SHORT COMMUNICATION

Nutritional benefits of filial cannibalism in three-spined sticklebacks (*Gasterosteus aculeatus*)

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Abstract Although filial cannibalism (eating one's own offspring) occurs in numerous species, including several teleost fishes, its adaptive value is still not well understood. One often-discussed explanation is that individuals enhance their mass and body condition by consuming part of their eggs. However, evidence for this assumption is scarce thus far. In this study, male three-spined sticklebacks (*Gasterosteus aculeatus*), a species with paternal care, were allowed to care for a batch of eggs or for an empty nest under food-deprived conditions. All brood-caring males cannibalised at least part of their eggs and thus preserved their initial mass and body condition. Furthermore, mass as well as body condition was significant positively correlated with the number of cannibalised eggs. In contrast, empty-nest males that had no possibility to cannibalise eggs significantly lost mass and body condition. This is, to our knowledge, the first experimentally documented evidence that mass as well as body condition were preserved by filial cannibalism.

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Introduction

Cannibalism is widespread in the animal kingdom (Polis 1981). It is advantageous when conspecifics represent a food source for the cannibalistic individual (Klug and Bonsall 2007). In contrast, cannibalising relatives leads to a reduction of fitness. However, cannibalism of relatives is not uncommon (Pfennig 1997), leading to the assumption that in some cases the benefits of cannibalism outweigh its costs. A special form of cannibalism of relatives is filial cannibalism (the consumption of own offspring), which is particularly common in fishes (Klug and Bonsall 2007; Manica 2002; Sargent 1992; for insects: Thomas and Manica 2003). However, the adaptive value of filial cannibalism is still not well understood (Klug and Bonsall 2007). One explanation is that brood-caring individuals cannibalise dead or infected eggs to keep their clutch healthy (Kraak 1996; Wootton 1976). Furthermore, eggs might be cannibalised to decrease egg density and consequently improve survivorship of the remaining eggs (e.g. Bakker et al. 2006; Klug et al. 2006). Another possible adaptive value is that individuals enhance their body condition by filial cannibalism (see Manica 2002 for a review), although it remains unclear whether the energetic content of cannibalised eggs is large enough to lead to a persistent increase of mass or body condition (Klug and Bonsall 2007; Smith 1992). Male scissortail sergeants (*Abudefduf sexfasciatus*) reduced filial cannibalism when they were fed additionally (Manica 2004). However, they did not completely stop cannibal-

ising, suggesting that filial cannibalism in this species might be both a response to energetic demands of parental care and a form of cleaning behaviour (Manica 2004). In cardinal fish (*Apogon doederleini*), a decrease in males' condition during the breeding season came along with an increase of filial cannibalism (Okuda and Yanagisawa 1996), while common gobies (*Pomatoschistus microps*) cannibalised part of their eggs more often when they were kept under food-deprived conditions (Kvarnemo et al. 1998). However, these studies did not document a direct effect of cannibalism on the cannibal's mass and body condition. Klug and St Mary (2005) experimentally manipulated filial cannibalism in the flagfish (*Jordanella floridae*) by covering some nests with a mesh throughout the duration of the breeding season. Here, filial cannibalism did not affect body mass. Flagfish, though, spawn relatively few eggs; thus, energetic benefits of filial cannibalism are perhaps less important in this species. In a field study on long-snout clingfish (*Diademichthys lineatus*), males that increased body condition and size during the breeding cycle cannibalised more eggs (Gomagano and Kohda 2008). However, in this study, it could not clearly be discriminated whether cannibalistic males increased their body condition and size by cannibalising their offspring or whether faster growing males consumed more eggs. Direct evidence for an effect of filial cannibalism on the cannibal's mass and body condition is lacking thus far (Manica 2002).

The present study aimed to answer the question of how cannibalism influences changes in mass and body condition during the breeding cycle in three-spined stickleback (*Gasterosteus aculeatus*) males. In this species, males show paternal care during which they guard the brood for up to several weeks (Wootton 1976). Additionally, they clean the clutches and provide them with oxygen by fanning with their pectoral fins. These behaviours lead to high energetic costs as expressed by a higher energy expenditure of caring males (Smith and Wootton 1999). Furthermore, three-spined stickleback males reduce foraging and food intake during the breeding cycle (Wootton 1976). Consequently, they lose mass and body condition during this time (Sargent 1985; Smith and Wootton 1999), although there is some variation within and between population (Sparkes et al. 2008). To reduce this loss, males might cannibalise at least part of their own eggs as an investment in future reproduction (Rowher 1978; Whoriskey and FitzGerald 1985). Indeed, filial cannibalism occurs frequently in this species (Frommen et al. 2007; van den Assem 1967; Whoriskey and FitzGerald 1985). In the present study, three-spined stickleback males were allowed to care for a nest containing their own eggs or for an empty nest under food-deprived conditions. The number of consumed eggs was estimated, and changes in mass and in body condition during the breeding cycle were calculated, allowing us to draw conclusions on the influence of cannibalism on changes in these variables.

