The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*

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Abstract. Theoretical arguments concerning the evolution of parental care depend on the relative costs of caring to the two sexes. In this study experimental manipulations of parental care were used to compare the costs of care between the sexes in the biparental St Peter's fish. For both males and females parental care had costs to growth and increased the number of days until the next reproductive cycle. In females, care also decreased subsequent fecundity, as expected from an observed positive correlation between female fecundity and body weight. The results provide strong evidence for high costs of care for females and distinguish between two components of the costs of reproduction: the costs of gamete production and the costs of care.

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Comparing the benefits of parental care (increased offspring survival) and its costs (reduced survival, energy intake and opportunities to mate) for males versus females in a species where either sex can care for young is one way of attempting to understand the evolution of parental care patterns (Gross & Sargent 1985; Clutton-Brock 1991). Few species, however, show such flexible care behaviour and where both sexes care for offspring, each sex may care in a different way. In this study I investigated the costs of care in the biparental cichlid fish, St Peter's fish, a species with flexible parental care patterns and in which both sexes exhibit identical care behaviour (mouth brooding; Trewavas 1983). I compared the costs to males and females by experimentally manipulating parental effort while controlling environmental quality and body size.

Male and female St Peter's fish usually divide the clutch at spawning, incubating about half each. Either parent can, however, and occasionally does, desert after spawning, leaving its partner to care alone. Therefore, spawning may be followed by one of three patterns of care: biparental care, male-only care or female-only care.

Other fish studies provide a useful indication of which activities are likely to be costly for each sex. For example, egg production is thought to be substantially more energetically costly than sperm production (Blumer 1986) and consequently, females would be expected to bear a larger energetic cost in gamete production. In

St Peter's fish, oral incubation prevents feeding and so is costly to both sexes (Johnson 1974). Reduced feeding is presumably experienced to the same degree in both sexes, but the consequences and hence fitness costs, of starvation may differ between the sexes. Parental care may, for example, reduce a parent's growth rate, which may have important consequences for future fecundity in females and future mating success for males (Gross & Sargent 1985; Berglund & Rosenqvist 1986). In most species the maximum reproductive rates of males are typically higher than those of females, so males probably incur higher costs in lost mating opportunities during parental care (Gross & Sargent 1985). For both sexes the direct costs of caring probably end at the same stage, when the young are released: unlike other cichlids, parental St Peter's fish do not continue to guard the young once they have been released from the parent's mouth (Keenleyside 1991).

This is the first study on a biparental cichlid to distinguish between the costs of parental care in the two sexes and to examine how these affect future reproductive attempts.

METHODS

Female Costs: Experiment 1

I carried out the study between May and September 1993 on the banks of Lake Kinneret

in northern Israel using 70 individual fish. I used a concrete pond measuring 13×4.5 m (part of the facilities of the Israeli Ministry of Agriculture's Experimental Fisheries Station) which was dried and scraped clean of algae prior to the experiment. The pond had a continual flow of fresh water from Lake Kinneret, providing a semi-natural environment. The experiment was performed in natural daylight, which varied between 14:10 and 12:12 h light:dark. Water temperatures during the experiment ranged from 24 to 30°C and dissolved oxygen levels varied from 7.1 to 8.3 ppm. Each was monitored weekly. Although the lake water contained high concentrations of phytoplankton, the diet of the fish was supplemented by the addition of 10 g of soya pellets to each enclosure each day. This supplemental feeding was intended to improve fish condition and stimulate spawning.

Fish were collected in April 1993 from Lake Kinneret, Israel, with the assistance of fishermen. After capture, the fish were anaesthetized (with Ethyl p-Aminobenzoate (Benzocaine), marketed by Sigma), sexed, measured and tagged behind the dorsal fin with a unique Carlin numbered tag (Neal, Finchley, London). Pairs of fish (one male and one female) were placed in each of 32 plastic fence enclosures in the pond. Each enclosure had a diameter of 1.5 m and a height of 70 cm. The plastic fence allowed water to flow through the enclosure. Rocks placed in the enclosure provided spawning sites and hiding places for the fish.

I randomly assigned pairs to one of two treatment groups: (1) non-caring group (broods of eggs were removed from their mouths on the day of the spawn); (2) caring group (broods of fry were removed 10 days after spawning). After the removal of eggs or fry the pairs in both treatments were left together to re-spawn. The second spawning was recorded, second broods were removed and the parents were reweighed. Egg removal did not in itself induce re-laying (personal observation).

