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The cost of parental care and egg cannibalism in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae)

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Summary. Male river bullheads guard and care for egg masses during a single brood cycle every breeding season. A study of two bullhead populations demonstrated that nesting males show a strong reduction in food intake rate and that their physical condition deteriorates during parental care. The estimated weight loss for the average guarding male was 18.8% in one population and 13.5% in the other. This could in part be responsible for the peak of male mortality observed during the second part of the breeding season. A high incidence of egg cannibalism was observed in males guarding eggs. Analysis of the developmental stage of individual egg masses demonstrated that heterocannibalism is very rare in this species and that the observed rate of egg cannibalism is mainly due to guarding males preying upon their own eggs (filial cannibalism). In both populations the frequency of filial cannibalism was negatively correlated with the male's chance of getting other food items. The probability of a male cannibalizing its own eggs was also significantly influenced by the time elapsed since the beginning of parental care. The observed limited cannibalism of progeny in the river bullhead cannot be explained as a male's strategy for obtaining energy to be used in subsequent brood cycles, as suggested for other fishes which show filial cannibalism. Rather, it can be interpreted as a behaviour aimed at avoiding the risk of dying of starvation before the eggs hatch. The observed criteria of female mate choice, i.e. a preference for males in good physical condition and for males that already have eggs in their nests, are consistent with the prediction of Rohwer's filial cannibalism theory, although other hypotheses cannot be excluded.

Introduction

For a long time the behaviour of parents that feed upon their own progeny (filial cannibalism) was thought to be pathological or difficult to reconcile with conventional evolutionary thinking. In most cases the significance of filial cannibalism is still poorly understood. Nevertheless, this phenomenon is apparently widespread in fishes where it is more common than in other vertebrates (for review see Dominey and Blumer 1984). Filial cannibalism in fishes is probably favoured by the fact that in many fish species eggs are within the size range of prey taken by adults, large numbers are often concentrated in small areas, and embryos have no means of avoiding predation by the parent (Dominey and Blumer 1984).

One evolutionary explanation for the occurrence of filial cannibalism in fishes with paternal care is that parental duties impose restrictions on foraging opportunities and that the consumption of part of their own progeny helps parents to maintain good condition for subsequent brood cycles (filial cannibalism theory, Rohwer 1978). This behaviour would be evolutionarily advantageous if the energy gained by the parent could be translated into a higher lifetime fitness. According to Rohwer (1978) filial cannibalism is expected to be advantageous in species that undertake several brood cycles during the same breeding season; in these species the parent has no time to recover during inter-brood cycles, unless it skips one or more brood cycles, thus reducing overall reproductive success. In the painted greenling, *Oxylebius pictus*, De Martini (1987) confirmed that males which go through several brood cycles lose more weight than males which go through few. On this basis filial cannibalism is not expected to occur in species which undertake only one brood cycle each breeding season.

The theory also predicts a conflict between males and females with the latter trying to dilute male predation by laying eggs in nests with multiple clutches: as a consequence males without eggs in their nest or defended territory are expected to be at a disadvantage in courtship. In this context, filial cannibalism may explain: why females prefer males that already have eggs in their nest (Ridley and Retchen 1981; Marconato and Bisazza 1986; Unger and Sargent 1988; Petersen 1989; Sikkel 1989; Belles-Isles et al. 1990; Goldschmidt and Bakker

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1990); egg-raiding in sticklebacks (Rohwer 1978); and nest take over (Constantz 1985; Bisazza and Marconato 1988; Unger and Sargent 1988).

This theory is largely based upon the biology of sticklebacks. Many studies on filial cannibalism have been carried out on this fish, but the results are equivocal. According to some authors (Kynard 1979; Whoriskey and FitzGerald 1985; Hyatt and Ringler 1989) filial cannibalism is not common in this species in nature and is less important than heterocannibalism. Other studies on *Gasterosteus aculeatus* and other stickleback species stress the importance of filial cannibalism (Salfert and Moodie 1985; Belles-Isles and FitzGerald 1991). Discrepancies are probably due to the difficulty of detecting filial cannibalism or distinguishing it from heterocannibalism at some sites (Belles-Isles and FitzGerald 1991).

In recent years the occurrence of filial cannibalism has been documented in the field in several brood-cycling fish: *Chromis notata* (Ochi 1985), *Oxylebius pictus* (De Martini 1987), *Stegastes rectifraenum* (Petersen and Marchetti 1989), *S. dorsopunicans* and *Microspathodon chrysurus* (Petersen 1990), and may occur also in fish without brood cycling (Hoelzer 1988; Marconato and Bisazza 1988). Marconato and Bisazza (1988) reported a high incidence of empty stomachs among guarding male river bullhead (*Cottus gobio*) and suggested that in species with a single long brood cycle per season, males may eat some of their own eggs to reduce the risk of dying of starvation before the eggs hatch. If so, filial cannibalism is a more general phenomenon than expected on the basis of Rohwer's theory.

