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Food access, brood size and filial cannibalism in the fantail darter, *Etheostoma flabellare*

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Abstract We compared the occurrence of filial cannibalism in fed and starved male fantail darters (*Etheostoma flabellare*). All males in the experiment consumed eggs, and 56% ate all of their eggs. A male's initial body condition did not explain the number of eggs that he ate. Neither did non-fed males eat more eggs than fed males. Fed males were able to maintain better body condition during the experiment, but the change in body condition also depended on the number of eggs eaten. Thus, males who ate more eggs were able to maintain better body condition. The most important determinant of whether or not a male ate all of his eggs was his initial egg number. Males with small egg masses ate all of their eggs whereas males with large egg masses were only partial cannibals. There was, however, no difference in the total number of eggs eaten by total and partial cannibals. We conclude that eggs are only partially eaten for energetic reasons. We also suggest that small egg masses are completely consumed because the costs of caring for a small egg mass may exceed the expected reproductive benefits of a small egg mass.

Key words Filial cannibalism · Paternal care · Condition change · Brood size · *Etheostoma flabellare*

Introduction

The consumption of one's own viable offspring, filial cannibalism, is a common phenomenon (reviewed in

Elgar and Crespi 1992), particularly among fishes with paternal care (FitzGerald and Whoriskey 1992). Filial cannibalism may be a way for the parent to obtain additional energy, which might be necessary for the parent to complete the brood cycle and initiate additional ones (Rohwer 1978). Ultimately then, the lowered present reproductive success would, through energy gains, result in an increase in future reproductive success. Sargent (1992) formalised the verbal model of Rohwer (1978) using a dynamic optimisation approach. In this model the parent would eat eggs to gain energy and thus be able to finish the brood cycle with a positive energy budget. The model was able to replicate realistically the pattern of filial cannibalism that has been observed in empirical situations (Sargent 1992), which suggests that increased future reproductive success through energy gained by egg eating could be an important factor in the evolution of filial cannibalism.

Energy based filial cannibalism predicts that parents with low energy reserves or limited access to food should show more cannibalism (Sargent 1992). Some previous studies aimed at testing this found that parents with limited food access will often consume more of their own offspring (Hoelzer 1992; Marconato et al. 1993). Other studies, however, have found that cannibalism is unrelated to food ration (Lavery and Keenleyside 1990; Belles-Isles and FitzGerald 1991) and occurs with equal frequency in fed and non-fed parents.

An important assumption of the energy-based models is that offspring function as an alternative energy source for the parents. It has even been suggested that paternal males might parasitize the foraging efforts of females by eating part of the clutches (DeMartini 1987). Although this is a reasonable assumption, no-one has yet shown that egg eating really enhances parental body condition.

The fantail darter, *Etheostoma flabellare*, is a small stream-living percid fish with paternal care of eggs (Kuehne and Barbour 1983; Page 1983). Males establish nests under flat rocks in the spring. They mate with one to several females who attach the eggs to the ceiling of the nest (Winn 1958). The time required by eggs to de-

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velop can be up to 35 days according to Winn (1958). The parental phase could thus be very costly to males, which suggests that filial cannibalism may be an important means for males to restore their energy budgets. Female fantail darters prefer to mate with egg guarding males (Knapp and Sargent 1989). This preference for already mated males would be adaptive if, by placing her eggs among other female's eggs a female reduces the risk of having her own eggs consumed by the male.

The aim of our study was to test the energy-based filial cannibalism models of Rohwer (1978) and Sargent (1992). Specifically, we test the following predictions of Sargent (1992):

1. Filial cannibalism should increase with decreasing body condition as the fitness value of extra energy should be higher for starved individuals. Therefore we compared egg consumption in starved and fed fish.
2. Males with small egg numbers should show total filial cannibalism more frequently as the cost of caring for these eggs would never outweigh the benefits.
3. Partial egg consumption should increase with increasing egg numbers.
4. We also predict that if egg consumption is energetically advantageous, individuals who eat eggs should have better body condition than non-cannibals.

Materials and methods

The study was done during the fantail darter breeding season in April 1993 and 1994. Males were collected from Shelby Branch, a second order spring-fed stream in central Kentucky, after they had established nests and received eggs on tiles provided by us as artificial nest sites. The tiles measured 15 × 15 cm. The nests and the males guarding them were collected when the eggs were at most 2 days old.

The standard length and initial body weight of the males were measured and their eggs counted. After that they were put into 150-l experimental aquaria. The aquaria had a 4-cm-thick layer of dark, 4–5 mm coarse gravel on the bottom. Each aquarium was equipped with an air-driven under-gravel filter and a 40-W light source. The tanks had a natural dark:light cycle and water temperature was maintained at 18° C. The nests were carefully placed over a small deepening in the gravel so that the eggs would not be damaged. After that, the male was released underneath the nest, where he would stay and resume parental activities.

