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The benefits of uniparental versus biparental mouth brooding in Galilee St. Peter's fish

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In Galilee St. Peter's fish *Sarotherodon galilaeus* the care system is naturally labile; biparental, male-only and female-only care all exist in one population. This unusual flexibility facilitates comparisons between the forms of care. The costs of parental care were considered in a previous study. Here, the benefits of parental care were quantified by observing wild fish, both held in pond enclosures and free-swimming in Lake Kinneret, Israel. Parental care was shown to be essential for offspring survival in St. Peter's fish. The reproductive success of parents who shared incubation duties was nearly twice as high as that of parents caring alone. However, per brood (or mouth cavity) reproductive success was 20% higher for uniparental parents. Both sexes were equally capable and efficient in care; when both sexes cared, they each incubated a similar number of eggs and released a similar number of fry. The results are discussed in terms of the relationship between caring strategies and clutch size.

Key words: cichlid; *Sarotherodon galilaeus*; benefits of care; evolution; mouth brooding.

INTRODUCTION

Galilee St. Peter's fish *Sarotherodon galilaeus* (L.) is well suited for investigations of parental care behaviour for two reasons: both sexes care in an identical manner (mouth brooding), and the care pattern is flexible. Identical caring behaviour simplifies a cost/benefit comparison between males and females, while the existence of male-only, female-only and biparental care in the same population (Fishelson & Heinrich, 1963) facilitates comparisons of the reproductive success of the various parental care forms.

Although parental care is generally not associated with fishes, it occurs in 21% of bony fish families (Gross & Sargent, 1985). Moreover, fishes show the greatest variety of parental care of any vertebrate group, including viviparity, ovoviviparity and many forms of external egg and fry care (Clutton-Brock, 1991). Typically, fish species that show care will modify a small area of the substratum on which they spawn, and then protect eggs against predation and aerate the eggs. However, parental care in fish can also include activities such as elaborate nest building, incubation and feeding of young (Hildenmann, 1959; Breder & Rosen, 1966; Blumer, 1982; McKay, 1986). Species of fish that incubate their young may do so in their mouth cavities (e.g. marine catfishes and cichlids; Oppenheimer, 1970), in ventral brood pouches (e.g. sea horses and pipefishes; Vincent *et al.*, 1992), on hooks (e.g. Genus *Kurtus*; Balon, 1975),

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embedded in skin (e.g. American banjo catfish; Marshall, 1965) or in gill chambers (e.g. cave fish; Breder & Rosen, 1966). In fish, as in other vertebrates, the main functions of parental care are to protect the young from predators and to promote offspring growth and development (Keenleyside, 1979).

St. Peter's fish belongs to the family Cichlidae, in which parents protect and aerate eggs in nests, caves, pits, or in their mouths. More unusually for fish, cichlid species also protect, herd, and sometimes even provide food for free-swimming fry (Hildenmann, 1959; Keenleyside, 1991; Wisenden *et al.*, 1995). Many cichlid species show biparental care, which is rare in fish in general; biparental care is confined to only 24 of the 424 bony fish families (Blumer, 1982). Biparental cichlids are usually substrate guarders that show sexual differentiation in care behaviour: typically females perform hygienic duties and fan the eggs, while males guard the territory and chase away predators (Perrone, 1978; Itzkowitz, 1984). In mouth-brooding cichlids, uniparental female care is most common (Fryer & Iles, 1972). Thus, as a mouth-brooding cichlid showing both uniparental and biparental care, St. Peter's fish is very unusual.

St. Peter's fish are sequentially monogamous (Johnson, 1974). A male and female together dig a simple nest; then the female deposits batches of 20–40 eggs in the nest, and the male glides over them fertilizing one batch at a time (Ben-Tuvia, 1959; Fagade *et al.*, 1984). The clutch remains in the nest untouched for approximately 15 min before the male, the female or both pick up the eggs for oral incubation (Fishelson & Heinrich, 1963). Desertion usually occurs before any eggs are picked up (pers. obs.). After the eggs are picked up, the pair bond dissolves and parents incubate separately making the transfer of eggs and fry between parents unlikely. The eggs hatch after approximately 5 days and the fry remain inside the mouth until the yolk sac is completely absorbed which takes 4–18 days depending on water temperature. Once the fry are released, usually they are not taken into the mouth again (Fishelson & Heinrich, 1963). While in the mouth, the eggs and fry are protected and are well supplied with water rich in oxygen. During oral incubation parents do not feed (Fryer & Iles, 1972; Akintunde, 1982) and the buccal cavity distends downwards to form a brood pouch (Rana, 1986).