In this paper we investigate the occurrence of egg cannibalism in two populations of river bullheads living in different habitats. The river bullhead is a freshwater bottom-dwelling fish. In late winter males establish and defend nest sites under stones. The female spawns all her eggs in a hemispherical mass attached to the nest ceiling. A male may mate with up to ten females. Parental care lasts 3–4 weeks during which the male fans the eggs by constant movement of its fins.

The aims of this field study were to determine the extent to which parental care reduces foraging opportunities of males, to estimate its costs both in terms of decreased male physical condition and increased mortality rate, and to confirm that egg cannibalism is mainly due to parent males feeding upon their own progeny. The following predictions about factors affecting the rate of filial cannibalism in *C. gobio* were tested: (1) males should cannibalize more as the parental care cycle progresses, since their physical condition will worsen; (2) other things being equal, males that succeed in obtaining other food are expected to cannibalize less frequently; (3) a high density of nesting males will lead to increased energy expenditure for nest defence and reduced foraging activity, and so should lead to an increase in the rate of filial cannibalism. Additional predictions are derived from the current filial cannibalism theory (Rohwer 1978; Dominey and Blumer 1984; FitzGerald 1992): (4) given the choice, males should eat younger eggs because these require a higher investment in care; (5) small males are expected to eat fewer eggs because they require fewer eggs per unit time for maintenance than large males; (6) the number of eggs eaten by a parental male should be independent of the total number of eggs he is brooding. This last prediction holds true only if a higher number of eggs does not cause higher costs.

Other predictions concern the behaviour that females are expected to adopt in order to reduce the chance that their own eggs will be eaten by the guarding male. First, females should prefer to mate with males in good physical condition because these are less likely to cannibalize their eggs. Second, females are expected to prefer spawning with males that already have eggs, in order to dilute potential cannibalism of eggs. However, if males selectively eat younger eggs, females should avoid nests with egg clutches at an advanced developmental stage. This should favour a synchronization of spawnings within the same nest.

Methods

The first study population inhabits a mountain river in Northern Italy, the river Brenta (hereafter referred to as the river) which, in the study area, has an average width of about 25 m and a depth ranging from 10–15 cm in riffles to 150 cm in pools. Here most of the river is less than 20 cm deep and the bottom is a mixture of pebbles and stones with occasional large rocks. Temperature varies between 5–6° C in winter and 12–13° C in summer. In this habitat bullheads are characterized by a low growth rate, a long life span (maximum age 10 years) and a low population density (0.2–0.7 adults/m^2) (Marconato 1991; Perini 1991).

The second study area is a portion of the Menegatta brook (hereafter referred to as the brook), a small and highly productive water body, average width 3.2 m, originating from a spring in the plain and running for about 4 km through an agricultural area near the town of Vicenza (Northern Italy). More details on this study area are reported by Marconato and Bisazza (1988). In this habitat bullheads are characterized by a high growth rate, a short life span (maximum age 4 years) and a high population density (0.9–2.6 adults/m^2) (Marconato 1991; Perini 1991). The distance between the two study sites is about 20 km. During the 1987 breeding season, from late February to late April, the two areas were sampled weekly for nesting males. On each sampling day a section of the area was searched thoroughly for bullheads by overturning rocks and any other suitable hiding place. Animals were caught by stunning them with a low-potential electrofishing apparatus. Each specimen was sexed and measured (total length). The position of each nest site was recorded on a map, a nest site being defined as the area occupied by a breeding male under a stone whose lower surface had clearly been polished. These data were later used to estimate the density of breeding males within a range of 5 m from a nesting male. The size of the nest site was estimated by calculating the area of the polygon which best approximated its shape. The water depth next to the nest was also recorded. After capture, breeding males and, if present, the egg mass or masses in the nest, were preserved in 10% formalin for later analysis. In the laboratory the condition factor K (ratio of body weight to body length) and stomach contents of each animal were determined as described by Marconato and Bisazza (1988). Thirty males with eggs, found in the brook at different dates, were transferred alive to the laboratory and their stomach contents were not analysed. In a few other fishes of both populations the contents of the stomach could not be determined or weighed. Five guarding males (two from the river and three from the brook) suspected to be heterocannibals (see Results) were not included in the analysis of the determinants of filial cannibalism.

We recorded the developmental stage of a sample of eggs from each egg mass in the nest and of all eggs found in the stomach. Sixteen developmental stages were used. These stages were based on observation of eggs fertilized and raised in the laboratory at water temperatures of 13–14° C. Each stage lasted 24 h. The devel-

