, (see also Neff & Gross 2001; Neff 2003) despite the many reports of sneaking in this taxon (reviewed in Taborsky 1994). Sneaking was only simulated, but no sperm was released in the nest, suggesting that fish responded simply to perceived paternity. Neff & Gross (2001) and Neff (2003) also found a response to perceived rather than genetic paternity in male sunfish guarding eggs, and suggested that fathers might be able to detect genetically related offspring only after hatching. In the scissortail sergeant, there is no care for hatched larvae, so fathers might have to rely fully on perceived paternity.

In the present study, filial cannibalism responded to changes in the costs and benefits of parental care, as expected from the theoretical framework proposed by Rohwer (1978). These results stress that filial cannibalism should be regarded as an integral part of parental care rather than a special behaviour. The variable response obtained when sneaking was simulated indicates that filial cannibalism is only one of the options for parental males, who can also change their effort in defending the offspring or spend more time foraging. Dynamic resource

models, which can take into account variable effort, would probably help to explain the relation between these nonmutually exclusive strategies.

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