In this study, the potential benefits of parental care in St. Peter's fish were investigated by addressing the following three questions. (1) Is parental care necessary for offspring survival and development? (2) Is biparental care more successful than uniparental care and if so, by how much? (3) Does one sex provide superior parental care, i.e. does one sex incubate or release greater numbers of young than the other?

MATERIALS AND METHODS

St. Peter's fish were observed in the wild in Lake Kinneret, Israel (32°45′–32°13′ N and 35°38′ E) and in large enclosures placed in a concrete pond beside the lake, during the 1992, 1993 and 1994 breeding seasons.

IS PARENTAL CARE NECESSARY FOR OFFSPRING SURVIVAL AND DEVELOPMENT?

To consider the importance of parental care, eight pairs of parents were removed after spawning and the effect on clutch survival was assessed. Spawning behaviour of

St. Peter's fish was observed in two regions of the lake: (1) Mezudia, in the northern Buteiha plain, a marshy area with isolated shallow lagoons and an important cichlid breeding area (Ben Tuvia, 1959); and (2) the western shore between Kibbutz Ginosar and the Yigal Allon Limnological Laboratory. At each site, 50-m transects were made and all fish observed were noted. If a breeding pair of *S. galilaeus* was encountered, their spawning behaviour was observed. In five pairs, parents were frightened away from their clutches by the observer approaching the nest and standing in the water by the nest for 10 min. The nest was approached only after spawning movements had ceased and parents had begun to perform the circle display over the eggs (Schwanck & Rana, 1991). These five pairs were chosen because their nests were extremely easy to see: they were built on light coloured substratum, far away from vegetation. After scaring away the parents, the fate of the eggs was monitored from the shore.

In addition, three males and three females were collected from Lake Kinneret with trammel nets. After capture, these fish were anaesthetized with Benzocaine, measured and tagged behind the dorsal fin with a uniquely numbered Carlin tag (Neal Ltd., Finchley, London). They were then placed paired in three plastic enclosures within a concrete pond (13 × 4·5 m) on the banks of Lake Kinneret at the Aquaculture Station, Ginosar. The enclosures were made of plastic fencing 70 cm in height, woven onto circular plastic-coated metal tubes 1.5 m in diameter. The enclosures were anchored in the water by rocks, which served an additional purpose as spawning and hiding places for fish. The pond had the benefit of natural daylight and a continual flow of fresh water from Lake Kinneret, providing a semi-natural environment for these fish [see Balshine-Earn (1995*a*) for details on the concrete pond and the enclosures]. After each pair spawned, both parents were removed and egg survival, in the absence of predators, was monitored.

IS BIPARENTAL CARE MORE SUCCESSFUL THAN UNIPARENTAL CARE AND IF SO, BY HOW MUCH?

To study the reproductive success of biparental *v.* uniparental care, St. Peter's fish were collected from Lake Kinneret and observed in enclosures during three breeding seasons (April–September, 1992–1994). Fish were marked individually as described above and placed (one male and one female, matched for size) in each of the 32 plastic enclosures inside the concrete pond. If both fish performed courtship behaviour (shakes and quivers), they were left together to spawn. If aggressive behaviours (chases, mouth fights) ensued, then the pair was split and each fish was given a new partner. After a single breeding cycle, each pair was replaced. In total, 190 different pairs' spawning behaviour inside enclosures was observed. The form of care was determined by observing which sex picked up eggs. Broods were removed from some of these pairs at the egg stage (<day 4) and from others when most of the yolk sac has been absorbed (day 10–14). The reproductive success (defined as the number of young to reach independence) between biparental and uniparental care was compared. The proportions of uniparental and biparental care observed in enclosures were compared to the proportions of each care state observed in the lake.