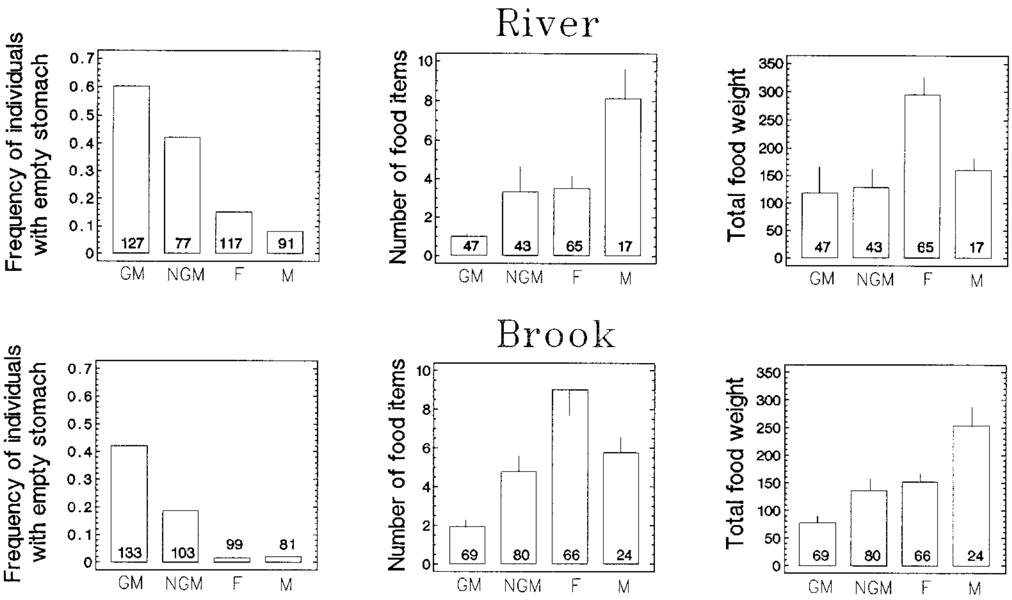

Fig. 1. Foraging opportunities of different groups of animals (*GM* = guarding males, *NGM* = non-guarding males in the breeding season, *F* = females in the breeding season, *M* = males outside the breeding season; *GM* + *NGM* = nesting males). *Numberals within columns* are sample sizes. The occurrence of empty stomachs differed significantly among groups (χ^2 test, $P<0.01$) with the exception of *F* versus *M* in both populations (river, $\chi^2=2.8$, $P=0.08$, NS; brook, $\chi^2=0.04$, $P=0.66$, NS). Excluding males with empty stomachs, the number of food items was significantly different among groups in both populations (Kruskall-Wallis ANOVA: river, $\chi^2=53.2$, $P<0.001$; brook, $\chi^2=72.2$, $P<0.001$). Each group differed from every other (Mann-Whitney *U*-test, $P<0.01$), with the exception of *F* versus *M* in the brook ($Z=1.55$, $P=0.11$). The total weight of food items in the stomachs was significantly different among groups in both populations (Kruskall-Wallis one-way ANOVA: river, $\chi^23=39.6$, $P<0.001$; brook, $\chi^2=48.8$, $P<0.001$). Each group differed from each other (Mann-Whitney *U*-test, $P<0.01$) with the exception of GM versus NGM in both populations (river, $Z=0.69$, $P=0.48$; brook, $Z=1.56$, $P=0.11$)

opmental stage of the first egg mass spawned in a nest was used to time the steps of the parental care cycle.

Evidences of filial cannibalism were derived from similarities in the developmental stage between ingested and guarded eggs. Although females river bullheads are not synchronized in their spawning, neighbouring males may guard eggs at the same developmental stage as those of the cannibalistic male. We therefore compared the frequency of concordance between developmental stage of embryos cannibalized and guarded by a parental male with the frequency of concordance between developmental stage of eggs cannibalized by that male and those guarded by a male found in the same area and at the same date. By convention we chose the nearest sampled guarding male.

For the purposes of this study, we define the parental care cycle as the period that starts when the male receives his first egg mass and ends when the last egg mass hatches.

In the river and the brook populations, four and seven additional fish samples were collected, respectively, at nearly regular intervals over the rest of the year. On each sampling occasion, both during and outside the breeding season, the whole study are was thoroughly searched for dead bullheads.

To obtain estimates of bullhead population density at the study area, a 30-m section was electrofished three or four times in different months of the year (Leslie's removal method; see Perini 1991 for details).

Parametric statistics were used except when departure from normality or lack of homogeneity of variance required non-parametric tests.

Results

Foraging opportunities and male condition

The river bullhead feeds mainly on small crustaceans, Oligochaeta and the nymphs and larvae of aquatic insects. Occasionally, larger individuals prey upon other fish species including conspecifics: during this study two large males were found each with a bullhead in their stomach; in one case the prey was a ovigerous female. The rate of food intake differed greatly between the two populations under study. In samples taken outside the breeding season, brook individuals were found to eat on average 54% more food than river individuals (river, $n=59$, mean ± SD = 0.118 ± 0.073 g; brook, $n=56$, 0.182 ± 0.124 g; $t=3.38$, $P<0.001$).