Materials and methods

Experimental subjects and design

About 500 three-spined sticklebacks from an anadromous population were caught during their spring migration in April 2006 on the island of Texel, the Netherlands, and were brought to the lab. Here, both sexes were kept together in a large outside-tank (750 l) with air ventilation and a constant supply of tap-water at a flow rate of $3 \ l \ min^{-1}$. They were fed with *Chironomus* spp. larvae daily in excess.

Experiments were conducted between July and August 2006. Holding tanks ($40.5 \times 20.5 \times 25$ cm) were placed in an air-conditioned room under summer conditions (day length 16L/8D, temperature 17 ± 1°C). Tanks were separated from each other by grey opaque partitions. Each tank contained 16.5 l of tap-water, one sand-filled Petri dish ($\varnothing$ 9 cm), an airstone and 2 g of java moss (*Vesicularia dubyana*) for nest-building. One nuptial-coloured male was placed into each tank. Nest-building of all males was stimulated daily by presenting a gravid female for 15 min. After the males had finished building their nest in the Petri dish, they were haphazardly allocated to one of the two treatments: 22 males were allowed to spawn with a single female, and 18 males were not allowed to receive any eggs. Afterwards, males were removed from their tanks to measure their standard lengths (SL) and masses (M_1). Changes in mass might be dependent on males' SL. Therefore, we additionally calculated their body condition (BC_1) as $BC = 100 M[g] / SL[cm]^3$ following Bolger and Connolly (1989). After that, males without eggs were returned to their tanks, where they re-started caring for the empty nest. Males with eggs were put in a dark room to minimise stress. The Petri dishes containing the nests of these males were taken out of the tank to determine the number of eggs. The nests were opened at the bottom, and eggs were removed carefully and stored in tap-water. The total egg mass per nest was measured to the nearest milligramme. Furthermore, a counted sub-sample of 35 eggs was weighed, and the average mass of one egg was calculated to determine the number of eggs from the total mass of the brood (Frommen et al. 2007; Kraak et al. 1997). Thereafter, all eggs were returned to the male's nest. Finally, the repaired nests and the males were returned to their tanks. Males were at least 30 min and at most 90 min separated from their nest. Of 22 males, 19 started brood-caring behaviour after being re-introduced, suggesting that they accepted their nests after manipulation. These males cared for their nest during the

whole experiment, which lasted 7 days (±1 h). Three males did not re-accept their nest but rather destroyed it completely. They were excluded from further analysis. Three-spined stickleback males reduce foraging and food intake while brood-caring. To simulate natural conditions, food ration of all males was reduced to 30 Chironomus spp. larvae every second day, which has been shown to be a mild food limitation in previous studies (Feuth-de Bruijn and Sevenster 1983; Frommen et al. 2007). After 7 days, the degree of cannibalism was determined by counting the number of all surviving eggs. As the growth rate during the short time span of 7 days under food-deprived conditions is negligible for adult three-spined sticklebacks (Allen and Wootton 1982), SL was not determined again after the experiment. However, M_2 and BC_2 were determined as described above and the gain or loss of M and BC was calculated.

Data analyses

Parametric statistics were applied when data did not significantly deviate from normal distributions according to Kolmogorov–Smirnov tests with Lilliefors correction. Cohen's effect size d (Cohen 1992) was calculated for the comparison of body measurements of the two groups of males, i.e. with and without eggs. For analyses, the SPSS 12.0 statistical package was used. p values are two-tailed throughout.

Results

At the beginning of the experiment, males with and without eggs did not differ significantly in SL, M_1 and BC_1 (Table 1). After the experiment, they did not differ significantly in M_2, but differed significantly in BC_2

(Table 1). The effect size was largest for differences in BC_2 (Table 1).