St. Peter's fish mate assortatively by size, but in a given mating pair the male is usually slightly larger than the female (Balshine-Earn, 1995*a*). No systematic size differences were found between parents involved in biparental care (mean ± S.E. = 121·0 ± 3·1 g) and uniparental care (119·0 ± 5·5 g, unpaired *t*-test: $t = 0{\cdot}31$, $P = 0{\cdot}76$). Fish brooding eggs biparentally were similar in weight to those brooding eggs uniparentally (mean body weight ± S.E.: biparental males and females = 111·0 ± 4·2 g, uniparental males and females = 105·0 ± 7·5 g; unpaired *t*-test: $t = 0{\cdot}66$, $P = 0{\cdot}52$). Similarly, parents brooding fry biparentally were similar in weight to parents brooding fry uniparentally (mean body weight ± S.E.: biparental males and females = 127·3 ± 4·2 g, uniparental males and females = 129·3 ± 7·4 g; unpaired *t*-test = 0·22, $P = 0{\cdot}83$).

DOES ONE SEX INCUBATE OR RELEASE GREATER NUMBERS OF YOUNG THAN THE OTHER?

To evaluate whether male and female St. Peter's fish were equally good at providing care: (1) male and female clutches (eggs and fry) from lake fish were compared; and (2) the proportion of eggs and fry in a clutch incubated by each sex in enclosures was compared.

First, fish were examined twice a week with local fishermen in Lake Kinneret from 15 April to 29 June 1992, 5 May to 13 September 1993, and 27 April to 23 July 1994. Sampling began when the water in the littoral zone spawning grounds reached 18–20° C, the minimum required spawning temperature for St. Peter's fish (Johnson, 1974; Ben-Tuvia *et al*., 1992). Fish were examined in the boats as soon as the nets were pulled out of the water and any signs of caring (determined by the presence of eggs/fry in the mouth or the presence of a brood pouch) were recorded. All females and males caught with intact broods of either eggs or fry were examined. Brood size and body size were log transformed to normalize the data and parametric analyses were employed.

Second, the numbers of eggs and fry incubated by biparental males and females in the enclosures were compared. In addition, cases of male-only and female-only care were compared to determine if one sex providing care alone was more successful than the other. Cases of uniparental care were examined further to determine whether season or body size affects either male-only or female-only care.

RESULTS

PARENTAL CARE IS NECESSARY FOR OFFSPRING SURVIVAL AND DEVELOPMENT

In the lake and in enclosures, removal of both parents had deleterious effects on clutch survival. In the lake, three clutches of eggs were preyed upon quickly in <1 h, by a freshwater crab, a turtle, and a group of three *S. galilaeus* conspecifics. The two remaining egg clutches also disappeared between 2 and 3 h after oviposition.

In the absence of predators, in the enclosures egg clutches remained intact for 6–8 h of daylight but had virtually disappeared by the next morning. In only one enclosure, a few eggs were found still stuck to the substratum (19 eggs left, of an estimate of several hundred). Probably the eggs were washed away by water movements as St. Peter's fish eggs are initially adhesive but the adhesive filaments dissolve soon after buccal incubation begins (Kraft & Peters, 1963; Rana, 1988).

BIPARENTAL CARE IS MORE SUCCESSFUL THAN UNIPARENTAL CARE

Pond observations

Out of 190 unmanipulated enclosure spawns, 151 resulted in biparental care and 39 resulted in uniparental care (24 cases of female-only care and 15 cases of male-only care). The median number of fry released by an individual fish providing uniparental care was 650 while two parents released a median of 1059 fry together; thus two caring parents released more fry than one caring alone (Mann–Whitney U-test, $z = -3{\cdot}284$, $P = 0.001$). Pairwise comparisons (Seigel & Castellan, 1988) are shown in Table II. The egg broods incubated by individual fish did not differ in size between parents who cared alone (Table I; median = 590 eggs, $n = 17$) and parents who shared incubation duties (median = 573, $n = 112$; Mann–Whitney U-test: $z = -0{\cdot}242$, $P = 0{\cdot}81$). However, the uniparental broods of fry (median = 650 fry, $n = 22$) were significantly larger than biparental broods of fry (per parent) (median = 514 fry, $n = 190$; Mann–Whitney U-test, $z = -2{\cdot}75$, $P = 0{\cdot}006$). Brood size did not decrease between the egg and fry stages. When egg and fry broods were combined, uniparental broods (median = 628, $n = 39$)

Table I. A comparison of brood size (eggs and fry) from unmanipulated enclosure spawns resulting in uniparental and biparental care*

	Median (egg) brood size	*n*	Median (fry) brood size	*n*
Uniparental care	590	17	650	22
Biparental care	1162	56	1059	95
♀-only care	550	13	630	11
♀-biparental care	603	56	554	95
♂-only care	793	4	650	11
♂-biparental care	499	56	499	95

*These are independent observations, not repeated observations at two different stages of development (egg and fry) from the same individuals.