In both populations stomach contents, and hence presumably foraging opportunities, varied widely among different subsets of animals (Fig. 1). Nesting males (guarding plus non-guarding males) had empty stomachs more frequently than females (river, $\chi^2=51.4$, $P<0.001$; brook, $\chi^2=28.7$, $P<0.001$) or males outside the breeding season (river, $\chi^2=46.1$, $P<0.001$; brook, $\chi^2=35.5$, $P<0.001$). Even when nesting males foraged, the quantity of prey in their stomach was reduced. Among nesting males those guarding eggs experienced a significant reduction in foraging opportunities as compared to non-guarding males. Empty stomachs were more frequently found in the river than in the brook population, both among guarding and non-guarding males (guarding males: $\chi^2=8.88$, $P=0.003$; non-guarding males: $\chi^2=11.59$, $P=0.001$). In both populations the amount of food eaten by guarding males did not change during the parental cycle (river, $n=127$, $r=0.07$, NS; brook, $n=131$, $r=-0.13$, NS).

We also used multiple regression analysis (stepwise procedure) to test whether features of the nest (nest size,

Table 1. Correlation coefficients from a stepwise multiple regression of the weight of stomach contents (log transformed) and factors potentially affecting the rate of food intake of nesting males of the river bullhead

Variable	River $n=204$		Brook $n=234$	
	Correlation coefficient	P	Correlation coefficient	P
1. Date	+0.26	<0.0002	+0.08	NS
2. Water depth (cm)[a]	−0.16	<0.019	−0.07	NS
3. Number of egg masses	−0.13	<0.049	−0.28	<0.0001
4. Male total length (mm)	+0.03	NS	+0.04	NS
5. Nest size (mm^2)	+0.02	NS	−0.00	NS
6. Male density[b]	−0.00	NS	−0.05	NS

NS, not significant at $P>0.05$

[a] Water depth as measured at the nest site

[b] Calculated as the number of nesting males found less than 5 m from the male

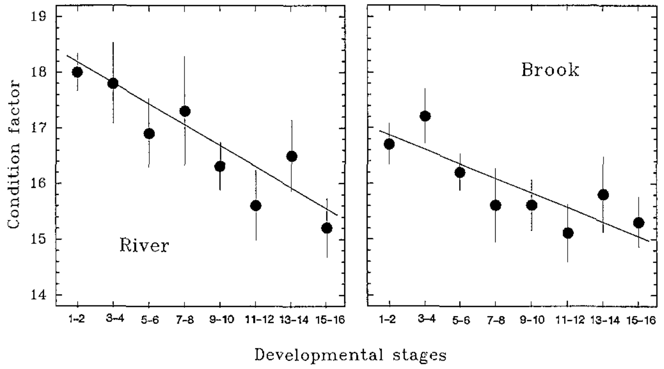

Fig. 2. Condition factor (*K*) of bullhead males guarding eggs at different developmental stages. *K* decreases with time elapsed since the first egg mass was spawned in the nest, i.e. with the progress of parental care. *Regression lines* calculated with all the data points (river $n=127$; brook $n=131$). *Vertical bars* ± SD

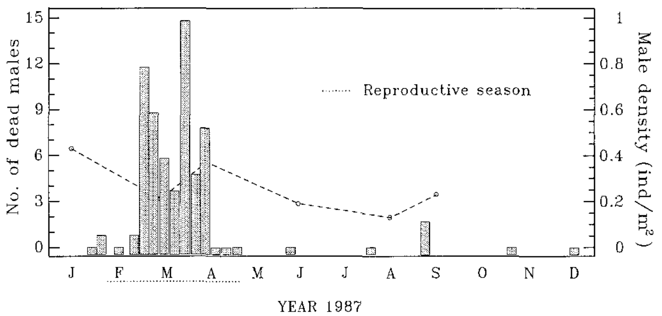

Fig. 3. Number of male bullheads found dead in the brook study area during the year. Searches for dead bullheads were made weekly from January to May and monthly for the rest of the year. The *broken line* is the estimate of male density on a section of the study area

water depth, density of males in the surrounding area), male size and mating status, and time of sampling, influenced the rate of food intake of nesting males (Table 1). In both populations the variable 'number of egg masses' was a significant predictor of the rate of feeding, thus confirming that males when involved in parental care ate less food. In the river two additional variables entered the model: a larger amount of food was eaten by males which nested in shallow water and later in the season.

In both populations the condition factor (*K*) of guarding males decreased with the time spent guarding (Fig. 2): river, $K=-0.18\ S+18.3$, $n=127$, $r=-0.39$, $P<0.001$; brook, $K=-0.12\ S+16.9$ $n=131$, $r=0.29$, $P<0.001$; where S is the developmental stage of the oldest egg mass found in the nest. Males at the end of the parental cycle showed the same average body condition in both locations (river, $N=13$, $K=15.2\pm1.9$; brook, $n=17$, $K=15.3\pm1.8$; $t=0.15$, $P=0.883$). However, males at the beginning of the parental cycle had a higher condition factor in the river than in the brook (river, $n=43$, $K=18.1\pm2.2$; brook, $n=42$, $K=16.7\pm2.4$; $t=2.92$, $P<0.005$) indicating a greater weight loss during parental care in this population.