Sometimes the fish spat out the eggs/fry before the entire brood could be collected. In eight (caring treatment) and 12 (non-caring) cases entire broods were removed for both spawns facilitating comparisons within individuals between spawns. All eggs and fry collected were weighed on an analytic balance and counted, and 10 eggs/fry from each brood were measured (total length and width). Broods were then dried in a drying oven for 24 h at 100°C and reweighed.

Fish collected during routine sampling with fishermen during June, July and August 1993 in the northern basin of Lake Kinneret (known as 'the Betecha') were measured and their gonads removed and examined to investigate how body size affects fecundity in females and testes weight in males.

Male Costs: Experiment 2

I conducted the second experiment between 5 May and 30 July 1994 using the same concrete pond, enclosures and fish tagging techniques as in the previous experiment. Natural daylight again varied between 14:10 and 12:12 h light:dark. Water temperature during the experiment ranged from 22 to 31°C and was monitored daily. The diet of the fish was supplemented by the addition of 20 g/day of soya pellets to each enclosure each day.

One male and one female were placed in each of the 32 fenced enclosures in the pond. Some enclosures were used twice in the experiment. I randomly assigned males to one of two treatment groups: (1) non-caring group (egg broods were removed from their mouths 1 day after the spawn); (2) caring group (broods were not removed). All females were also removed 1 day after they spawned and a secondary female with swollen genitalia and abdomen (indicating readiness to spawn) was added to each enclosure. The new pairs in both treatments were then left together to re-spawn. Three 15-min focal watches were made of each pair (at 1, 3 and 24 h) after the second female was added. I recorded courtship and aggressive behaviour and the time each new pair spent in close proximity (less than one fish body length apart).

The second spawning was recorded, and 4 days later broods were removed for measurement and both sexes were reweighed. Again, all eggs and fry collected were counted and weighed on an analytic balance, and 10 eggs/fry from each brood were measured (total length and width). Broods were then dried in a drying oven for 24 h at 100°C and reweighed. In addition, the fertility rate between treatments was compared.

Table I. Size of broods of the caring and the non-caring groups in relation to the type of care given to each spawn in experiment 1

	Spawn 1	Spawn 2
Caring group		
Biparental care	14	12
Female-only care	3	3
Male-only care	3	2
Unknown	0	3
Total	20	20
Non-caring group		
Biparental care	8	9
Female-only care	4	3
Male-only care	2	1
Unknown	1	2
Total	15	15

Parents in the caring group had their fry removed on day 10 and non-caring parents had their eggs removed on day 0.

Figure 1. The inter-spawn interval (+SE) for caring and non-caring females.

Figure 2. Mean (+SE) change in brood weight for caring versus non-caring females between spawns.
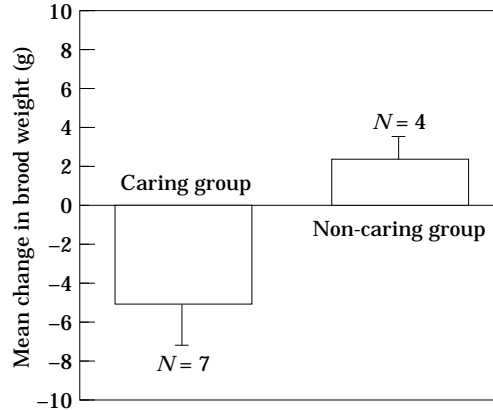
RESULTS

Female Costs: Experiment 1

Thirty-five pairs spawned in total, 20 pairs in the caring treatment and 15 pairs in the non-caring treatment. (The non-caring treatment included six pairs from a pilot study in the same pond and under similar conditions in June 1992.) Males were heavier than females in both treatments but individuals of the same sex did not significantly differ in weight between the two treatments ($\bar{X}$: caring group: males, 170·7 g, females, 148·2 g; non-caring group: males, 163·9 g, females, 132·3 g; two-way ANOVA: Sex, $F_{1,67}=16\cdot335$, $P=0\cdot0001$; Treatment, $F_{1,67}=2\cdot898$, $P=0\cdot10$, Treatment*Sex, $F_{1,67}=0\cdot462$, $P=0\cdot50$).

Providing care to one brood did not affect whether the subsequent brood received uniparental versus biparental care. In the second spawn (after the treatment) five of the 20 spawns resulted in uniparental care in the caring group and four spawns of 15 resulted in uniparental care in the non-caring group (Table I; $G=0\cdot10$, $df=1$, $P>0\cdot80$).

Caring had appreciable costs to females. First, the inter-spawn interval (mean number of days between spawns) was longer for females that cared (24 days) than those that did not (13 days; Fig. 1; Mann–Whitney U-test: $z= -4\cdot569$, $N_1=17$, $N_2=15$, $P=0\cdot0001$).