Males were randomly assigned to one of two treatments. Those males assigned to the starvation treatment received no food, whereas the other group of males, the fed males, received *ad libitum* food consisting of earthworms, *Daphnia* spp., isopods and amphipods. Unless a male ate all his eggs the experiment ran for 12 days. The eggs would start to hatch shortly after age 12 days and we did not want to confound our estimate of cannibalism with hatching. Each male was checked daily for the presence of eggs. After 12 days or when a male had lost all his eggs he was captured, reweighed and killed in MS-222 for further treatment.

To measure change in body condition we estimated it by scaling fresh weight to standard length^{2.66} ($r = 0.994$, $df = 40$, $P < 0.001$). Using standard length^{2.66} explains 80% of the variation in fresh weight. This estimate is in turn highly correlated with condition estimates based on dry weight ($r = 0.885$, $df = 17$, $P < 0.001$).

We used parametric tests whenever data fulfilled the assumptions of these tests. Otherwise we used non-parametric tests.

Results

The fish from the two years did not differ in any of the traits measured (Table 1), so we pooled the two data sets for further analyses.

All 41 males consumed eggs. Roughly 43.9% of the males were partial cannibals, and consumed on average 184.9 ± 146.9 (mean \pm SD) of their eggs. The rest of the males (56.1%) consumed all their eggs (191.9 ± 152.0). The frequency of partial and total cannibalism did not differ between fed and starved fish (43% and 57%, respectively; $\chi^2 = 0.02$, $P = 1.00$). There was no difference in body length between the two behavioural categories. Partial cannibals were on average 65.8 ± 4.1 mm ($n = 18$) in standard length and total cannibals 64.3 ± 4.1 mm ($n = 23$; t -test, $t = 1.22$, $df = 39$, $P = 0.229$).

Total cannibals finished their egg masses in an average of 4.6 ± 3.1 days, and this time did not depend on treatment ($t = 0.35$, $df = 21$, $P = 0.727$). Neither did the total number of eggs (175.9 ± 144.1) or the daily number of eggs (14.4 ± 11.6) eaten by partial cannibals depend on the treatment (total number of eggs eaten, Mann-Whitney $U = 40.0$, $P = 0.965$; number of eggs eaten per day, Mann-Whitney $U = 40.0$, $P = 0.965$).

The number of eggs eaten was not associated with a male's initial body condition ($r = 0.086$, $df = 39$, $P = 0.598$) but fed fish were able to improve their condition whereas non-fed fish lost condition (ANCOVA,

Table 1 A comparison of the fish from the two years over which the experiment was run. The values given are means with standard deviations in parenthesis. The last two columns give the t -value with the corresponding probability

Trait	Year		t	P
	1993 $n = 22$	1994 $n = 19$		
Standard length, mm	66 (3.50)	64 (4.70)	1.15	0.257
Initial weight, g	3.91 (0.71)	3.62 (0.65)	1.32	0.192
Initial condition	9.77 (0.88)	9.62 (0.66)	0.61	0.544
Initial number of eggs	316 (206)	237 (162)	1.37	0.177
Daily change in condition	-0.15 (0.44)	0.04 (0.22)	1.75	0.089

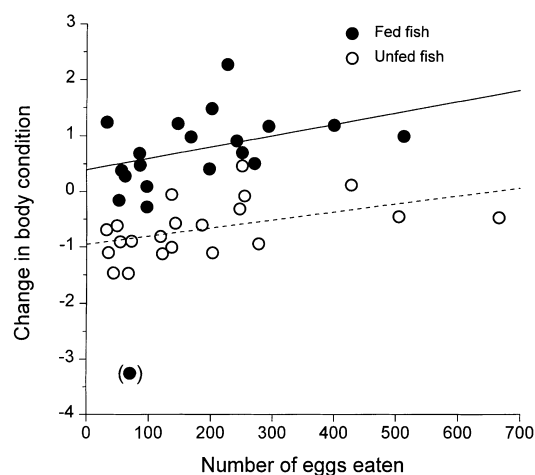


Fig. 1 The relationship between change in condition and the number of eggs eaten shown separately for fed and unfed fish. Fed fish have a more positive change in condition and in both groups the number of eggs eaten increases condition in a similar way. The regression lines for fed (solid line; change in condition = $0.395 + 0.002$ eggs eaten, excluding the apparent outlier) and for non-fed fish (dashed line; change in condition = $-0.952 + 0.001$ eggs eaten) are parallel. Pooling the data shows that keeping condition constant requires that a male eats 181 eggs (excluding the apparent outlier)

$F_{(1,38)} = 26.86$, $P < 0.001$, Fig. 1). The number of eggs eaten, used as a covariate in the above analysis of covariance, had a significant positive effect on the change in body condition ($F_{(1,38)} = 6.36$, $P = 0.016$, Fig. 1). Thus fish who ate more eggs also increased their condition more.