The average condition factor did not differ between guarding and non-guarding males [Student *t*-test; river ($n=204$): $t=1.88$, NS; brook ($n=234$); $t=0.12$, NS]. This arises because recently spawned males have a higher condition factor than non-guarding males. In the river this difference is highly significant ($N=139$, $t=4.31$, $P<0.001$), in the brook it is only marginally significant ($N=171$, $t=1.94$, $P<0.054$). In both populations males smaller or larger than the average size lost weight at the same rate [two-way ANOVA, river: parental stage, $F(3,126)=6.9$, $P<0.001$; male size, $F(1,126)=0.72$, NS; interaction, $F=1.53$, NS. Brook: parental stage, $F(3,130)=3.87$, $P=0.01$; male size, $F(1,130)=1.68$, NS; interaction, $F=1.66$, NS].

Comparing the value of the condition factor of guarding males at the beginning of the parental cycle with that of males at the end of the cycle, we calculated that, on average, weight loss was about 18.8% in the river and 13.5% in the brook.

Dead animals were rarely found in the river, perhaps because of the relatively low population density in the river and of the presence, in this habitat, of predatory fish (e.g. the brown trout) that prey upon bullheads. All dead bullheads found in the brook were adults, and 91% were males despite a female-biased sex ratio at the study site (males:females, 1:1.4). Male mortality (Fig. 3) increased strongly by the end of March, in the middle of the breeding season, and remained high through April. Data on male density at the study site are also reported in Fig. 3: density changed little during the year, and this observation together with the fact that most dead animals were males suggests that the observed variation in male mortality is related to reproduction.

Egg cannibalism

During the spawning season 205 nesting males were collected in the river and 266 in the brook. Overall 38% of males in the river and 38.7% of males in the brook were without egg masses in their nest at the moment of capture.

Conspecific eggs were found in the stomach of 23% of males in the river and 16.2% in the brook ($\chi^2 = 3.42$, $df = 1$, $P = 0.06$). The analysis of eggs that had been eaten showed that they were always fertilized and in most cases showed a normal development. The maximum number of eggs found in one stomach was 50 ($n = 43$, average $\pm$ SD $= 14.0 \pm 15.4$) in the river and 75 ($n = 38$, average $\pm$ SD $= 14.3 \pm 17.8$) in the brook.

The percentage of cannibals among guarding males was 34% in the river and 28% in the brook; among non-guarding males the percentages were 3% and 5% respectively. The differences were highly significant in both populations (river, $\chi^2 = 24.9$, $P < 0.001$; brook, $\chi^2 = 22.6$, $P < 0.001$). Differences between populations in the frequency of cannibalism were not significant either for guarding males ($\chi^2 = 1.01$, $P = 0.31$) or for non-guarding males ($\chi^2 = 0.62$, $P = 0.43$).

The condition of the eggs found in the stomachs of guarding males was good enough to allow the determination of the developmental stage in 20 fish from the river and 23 from the brook. In 90% of river fish and 87% of brook fish the developmental stages of eggs in the stomach corresponded to the stage of egg masses in the male's nest. Pooling the two populations, there are five cases where the stages of eggs eaten differed from those in the nest. These guarding males very likely preyed upon eggs of others. Indeed, the average number of eggs found in their stomach was three times larger than that recorded for other guarding males (Mann-Whitney *U*-test, $n = 81$, $P = 0.003$).

The possibility that these males were heterocannibals cannot be excluded by these data alone, since egg developmental stages could be similar in the nest of neighboring males. In the river, the developmental stage of eaten eggs corresponded in 18 out of 20 cases with the stages of egg masses found in the cannibal's nest, and in 0 out of 20 cases with those found in the nest of a near-neighbour male ($\chi^2 = 32.7$, $P < 0.001$). In the brook, only 4 out of 23 cases showed a coincidence between eaten eggs and a neighbour's eggs, against 20 out of 23 cases of coincidence with the eggs present in the cannibal's nest ($\chi^2 = 22.3$, $P < 0.001$). A male's own nest is thus clearly the main source of conspecific eggs eaten by that male. The analysis of stomach contents of 65 river females and 66 brook females revealed no case of egg cannibalism, even though we observed that females readily ate unguarded eggs in the laboratory.