Second, caring had costs to females in terms of subsequent relative fecundity. Caring females were more fecund in their first brood (7 of 8 cases) than in their second whereas non-caring females laid more eggs in their second brood (9 of 12 cases; $G=5\cdot52$, $df=1$, $P<0\cdot02$). (The range of change in fecundity was from -830 to $+656$ fry for caring females and -348 eggs to $+1395$ eggs for non-caring females.)

Third, caring reduced the weight of the subsequent brood conferring a further cost on females. Six out of seven caring females had lighter broods (average reduction$=5\cdot2$ g wet weight) the second time around while all four non-caring females had heavier broods (average increase$=2\cdot3$ wet weight; Fig. 2; Fisher's exact test: $P=0\cdot023$). Both the magnitude and direction of change were significant (Mann–Whitney U-test: $z= -2\cdot378$, $P=0\cdot02$).
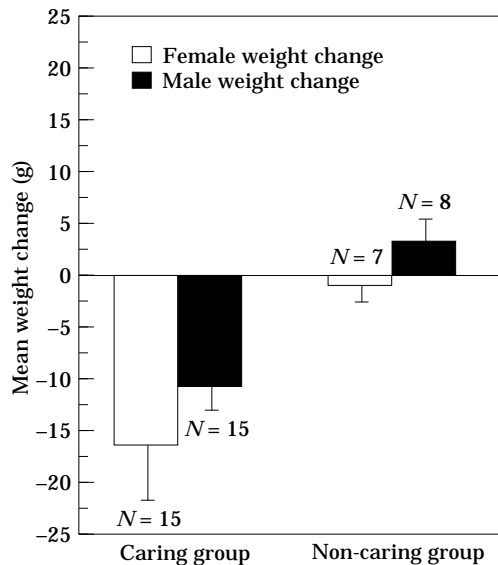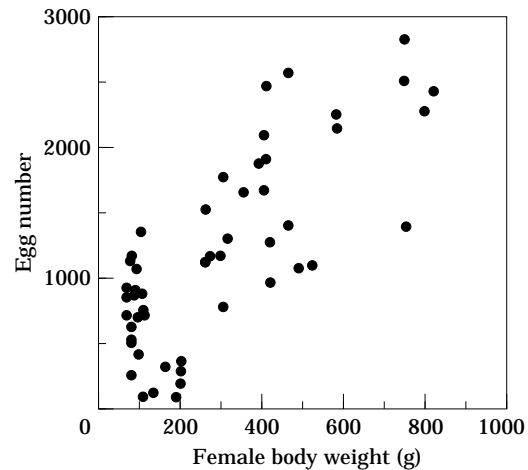
Figure 3. Comparison of weight loss between males and females and between caring and non-caring individuals.

Figure 4. Female fecundity in relation to body size ($r_S = 0.687$, $N = 51$, $P = 0.0001$).

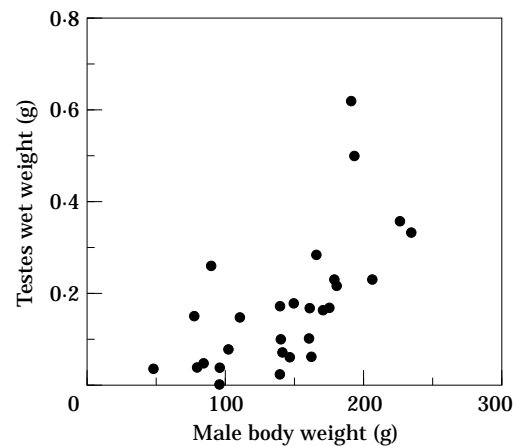**Figure 5.** Testes size in relation to male body weight ($r_S = 0.718$, $N = 28$, $P = 0.0002$).

Neither caring nor non-caring females varied the size of fry/eggs produced between the first and second spawns ($\overline{X}$ length × width (mm); caring females: spawn 1, 8.7×2.5 mm, spawn 2, 8.9×2.2 mm: non-caring females; spawn 1, 2.4×1.9 mm, spawn 2, 2.5×1.9 mm). Three out of seven caring females and two out of four non-caring females examined had larger offspring in their second broods (Fisher's exact test: $P > 0.45$). Thus, caring females laid lighter clutches than non-caring females, by producing fewer but not smaller offspring.