All brood-caring males cannibalised at least part of their clutch (ranging from 43% to 100% of the clutch). Mass (paired t test, $N=19$, $t=0.676$, $p=0.508$, Fig. 1) and body condition (paired t test, $N=19$, $t=0.946$, $p=0.357$, Fig. 1) of these males did not significantly change during the experiment. In contrast, males without eggs showed a significant decline in mass (paired t test, $N=18$, $t=10.676$, $p<0.001$, Fig. 1) and in body condition (paired t test, $N=18$, $t=9.991$, $p<0.001$, Fig. 1). Cannibalising males showed a significantly different change in mass (t test for unequal variances, $N_1=19$, $N_2=18$, $t_{23.719}=3.231$, $p=0.004$, Fig. 1) and in body condition (Mann–Whitney U test, $N_1=19$, $N_2=18$, $z=-3.016$, $p=0.003$, Fig. 1) compared to males without eggs. Furthermore, their change in mass (Pearson correlation, $N=19$, $r_p=0.763$, $p<0.001$, Fig. 2) and in body condition (Pearson correlation, $N=19$, $r_p=0.775$, $p<0.001$, Fig. 2) was positively correlated with the number of cannibalised eggs.

Partial and full clutch cannibals did not differ significantly in their initial mass and body condition (Student's t test, $N_{partial}=7$, $N_{total}=12$, $t_{17}=1.182$ and 0.507, $p=0.254$ and 0.618, respectively) or in change of mass and body condition during the experiment (Student's t test, $N_{partial}=7$, $N_{total}=12$, $t_{17}=0.754$ and 0.571, $p=0.461$ and 0.575, respectively). Furthermore, initial clutch size of partial and total cannibals did not differ significantly (Student's t test, $N_{partial}=7$, $N_{total}=12$, $t_{17}=0.450$, $p=0.658$).

Discussion

Filial cannibalism has been frequently discussed as a foraging strategy in many animal species (Klug and Bonsall 2007; Rowher 1978; Sargent 1992). However, although it

Table 1 Results of the Student's t tests comparing body measurements of the two groups of males

		∅	SD	t	p	d
SL [cm]	With eggs	5.23	0.37	−0.993	0.328	−0.326
	Without eggs	5.35	0.39			
M1 [g]	With eggs	1.81	0.40	−0.375	0.710	−0.123
	Without eggs	1.86	0.45			
M2 [g]	With eggs	1.80	0.41	0.087	0.931	0.028
	Without eggs	1.78	0.44			
BC1	With eggs	1.25	0.09	1.851	0.073	0.594
	Without eggs	1.19	0.09			
BC2	With eggs	1.24	0.09	3.139	0.003	1.037
	Without eggs	1.14	0.09			