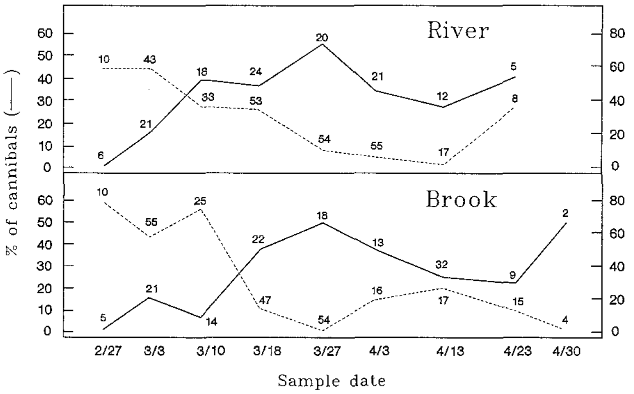

Fig. 4. Variations in the frequency of filial egg-cannibalism during the breeding season. The frequency of egg masses at developmental stage ≤ 2 is also reported. *Numbers* are sample size

The frequency of guarding males with eggs in their stomach (hereafter referred to as FC males) varied throughout the breeding season and followed a very similar pattern in the two populations (Fig. 4). The percentage of cannibals, very low at the beginning of the season, increased constantly and reached a maximum by the end of March, then dropped, to rise again towards the end of April. There was a inverse relationship between the frequency of cannibals and the frequency of males at the beginning of the parental cycle in both populations (river, $n = 8$, $r = -0.68$, $P = 0.05$; brook, $n = 8$, $r = -0.92$, $P < 0.001$).

The occurrence of cannibalism is also apparently related to food availability. In both populations cannibals were significantly less frequent among males that have at least one other food item in their stomach than among males with otherwise empty stomachs (river, $\chi^2 = 3.92$, 1 *df*, $P < 0.05$; brook, $\chi^2 = 3.98$, 1 *df*, $P < 0.05$).

The occurrence of cannibalism increases with time since the onset of parental care. In both populations we found a significant relationship between percentage of cannibals (CAN) and developmental stage (*S*) of the first egg mass laid in the nest (River: CAN $= 2.98\ S + 17.0$, $n = 16$, $r = 0.55$, $P = 0.03$; brook: CAN $= 3.63\ S + 3.32$, $n = 16$, $r = 0.66$, $P = 0.006$).

Discriminant analysis (Table 2) confirmed the effect of time elapsed since the beginning of parental care on the probability of a male cannibalizing its own eggs. The longer the male guarded, the more likely he was to cannibalize. For the brook, this was the only variable that entered the model, while for the river the variable "water depth" at the nest site also significantly affected the incidence of egg cannibalism: males in deeper water were more likely to feed on their own eggs.

Among river FC males, the number of cannibalized eggs increased with the number of egg masses in the nest. Brook males that had a chance to eat other food tended to eat fewer eggs (Table 2). In both cases the explained variance in the number of cannibalized eggs is low (13% in the river and 10.3% in the brook).

Table 2. Variables tested for their effect on the occurrence of cannibalism (discriminant analysis) and on the number of eggs eaten (multiple regression, stepwise procedure on guarding males with eggs in their stomachs only)

Variable	Dependent variable: cannibal/non-cannibal				Dependent variable: number of eggs eaten			
	River ($n=125$)		Brook ($n=129$)		River ($n=41$)		Brook ($n=34$)	
	F	P	F	P	r	P	r	P
1. Egg mass dev. stage[a]	8.11	<0.005	19.7	<0.0001	+0.07	NS	−0.00	NS
2. Water depth (cm)[b]	6.5	<0.008	0.1	NS	−0.04	NS	−0.02	NS
3. Food	3.5	NS	1.6	NS	−0.12	NS	−0.32	<0.04
4. Number of egg masses	0.4	NS	1.2	NS	+0.36	0.018	−0.06	NS
5. Male total length (mm)	0.22	NS	0.3	NS	+0.25	NS	−0.22	NS
6. Male density[c]	0.1	NS	0.1	NS	−0.07	NS	+0.20	NS
7. Date	0.0	NS	0.2	NS	−0.13	NS	+0.05	NS

NS, not significant at $P>0.05$

[a] Developmental stage of the first egg mass spawned in the nest

[b] Water depth as measured at the nest site

[c] Calculated as the number of nesting males found less than 5 m from the male

We tested whether cannibalized eggs were at an earlier developmental stage than other eggs in the nest. Since nests containing multiple egg masses at different stages were too few to analyse each population separately, the data from the two populations were pooled. In 13 cases cannibalized eggs were younger than the average age of eggs in the nest, in 6 they were older and in 4 the eggs were at the same developmental stage. The difference between the age of eaten eggs and the age of eggs in the nest is not significant (paired t-test, $n=23$, $t=1.98$, $P=0.06$).

In the laboratory, the complete digestion of eggs took 22–24 h at a water temperature of 13–14° C (unpublished data). Using the average number of eggs eaten by males with egg masses at different developmental stages, we estimated that a male guarding a single egg mass would eat in total an average of 98.2 eggs in the river and 97.1 eggs in the brook. Since, for males with multiple clutches, parental care lasted longer than the time necessary for the development of a single egg mass (at 13° C, river: +2.86 days, brook: +2.95 days) in this case the average number of eggs eaten during one parental cycle would increase to 117.3 and 128.9 respectively. These numbers correspond to about one-fifth of the average egg mass (638 eggs) spawned in the river, and to half of the average egg mass (272 eggs) spawned in the brook.