Table II. Reproductive success: multiple pairwise comparisons from Kruskal–Wallis one-way analysis of variance between care forms and number of fry released*

Pair	Critical value	$\lvert \bar{R}_1 - \bar{R}_2 \rvert$	*P*
Cases of no care *v.* uniparental care	22·6	33·2	<0·001
Cases of no care *v.* biparental care	31·2	67·2	<0·001
Cases of uniparental care *v.* biparental care	22·1	34	<0·001

*There were eight cases of no-care (five field clutches and three enclosures clutches), 151 cases of biparental care and 39 cases of uniparental care. Median values of clutch size for each were used to estimate the reproductive success of each care type. $\bar{R}_1$-$\bar{R}_2$ is the difference between the mean reproductive success of the forms of care. See Seigel and Castellan (1988) for an explanation on how to calculate critical values. Uniparental care was significantly more successful than no care while biparental care was significantly more successful than both uniparental and no care.

were larger per individual fish than broods incubated by individuals caring with their partners (median = 534, $n = 151$; Mann–Whitney *U*-test: $z = -2·4$, $P = 0·02$).

Field observations

In 3 years, 87 spawns of St. Peter's fish were observed in Lake Kinneret. Both parents took eggs in 65 cases, the female alone in 15 cases and the male alone in seven cases. The proportion of biparental *v.* uniparental care was similar in lake and pond spawns ($G = 1·05$, d.f. = 2, $P > 0·40$). Wild fish were unmarked and consequently there was no information on their size, condition or clutch size.

NEITHER SEX PROVIDES SUPERIOR PARENTAL CARE

Pond observations

Males and females involved in biparental care incubated similar numbers of eggs and fry (Fig. 1; Mann–Whitney *U*-tests: $z(\text{eggs}) = -0·595$, $P = 0·55$; $z(\text{fry}) = -0·476$, $P = 0·63$). There was no significant difference in body weight between the sexes in the biparental pairs (mean body weight ± S.E.; egg

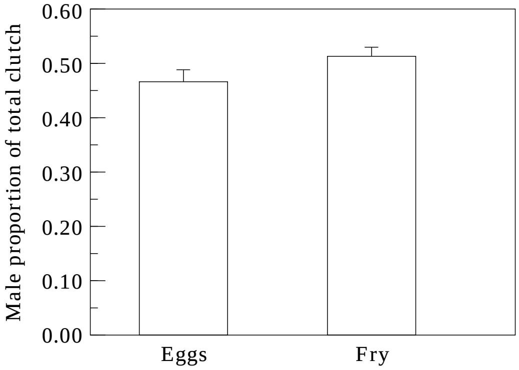

FIG. 1. Males incubated about 50% of the clutch [eggs ($n=56$) and fry ($n=95$)]. The data were collected from biparental pairs in enclosures. Error bars show standard errors.

TABLE III. A comparison of body weight, the timing of spawning, clutch size, and the frequency of male-only and female-only care in captive St. Peter's fish that spawned in enclosures inside a concrete pond

	Male-only care	Female-only care	*G* or *z* statistic	*P*
Total number of cases	15	23	$G=1{\cdot}65$	>0·10
Mean body weight of parents (g) ± S.E.	124 ± 8	114 ± 8	$z=-1{\cdot}314$	0·19
Season:				
Early (May–June)	6	12	$G=1{\cdot}41$	>0·20
Late (July–August)	9	11	$G=0{\cdot}19$	>0·60
Median clutch size	650	596	$z=-1{\cdot}176$	0·24

group: males = 118 ± 5·7 g, females = 106 ± 5·9 g, paired *t*-value = 1·251, $P=0{\cdot}22$; fry group: males = 127·8 ± 6·0 g, females = 126·5 ± 5·7 g, paired *t*-value = 0·19, $P=0{\cdot}84$).

No differences were found between male-only and female-only care cases in the probability of occurrence, parents' body weights or seasonal occurrence (Table III). Males and females incubating alone were brooding similar numbers of eggs and fry (Table III: Mann–Whitney *U*-tests, eggs: $U=31$, $P=0{\cdot}40$; fry: $z=-0{\cdot}493$, $P=0{\cdot}62$). Males and females incubating alone were of similar body weight (Mann–Whitney *U*-tests: $z=-1{\cdot}314$, $P=0{\cdot}19$).