At the beginning of the experiment, males with eggs ($N=19$) and without eggs ($N=18$) did not differ significantly in SL, M_1 and BC_1. After the experiment, the males did not differ significantly in M_2, but they differed significantly in BC_2. Given are means (∅) ± standard deviations (SD) and Cohen's effect size d
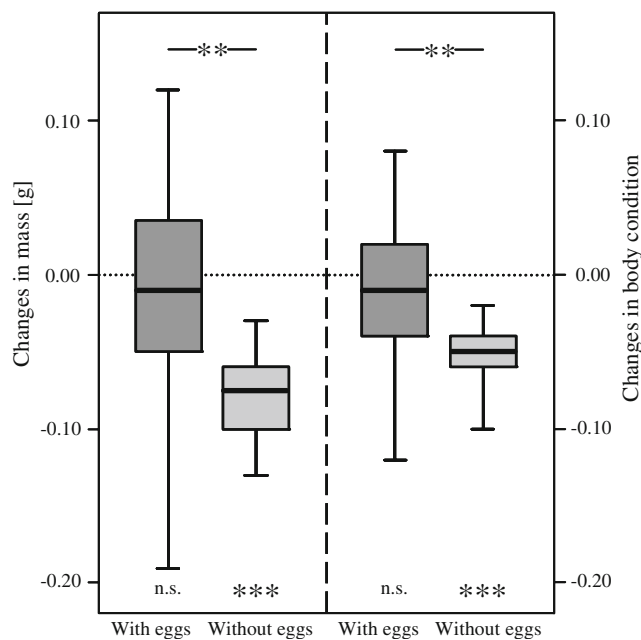
Fig. 1 Changes in mass and in body condition of males with eggs (*dark*) and without eggs (*light*) in their nests. Given are medians, quartiles and total range. *Upper statistics*: differences between the treatments. *Lower statistics*: differences between the first and second measurement of the respective males. *n.s. p>0.1, **p<0.01, ***p<0.001*
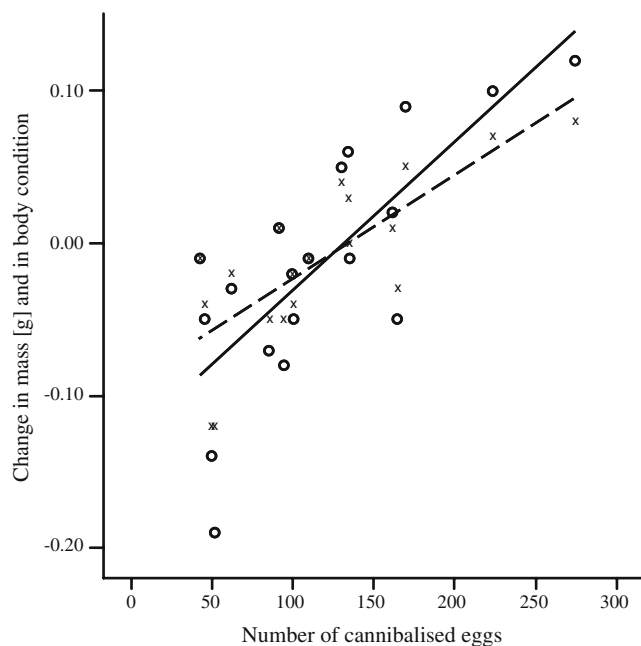
Fig. 2 Significant positive Pearson correlation of the number of cannibalised eggs with change in mass (*circles*) and in body condition (*crosses*). Egg cannibalism occurred in each experiment. The *solid line* represents the fitted linear regression of the changes in mass; the *dashed line* represents the fitted linear regression of the changes in body condition

has been shown that the rate of cannibalism increases with a decrease in body condition (see Manica 2002), direct evidence for a beneficial effect of filial cannibalism on body condition is scarce thus far. This study showed that males which cannibalised their own eggs preserved their initial mass and body condition, while nest-tending males without eggs showed a significant decline in these variables during the 7-day experiment. Furthermore, there was a positive correlation between changes in mass and body condition and the number of cannibalised eggs, which is in accordance with a recent study on long-snout clingfish (Gomagano and Kohda 2008).

In general, one can distinguish total and partial filial cannibalism. Partial filial cannibalism might represent an investment into present as well as future broods (Sargent 1992). Cannibalistic males might consume part of their eggs in order to be able to provide better care for the surviving eggs. Furthermore, cannibalistic males might be able to start a new breeding cycle faster (Manica 2002). In contrast, total filial cannibalism can only be an investment into future reproduction (Sargent 1992). Sticklebacks in this study consumed between 43% and 100% of their eggs. Partial and total cannibals did not differ in initial body measures or changes therein during the breeding cycle. Furthermore, clutch size of these males did not differ significantly, which is in contrast to a number of studies showing an effect of initial clutch size on partial and total filial cannibalism (reviewed in Manica 2002, but see Manica 2003 and Payne et al. 2003 for contrasting results). Thus, the cause of the decision for partial or total cannibalism remained unclear in this study.

One alternative explanation for the difference in loss of mass and body condition between parental and empty-nest males might be that they faced different behavioural tasks during the experimental phase. Whilst males with eggs mainly cared for the clutch (that is fanning behaviour, cleaning the eggs and repairing the nest), males without eggs modified the nest and occasionally performed fanning behaviour as part of courtship. However, brood-caring behaviour in sticklebacks is known to come along with an energetic effort that is assumed to be higher than the energy needed by non-caring males (Smith and Wootton 1999). Thus, one should have expected a higher loss in body condition in males caring for eggs, which was not the case. The set-up was thus conservative with respect to the different behaviours of males with and without eggs. Additionally, the positive correlation between the number of consumed eggs and changes in mass and body condition further strengthens our main argument.

In summary, this study indicates that male three-spined sticklebacks counter-balance the loss of mass and body condition during brood-care by cannibalising parts of their eggs. As sticklebacks' behaviour and ecology vary both

within and between populations (Belles-Isles and FitzGerald 1991; Dingemanse et al. 2007; Foster et al. 1998; Sparkes et al. 2008), an interesting follow-up study would be to examine under which circumstances such benefits of filial cannibalism occur under natural conditions.

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