Temporal pattern of spawnings

A total of 254 egg masses were found in the river and 293 in the brook. In the same nest there was a strong tendency for egg masses to be spawned in quick succession (Fig. 5). Thus in both populations in about 90% of cases the age difference between one egg mass and the next one spawned in the same nest was 2 developmental stages, i.e. 48 h or less. In more than 90% of cases the difference between the first and the last egg mass spawned in the nest was less than 6 stages, i.e. 6 days. In 61.4% of cases in the river, and 59.1% in the brook, the difference was only 2 stages. In both populations the frequency distribution of differences between the first and the last egg mass was significantly different from that expected if the laying of an egg mass was unaffected by the presence of other egg masses (river, $\chi^2=57$, 5 df, $P<0.001$; brook, $\chi^2=56.4$, 5 df, $P<0.001$).

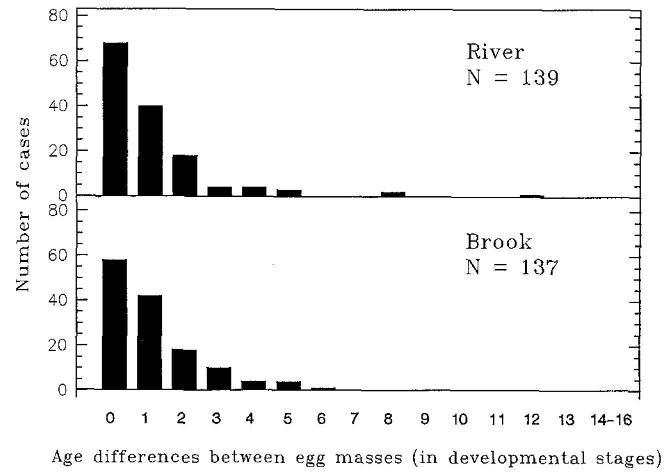

Fig. 5. Synchronization of egg mass deposition in the same nest. *Histograms* are frequencies of differences in the developmental stage of two masses spawned consecutively in the same nest

Discussion

Our data suggest that high rates of egg cannibalism in river bullhead populations are mainly due to cases of male filial cannibalism. The importance of this phenomenon for the reproductive strategy of this fish is confirmed by its occurrence in populations that live in different habitats and by the observation that the average number of eggs eaten by a male during the parental cycle represents a significant portion of its mating success. According to Rohwer (1978) filial cannibalism is expected to occur in fish species in which parental care imposes a strong reduction in foraging opportunities, leading to a deterioration in the physical condition of the parent. In the bullhead, nesting males showed a strong reduction in their food intake compared to other individuals of the population both during and outside the breeding season, and the reduction was more evident for males guarding eggs. Thorp et al. (1989) showed a reduction in foraging activity of nesting versus non-nesting males in two sunfish species, and Petersen (1990) observed a significant reduction in the feeding rate of guarding versus non-guarding male damselfish. Similar evidence exists for other fish species (Qasim 1957; Worgan and FitzGerald 1981; De Martini 1987; Mrowka 1987). Reduced food intake is presumably frequent in fishes with parental care. In both our bullhead populations, the weight of stomach contents decreased with the number of egg masses in the nest, possibly as a consequence of increased effort invested in parental care. This result is predicted by the parental-investment theory, according to which a positive correlation between level of parental care and offspring number is expected (Trivers 1972; Sargent and Gross 1985, 1986).

As a consequence of intense parental care (mainly fanning activity) and reduced food intake, bullhead males showed a strong deterioration in their physical condition. The deterioration was accentuated in the less productive habitat (the river). The average weight loss of guarding male bullheads in this study was estimated to be 13.5% and 18.8% of the total body weight in the brook and the river respectively. These values are similar to those recorded in other fishes with paternal care of eggs, e.g. the fathead minnow *Pimephales promelas* (weight loss = 17%; Unger 1983) and the sand goby *Pomatoschistus minutus* (weight loss = 14%; Lindstrom and Hellstrom 1993). We suggest that the increase in the mortality of male bullheads at the end of the breeding cycle is at least in part caused by the deterioration in their physical condition. A high cost of parental care, measured as a decrease in parental condition, survival and growth rate has been recorded in other fish species (Qasim 1957; De Martini 1987; Blumer 1986; Coleman and Fischer 1991) and high mortality rates during breeding and immediate post-breeding period are not uncommon among fishes (Wootton 1990).

Filial cannibalism is generally thought to occur in brood-cycling species where the energetic gain obtained by eating some eggs can be used in the subsequent parental cycle (Rohwer 1978). However bullhead males perform only one cycle of parental care during each reproductive season (Morris 1955; Marconato 1986). In bullheads male mortality increases during the breeding season and deserted egg masses are quickly preyed upon by other conspecifics (Marconato and Bisazza 1988). Thus, the observed filial cannibalism in this species, and possibly in other non-brood-cycling fishes with long and costly parental care, might be interpreted as a behaviour performed by the parent to avoid the risk of dying by starvation before the eggs hatch.