Field observations

Of the 1093 wild females caught, 156 were incubating intact broods (72 with egg broods and 84 with fry broods). Of the 1487 wild males caught, 138 had intact clutches (41 with egg broods and 97 with fry broods). Compared with males, significantly more females were caught brooding eggs ($\chi^2=9{\cdot}14$, $P<0{\cdot}01$) but the number of females and males caught brooding fry did not differ ($\chi^2=0{\cdot}93$, $P<0{\cdot}50$).

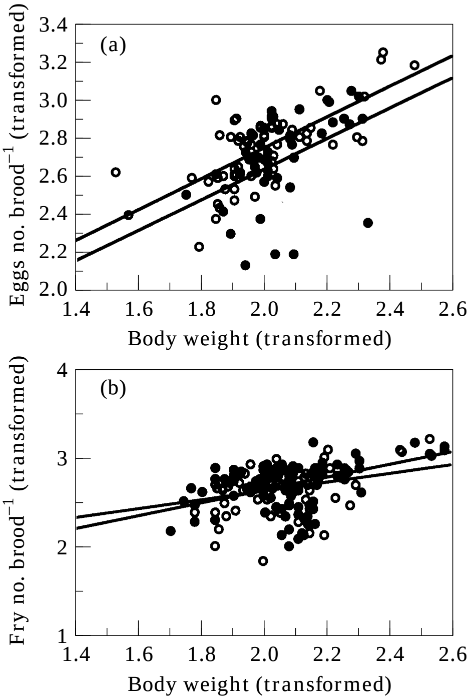

FIG. 2. Brood size and body size were log transformed to normalize the data and parametric analyses employed. (a) The allometric relationship between male (●) and female (○) body weight and the number of eggs incubated: y (males) = 1·0 + 0·8x, $r^2 = 0·203$; and y (females) = 1·1 + 0·81x, $r^2 = 0·50$. (b) The allometric relationship between male (●) and female (○) body weight and the number of fry incubated: y (males) = 1·6 + 0·5x, $r^2 = 0·110$; and y (females) = 1·2 + 0·7x, $r^2 = 0·20$. The data are from field observations taken while sampling with fishermen in Lake Kinneret.

In both males and females there was a positive correlation between body weight and brood size [Fig. 2(a), (b)]. Both sexes incubated similar numbers of egg and fry (ANCOVA, eggs: sex × body weight, $F_{2,109} = 0·978$, $P = 0·32$; fry: sex × body weight, $F_{2,177} = 0·002$, $P = 0·96$).

DISCUSSION

Parental care of fertilized gametes was shown to be essential for protection and appropriate development of young St. Peter's fish. Parents sharing incubation duties were more successful than parents providing uniparental care in terms of the total number of young released. However, per parent, uniparental broods were larger than biparental broods. Males and females were equally efficient at providing care.

Some form of parental care (male-only, female-only or biparental care) is found in all cichlid species (Keenleyside, 1991) and in the genus *Sarotherodon*, mouth brooding (male-only or biparental) is always observed (Trewavas, 1983). It is therefore not surprising that offspring did not survive in the absence of a care-giving adult. Parents and young undoubtedly co-evolve to given levels of care. Other studies of biparental cichlids report similar results; when one of a brooding pair is removed, the remaining parent cannot protect the brood of eggs or young fry as effectively (Keenleyside & Bietz, 1981; Nagoshi, 1987). It is also highly unlikely that eggs can develop appropriately in the absence of parental care. In incubators, unmixed St. Peter fish eggs are quickly covered with fungus that arrests development (pers. obs.). Inside the parent's mouth eggs are churned; these are periodic mouth movements that agitate the eggs (Baerends & Baerends-van Roon, 1950) and promote egg survival (Shaw & Aronson, 1954; Fishelson, 1966).

Two parents providing biparental care produced more fry than a single parent providing uniparental care; this probably occurs because two mouths can hold more young than one and perhaps provide the eggs and later fry, with better conditions for development. If one parent incubates the entire clutch, then too many eggs may be packed into one cavity, thus reducing survivorship. Rana (1986) showed an increase in the number of developmental abnormalities in fry when clutch sizes were above normal in two close relatives of St. Peter's fish, *Oreochromis niloticus* L., and *O. mossambicus* Peters. In the present study, fish with full mouths were observed occasionally attempting to pick up additional eggs; with each new mouthful, eggs would drip out of the already full mouth. It is possible that eggs and fry in such tightly packed mouths cannot be churned properly; however, in the current study there was no evidence that the survival of eggs and fry was lower with uniparental care.