Fourth, females lost weight between spawns whether or not they provided care, but the weight loss was significantly greater in those females that did care (Fig. 3; Mann–Whitney U-test: $z = -2.502$, $N_1 = 15$ caring females, $N_2 = 7$ non-caring females, $P = 0.01$). Female body weight was positively correlated with fecundity, heavier females laying more eggs (Fig. 4).

Caring had similar costs for males: caring males lost weight but non-caring males on average gained weight (Fig. 3; Mann–Whitney U-test: $z = -3.292$, $N_1 = 15$ caring males, $N_2 = 8$ non-caring males, $P = 0.001$). The weight loss caused by care may affect subsequent reproductive performance as females prefer the largest available mate (unpublished data). It is possible that large males are more fertile since body size is correlated with testes weight (Fig. 5), but this has not been investigated.

Females who provided care did not lose more weight than caring males (Fig. 3; Mann–Whitney U-test: $z = -0.871$, $N_1 = 15$ caring males, $N_2 = 15$ caring females, $P = 0.38$). Non-caring males and females did not lose or gain significant weight (Mann–Whitney U-test: $z = -1.27$, $N_1 = 8$ non-caring males, $N_2 = 7$ non-caring females, $P = 0.20$).

Male Costs: Experiment 2

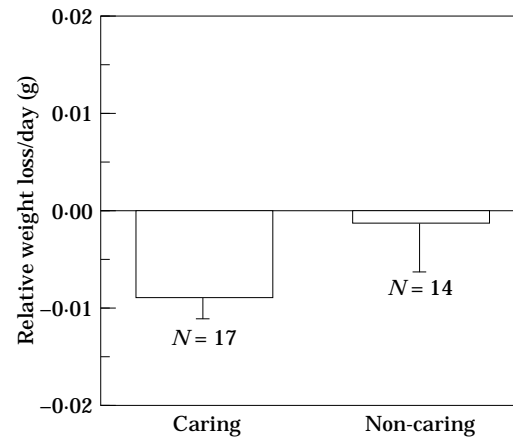Thirty-four males and 68 females spawned in this experiment.
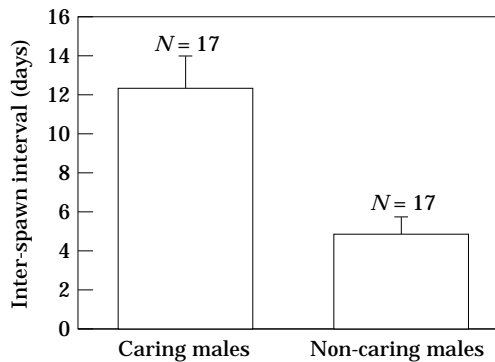
Figure 6. The inter-spawn interval (+SE) for caring and non-caring males in experiment 2.

Figure 7. Comparison of relative weight loss/day between caring and non-caring males.

Caring males took longer (12-day average) to spawn with their second females, compared with non-caring males (5-day average; Fig 6; Mann–Whitney U-test: $z= -3.203$, $P=0.0013$).

As in the previous experiment, caring males experienced a relative weight loss per day (Fig. 7; Mann–Whitney U-test: $z= -4.833$, $N=17$, $P=0.0001$) while in contrast to the last experiment non-caring males neither gained nor lost significant weight (Mann–Whitney U-test: $z= -1.501$, $N=14$ excluding three males that were not weighed until the day after their broods were removed, $P=0.13$). The difference between the relative weight loss per day in each treatment approached significance (Mann–Whitney U-test: $z= -1.912$, $P=0.056$).

The behaviour of caring males and non-caring males was similar. Both caring males and non-caring males spent most of the 15-min focal watches close to their secondary females ($\bar{X} \pm$ SE: caring males 8.9 ± 0.9 min, non-caring males 10.8 ± 0.9 min; Mann–Whitney U-test: $z= -1.446$, $N_1=17$ caring males, $N_2=15$ non-caring males, $P=0.15$). The frequency of courtship displays was similar for both treatments ($\bar{X} \pm$ SE: caring males 9 ± 1.5, non-caring males 13 ± 2.5; Mann–Whitney U-test: $z= -1.74$, $N_1=17$ caring males, $N_2=15$ non-caring males, $P=0.08$). The frequency of aggressive displays (mouthfights, bites and chases) was also similar between treatments ($\bar{X} \pm$ SE: caring males 2.2 ± 0.6, non-caring males 2.5 ± 0.9; Mann–Whitney U-test: $z= -0.075$, $N_1=17$ caring males, $N_2=15$ non-caring males, $P=0.94$).

Fertility rates, calculated for the second female's clutch on day 4 when fertilized eggs have discernible vertebrate columns emerging from the egg, did not differ between treatments (Mann–Whitney U-test: $z=0.053$, $P=0.96$).