If filial cannibalism is mainly a response to food shortage, those individuals which succeed in obtaining food are expected to show reduced filial cannibalism. In both bullhead populations a significant reduction in filial cannibalism was observed among males found with other food items in their stomach. In the river population males nesting in deep water ate less food and this could explain why they were more often cannibals. While most studies on filial cannibalism suggest a relationship between filial cannibalism and amount of food available to the parent, Belles-Isles and FitzGerald (1991) suggested that by eating eggs, male threespine stricklebacks gain access to nutrients that are lacking in other food items.

During our study, filial cannibalism increased with the progress of parental care and with the decline of male physical condition. We suggest that the higher rate of filial cannibalism by male river bullheads at advanced stages of the parental cycle is the consequence of the accumulating effect of reduced food intake throughout the parental care cycle.

The number of eggs in the nest should not influence the rate of filial cannibalism (Rohwer 1978). However, in one of the two populations we found that the number of eggs eaten was positively correlated with the number of egg masses in the nest. An explanation of this is that males with multiple masses have longer parental cycles, as different masses hatch at different times, and thus they incur a higher cost of parental care compared to males that have only one or few egg masses. It is also possible that a larger number of eggs in the nest needs a larger amount of care (e.g. fanning, cleaning) and demand more energy investment by the male. Fanning the eggs to provide oxygen is a depreciable care (*sensu* Clutton-Brock 1991) and in at least one species its rate has been demonstrated to increase with the number of attended eggs (Coleman and Fischer 1991).

Some of the predictions of filial cannibalism theory are based upon the idea that in species where filial cannibalism is important to maintain the parent in good condition, small parents, other things being equal, should require fewer eggs for their own maintenance than large parents (Rohwer 1978). However, in species in which males accumulate fat stores at the beginning of the breeding season the opposite is expected. The data on both the filial cannibalism rate of small versus large males and on the decline in their condition during the parental cycle suggest a lack of parental-size effect on filial cannibalism in the river bullhead.

According to the filial cannibalism theory, males should preferentially eat younger eggs in a mixed-age group of clutches because they require a longer parental investment as compared to older clutches. Evidence for this selective filial cannibalism has been found in a few studies (Petersen and Marchetti 1989; Petersen 1990). Our results raise the possibility that this occurs in bullheads, but the data are not conclusive due to the small sample size. However, considering that egg masses are at very similar developmental stages and are closely clumped, and that bullheads have very large mouths unsuited to picking up small food items such as individual eggs, we do not expect this species to be able to select cannibalized eggs on the basis of their age.

In both populations a large variance in nesting male density was observed. We expected that the presence of other nesting males in close proximity influenced both the rate of food intake and the amount of energy spent in nest defence, and hence the occurrence of filial cannibalism. However, our data did not support these conclusions in *Cottus gobio*.

If patterns of filial cannibalism are predictable, then females are expected to adopt tactics that reduce the probability that their own eggs will be eaten by the guarding male. First, females should prefer males that are in better condition and hence not likely to cannibalize eggs (Rohwer 1978). We do not have direct evidence for this female preference in *C. gobio*. However, males that have just spawned have higher condition factor values than unmated males, thus suggesting the existence of female choice for males with higher energetic reserves.

Another important prediction is that females will prefer males that already have eggs in their nests. While in other species the reason why females choose nests with eggs is still a matter of controversy (Ridley and Retchen 1981; Jamieson and Colgan 1989; Goldschmidt and Bakker 1990; Belles-Isles et al. 1990), in the bullhead female preference for males whose nest contains eggs has been clearly demonstrated (Marconato and Bisazza 1986; Bisazza and Marconato 1988) and is interpreted as a female tactic to dilute the effect of filial cannibalism on the female's own eggs. Females should also avoid nests with late-stage egg masses because males may preferentially eat younger eggs. As a consequence of this behaviour we might expect a synchronization of the developmental stages of masses present in the same nest. In both bullhead populations, strong synchronization of egg deposition in the same nest was observed. Laboratory observations suggest that the mechanism by which females localize nests with freshly spawned egg masses involves chemical cues. During spawning, females release pheromones that attract other ripe females to their nest (Bisazza and Marconato 1987).

Though all these female tactics are consistent with the predictions of the filial cannibalism theory, there are other possible explanations. Female choice of males in better condition is a feature of sexual selection expected to occur in most species even if filial cannibalism is not present; the fitness advantage for the female is either increased progeny survival due to selection of a better parent, or increased genetic quality of the progeny, or both. Female preference for males with eggs in the nest is predicted also by the parental investment theory (Sargent and Gross 1986): male propensity to invest in parental care is expected to increase with the number of eggs in the nest, thus increasing offspring survival. Synchronization of the developmental stages of different egg masses in the same nest could be the consequence of females avoiding the risk of male desertion, if the male cannot sustain a period of parental care much longer than that necessary for the first egg mass to hatch.

While most authors have stressed the importance of filial cannibalism in constraining female mating tactics, the above considerations suggest that the situation is more complicated. Further studies on fishes with filial cannibalism should address, possibly with an experimental approach, the factors responsible for female mating tactics.

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