In substratum-guarding species, two parents also tend to enjoy higher reproductive success than one parent but for an entirely different reason. In these species the care duties are divided and a single parent without a mate is unable to perform adequately both male (protection) and female (fanning) roles (Keenleyside 1991). As a result, after one parent deserts, the brood is usually eaten within a few days (Keenleyside, 1979, 1983; Keenleyside & Bietz, 1981; Dupuis & Keenleyside, 1982; Blumer, 1985, 1986*a*, 1986*b*).

If biparental care leads to higher reproductive success, this raises the question of why biparental mouth brooding cichlids are so rare. St. Peter's fish and 18 other species (17 cichlids and one *Apogon*) are the only known biparental mouth brooders (Breder & Rosen, 1966; Oppenheimer, 1970; Loiselle, 1985). Biparental mouth brooding is probably so uncommon because the incentives for the evolution of biparental care (effective protection for diffuse fry or for a breeding site) are removed once mouth brooding evolves. Mouth brooding releases parents from long-term defence of a nest and provides an alternative form of effective protection for free-swimming fry (Blumer, 1979; Gittleman, 1981; Barlow, 1984, 1991; Keenleyside, 1991). However, in St. Peter's fish biparental care is common (75–80% of spawns) probably because the eggs are usually too numerous to fit into a single fish's mouth. In general, uniparental mouth brooding species have relatively small clutches (Lowe-McConnell, 1955). Large clutch size may be maintaining biparental mouth brooding in extant species, including St. Peter's fish.

Uniparental broods may have been 20% larger than the broods incubated by individuals caring biparentally because fish caring alone may attempt to compensate for mate desertion by caring for more young than usual. On the other hand, it is also possible that 20% over a single parent's normal brood represents a clutch size threshold where the costs of brooding outweigh the benefits in terms of reproductive success. After spawning, St. Peter's fish circle above the eggs and every few minutes one member of the pair will break from the circle formation to approach the eggs, finally picking up the eggs for incubation (Schwanck & Rana, 1991; Balshine-Earn, 1995*b*). Thus, the visual inspection of eggs at close range provides an opportunity for clutch size assessment.

The benefits of care, in terms of offspring survival, are usually the same for both sexes (Clutton-Brock, 1991). As emphasized previously, when both male and female St. Peter's fish care, they incubate roughly equivalent numbers of eggs and fry. If the relative effectiveness of male and female are equal then why do males desert more often in St. Peter's fish?

Decreases in the benefits of care or increases in the costs of care (fitness, survival and growth) can cause male desertion. At least four factors decrease the benefits of caring for males and thus increase the likelihood of male desertion: (1) decreased offspring relatedness; (2) increased offspring age; (3) decreased offspring quality; and (4) decreased offspring quantity (Lazarus, 1990). In St. Peter's fish, variance in offspring relatedness is not likely to be a major evolutionary selective force, as males and females mate monogamously and sneakers have never been observed in natural spawns. When spawning fish were disturbed by conspecifics, the conspecifics ate the eggs rather than attempting to fertilize them (pers. obs.). In addition, offspring age does not influence the care decision in St. Peter's fish because desertions occur shortly after oviposition. The third factor, offspring quality, may influence parental care behaviour and the fourth factor, offspring quantity, certainly does: large clutches increase the probability of biparental care (Balshine-Earn, 1995*b*). In St. Peter's fish, neither offspring quality nor quantity is likely to vary between the sexes and thus do not explain why males tend to desert more often.

Hence, sexual differences in the costs of care may be responsible for the higher male desertion. In this study, it was shown that more females were caught incubating eggs, indicating a greater tenacity on females' part for mouth brooding in the early stages of parental investment. Males' higher potential for remating (Emlen & Oring, 1977; Clutton-Brock & Vincent, 1991) means males suffer higher caring costs in terms of lost mating opportunities (Balshine-Earn, 1995*a*) and this sexual difference in costs of care probably explains why males desert more often.

In conclusion, the benefits of parental care were shown to be high and shared equally between males and females. Furthermore, this study emphasizes that benefits and costs of care must be considered in concert to understand desertion in St. Peter's fish and the evolution of parental care patterns in general.

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