DISCUSSION

This study provides evidence for the costs of parental care in St Peter's fish. In females, caring led to longer inter-spawn intervals, weight loss and reduced energy invested in subsequent breeding attempts: fewer eggs and lighter broods were produced, although the size of individual offspring did not change. In males, caring led to weight loss and longer inter-spawn intervals.

The longer inter-spawn interval observed for caring females implies that care reduces the reproductive rate, and therefore that lost mating opportunities is a cost of parental care for females. Evidence that caring females take longer to re-spawn has been reported in two other cichlids, *Cichlasoma nigrofasciatum* and *Haplochromis* '*argens*' (Cichlidae) (Smith & Wootton, in press a, b). Furthermore, when parents terminate parental care early by cannibalism, the inter-spawn interval is reduced (Mrowka 1987; Lavery & Keenleyside 1990).

In the second experiment the higher reproductive rate of males was confirmed. The 'lost mating opportunities' cost of care is probably higher for male St Peter's fish as males were capable of spawning again almost immediately (1 day) whether or not they were caring while females

Animal Behaviour, 50, 1

required a minimum of 9 days and an average of 13 days to replenish eggs and re-spawn. Caring and non-caring males were equally eager to re-spawn. Further evidence that males suffer more than females from lost mating opportunities is that they are more likely to desert in other species. For example Keenleyside (1983) induced male *Herotilapia multispinosa* to abandon their broods by creating female-biased sex ratios (opportunities to breed again were high) but he could not induce females to do the same in male-biased sex ratios. These results have been confirmed for St Peter's fish (unpublished data).

Both sexes lost weight because of reduced feeding activity. Similarly, care has been found to cause loss of condition in other species such as: *Blennius incognitus* (Blenniidae) (Goldschmid & Kotrschal 1981); *Ictalurus nebulous* (Ictaluridae) (Blumer 1986); *Oxzylebius pictus* (Hexagrammidae) (DeMartini 1987); *Syngnathus typhle* (Syngnathidae) (Svensson 1988); *Gasterosteus aculeatus* (Gasterosteidae) (FitzGerald et al. 1989); *Cottus gobio* (Cottidae) (Marconato & Bisazza 1988). However, the cost of lost feeding opportunities may be higher in mouth-brooding species, such as St Peter's fish, than in the species mentioned above as care/incubation of young involves the mouth and impedes feeding (Fryer & Iles 1972). However, recent research has shown that some mouth-brooding species manage to feed at a reduced rate while caring (Yanagisawa & Sato 1990; Yanagisawa & Ochi 1991). Furthermore, in St Peter's fish both sexes have the opportunity to compensate for their losses in condition by eating a proportion of eggs, as seen in some paternal substrate guarders (DeMartini 1987). Whether St Peter's fish parents eat part of their clutch is not known. A common phenomenon in mouth-brooding cichlids is a gradual reduction in the number of zygotes; more eggs are laid than are brooded and more eggs are brooded than fry are released. This brood reduction may result from consumption of eggs for energy compensation or it may be caused by infertility, or space constraints in the mouth (brooding) cavity.

Although the currency of lost feeding opportunities (i.e. weight loss) is the same for both sexes the fitness consequences differ between the sexes. The decrease in body weight experienced by caring females is probably directly related to the high fecundity costs suffered: caring females produced fewer young and therefore lighter clutches compared with non-caring females while caring and non-caring males were equally able to fertilize eggs. Both males and females prefer large mates but the female's preference is stronger (unpublished data) and therefore the weight loss caring males experience is likely to affect their fitness by decreasing their ability to attract future mating partners. These different fitness consequences make it difficult to compare the cost of lost feeding opportunity between the sexes.

In this study, females produced a range of egg and fry sizes; however, individual females produced eggs or fry of a characteristic size between spawns, varying their clutch sizes in response to changes in parental expenditure. Egg size may be constrained more than egg number because once fry are released from the parents' mouths they enter a critical time in their development where larger fry have a survival advantage (Hutchings 1991). Females may experience strong selection pressure to make eggs as large as possible, since young in large eggs will develop slowly and be released as larger individuals rather than young emerging from small eggs (Rana 1985, 1988). Thus, although offspring size is known to vary in fish species (Blaxter 1969; van den Berghe & Gross 1989), offspring size may be less flexible than offspring number, as in birds (Lack 1954, 1968).

Finally, this study provides insight into some of the short-term costs of parental care, which together with the measured benefits of care may aid in our understanding of what factors were important in the evolution of parental care in fish.

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