Partial cannibals showed no tendency to increase cannibalism with larger clutch sizes ($r_s = 0.27$, $df = 17$, $P = 0.280$). Partial cannibals had on average twice as large egg masses as total cannibals ($t = 3.89$, $df = 39$, $P < 0.001$, Fig. 2A). However, the total number of eggs eaten did not differ for these two groups of fish (Mann-Whitney $U = 193.5$, $P = 0.723$, Fig. 2B).

Discussion

Filial cannibalism occurred independently of initial male condition and food access in this study. Since males with low energy reserves are expected to eat more eggs (Sargent 1992), these results would suggest that the primary reason for egg eating in the fantail darter is not energy gain. That egg eating is still energetically advantageous is indicated by the fact that males who ate eggs were able to maintain a better body condition. Although we cannot rule out that males who improved in condition ate more eggs, rather than vice versa, we feel that this is highly unlikely because unfed males had no other source of food and no other means to increase their condition. This also verifies one of the central assumptions of Rohwer (1978), that offspring could function as an alternative food source. So even if the consumption of eggs is energetically advantageous, the decision to eat

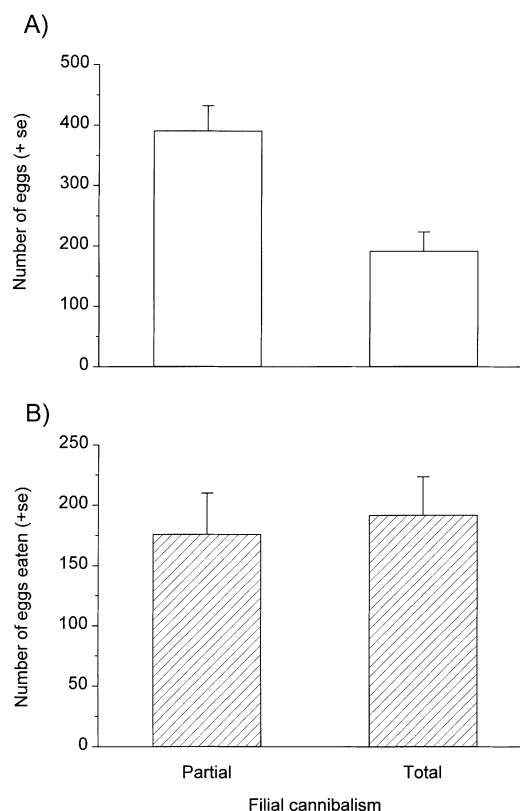


Fig. 2A, B A comparison of partial and total filial cannibals. **A** The initial egg mass size of partial and total filial cannibals. Males who eat all their eggs have clearly smaller egg masses. **B** The total number of eggs eaten. There was no difference between the two groups of males in the number of eggs consumed

eggs does not seem to be a function of energetic need for egg guarding fantail darter males. Perhaps eggs contain nutrients that are not otherwise available in the diets of parental male fantail darters. Future studies need to consider the possibility that parental fishes may be limited by more than one food-related resource (Sargent, in press).

The main difference between total and partial cannibals in the present study was their initial number of eggs. Males with small egg masses consumed all their eggs, whereas larger egg masses only resulted in partial cannibalism. This has been observed previously in other species. Examples come from species with female care (Mrowka 1987) and biparental care (Lavery and Keenleyside 1990). These observations suggest that small broods are more vulnerable to total parental cannibalism than large broods. In many fish species with paternal care, including the fantail darter, it has been shown that females prefer males who have already mated and thus have eggs in their nests (Ridley and Rechten 1981; Constanz 1985; Sikkell 1988; Unger and Sargent 1988; Knapp and Sargent 1989). It has also been shown that in such species females only prefer males with young eggs in their nest while males with old eggs are avoided (Sikkell 1989, 1994). A male with a few young eggs would therefore be attractive to additional females but a male

with a few old eggs would not. The cost of caring might be almost the same for small and large broods since the care fishes provide is often divisible (*sensu* Clutton-Brock 1992) but the benefits will be substantially smaller for small broods (Petersen and Marchetti 1989). Thus caring for small broods may never be beneficial in some species and this may be especially so if expected mating success is negatively correlated with egg age.

There was no difference in the total number of eggs eaten by partial and total cannibals. Thus, there might be a fixed amount of eggs that a male will consume during the brood cycle, perhaps to cover the energetic costs of the present brood cycle. If the number of eggs in the nest is smaller than this threshold then the male will consume all the eggs and consequently be classified as a total cannibal. The average number of eggs eaten was very similar to the number of eggs eaten by those males who maintained a constant body condition (see Fig. 1). It seems that males are unwilling to lose body condition during the brood cycle and that the brood cycle is completed only if the male is able to maintain a positive body condition and produce offspring. The loss of body condition is at least partly the cost a male pays for providing care. If this cost was relatively unchanged by the number of eggs a male had to care for (i.e. care was divisible) then it would make sense if the male always ate a constant number of eggs. As indicated above, the assumption of constant cost may often be true in fishes as a major part of care consists of guarding the nest against egg predators and other intruders (Wittenberger 1981; Clutton-Brock 1992). Also, because the fantail darter breeds in streams, it is likely that much of the oxygen needed by the eggs is provided by the constantly running stream water. Future studies will have to show whether there is a relationship between the number of eggs and cost of parental care. A fruitful experiment would be to manipulate the cost level, for example by exposing guarding males to different densities of egg predators; as the cost of care increases, the frequency of total filial cannibalism should increase.

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References

- Belles-Isles J-C, FitzGerald GJ (1991) Filial cannibalism in sticklebacks: a reproductive management strategy? *Ethol Ecol Evol* 3:49–62
- Clutton-Brock TH (1992) Parental care. Princeton University Press, Princeton
- Constanz GD (1985) Alloparental care in the tessellated darter *Etheostoma olmstedi* (Pisces: Percidae). *Environ Biol Fish* 14:175–183
- DeMartini EE (1987) Paternal defence, cannibalism and polygamy: factors influencing the reproductive success of painted greenling (Pisces, Hexagrammidae). *Anim Behav* 35:1145–1158
- Elgar MA, Crespi BJ (1992) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York
- FitzGerald GJ, Whoriskey FG (1992) Empirical studies of cannibalism in fish. In: Elgar MA, Crespi BJ (eds) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York, pp 238–255
- Hoelzer G (1992) The ecology and evolution of partial-clutch cannibalism by paternal Cortez damselfish. *Oikos* 65:113–120
- Knapp RA, Sargent RC (1989) Egg-mimicry as a mating strategy in the fantail darter, *Etheostoma flabellare*: females prefer males with eggs. *Behav Ecol Sociobiol* 25:321–326
- Kuehne RA, Barbour RW (1983) The American darters. University Press of Kentucky, Lexington
- Lavery RJ, Keenleyside MHA (1990) Filial cannibalism in the biparental fish *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) in response to early brood reductions. *Ethology* 86:326–338
- Marconato A, Bisazza A, Fabris M (1993) The cost of parental care and egg cannibalism in the river bullhead, *Cottus gobio* L (Pisces, Cottidae). *Behav Ecol Sociobiol* 32:229–237
- Mrowka W (1987) Filial cannibalism and reproductive success in the maternal mouthbrooding cichlid fish *Pseudocrenilabrus multicolor*. *Behav Ecol Sociobiol* 21:257–265
- Page LM (1983) Handbook of darters. TFH, Neptune City
- Petersen CW, Marchetti K (1989) Filial cannibalism in the Cortez damselfish *Stegastes rectifraenum*. *Evolution* 43:158–168
- Ridley M, Rechten C (1981) Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour* 76:152–161
- Rohwer S (1978) Parent cannibalism of offspring and egg raiding as a courtship strategy. *Am Nat* 112:429–440
- Sargent RC (1992) Ecology of filial cannibalism in fish: theoretical perspectives. In: Elgar MA, Crespi BJ (eds) Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, New York, pp 38–62
- Sargent RC (1997) Parental care. In: Godin J-G (ed) Behavioural ecology of teleost fishes. Oxford University Press, Oxford, pp 290–313
- Sikkel PC (1988) Factors influencing spawning site choice by female garibaldi *Hypsypops rubicundus* (Pisces, Pomacentridae). *Copeia* 1988:710–718
- Sikkel PC (1989) Egg presence and developmental stage influence spawning site choice by female garibaldi. *Anim Behav* 38:447–456
- Sikkel PC (1994) Filial cannibalism in a paternal-caring marine fish: the influence of egg development stage and position in the nest. *Anim Behav* 47:1149–1158
- Unger LM, Sargent RC (1988) Allopaternal care in the fathead minnow, *Pimephales promelas*: females prefer males with eggs. *Behav Ecol Sociobiol* 23:27–32
- Winn HE (1958) Comparative reproductive behavior and ecology of fourteen species of darters (Pisces-Percidae). *Ecol Monogr* 28:155–191
- Wittenberger JF (1981) Animal social behavior. Duxbury, Boston

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