ANIMAL BEHAVIOUR, 2004, **68**, 1283–1289
doi:10.1016/j.anbehav.2004.03.007

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Mouthbrooding and biparental care: an unexpected combination, but male brood care pays

CHRISTOPH GRÜTER & BARBARA TABORSKY
Behavioural Ecology, University of Bern

(Received 3 July 2003; initial acceptance 4 September 2003; final acceptance 9 March 2004; published online 29 September 2004; MS. number: 7779)

Biparental care is expected to occur if (1) the costs of desertion for a parent are high, because of greatly reduced survival prospects of offspring, or (2) the benefits of desertion are low. Among mouthbrooding fish, biparental care is rare because the mouth cavity provides a safe brooding site, thus reducing the selective advantages of shared brood care. *Eretmodus cyanostictus* is a monogamous mouthbrooding cichlid in which the entire clutch is brooded first by the female and then by the male. To test the hypothesis that females alone can produce viable young, we designed an experiment in which females were separated from their mates. Unassisted females prolonged incubation but released as many young as females assisted by males. However, they compensated only partially for male incubation and released smaller and less-developed young. This may substantially reduce offspring survival chances in the wild. The body condition of single females decreased more during incubation and they had a prolonged interspawning interval, but produced similar egg numbers and weights in the next clutch. Our results suggest that the male's brood care effort is an important cause of the maintenance of biparental care and monogamy in *E. cyanostictus*.

The parental care pattern found in a species is likely to reflect the outcome of a contest played between the sexes over evolutionary time (Westneat & Sargent 1996). Often the payoffs of the two alternatives, care giving or desertion of a brood, diverge substantially between males and females (Trivers 1972; Clutton-Brock 1991). Biparental care is likely to occur if it is significantly more effective than uniparental care, as in many altricial birds where it increases the survival chances of young considerably (Lack 1968; Oring 1982). Furthermore, biparental care should occur when the payoffs of desertion are low for both parents. This is the case if the remating probability is low or search costs for a new mate are high (reviewed in Clutton-Brock 1991).

Cichlid fish (Cichlidae) provide excellent opportunities to study sexual conflict and parental care decisions. They show a variety of parental care patterns (substrate breeding, delayed or immediate mouthbrooding, biparental, female-only and male-only care; Keenleyside 1991). In most substrate-breeding species both parents are needed for the defence of young and the breeding site. In contrast, most mouthbrooders show female-only care and sequential polygyny. Parents share brood care in only a few mouthbrooders (Oppenheimer 1970; Keenleyside 1991; Kuwamura 1997). A common explanation for the rarity of biparental mouthbrooding is that the mouth of one parent provides a sufficiently safe incubation site (Oppenheimer 1970; Barlow 1984; Gross & Sargent 1985). Biparental care in mouthbrooders would be expected only if (1) a large brood size requires both parents for incubation or (2) parents need to codefend the fry after release (Perrone & Zaret 1979; Clutton-Brock 1991). Although this appears to apply to most biparental mouthbrooders (e.g. Kuwamura 1986; Yanagisawa 1986; reviewed by Perrone & Zaret 1979; Clutton-Brock 1991), there are at least three exceptions. In the Lake Tanganyika cichlids *Eretmodus cyanostictus*, *Tanganicodus irsacae* and *Xenotilapia boulengeri*, females take up the whole clutch after spawning to incubate it for a while before the young are transferred to their mates who incubate them until independence. Young are not defended after release (Kuwamura 1986; Kuwamura et al. 1989; Morley & Balshine 2002).

We studied factors maintaining biparental care in *E. cyanostictus*. In this species, females incubate the young for about 8–12 days before males continue incubation for another 10–16 days (Neat & Balshine-Earn 1999; Morley &

Correspondence: B. Taborsky, Behavioural Ecology, University of Bern, Wohlenstrasse 50A, CH-3032 Hinterkappelen, Switzerland (email: barbara.taborsky@esh.unibe.ch).

0003–3472/04/$30.00/0

Balshine 2002). Apparently, parents starve during incubation (Morley & Balshine 2003). Females may gain little from desertion because the time until they are able to spawn again is much longer than the incubation period of the males (Morley 2000). However, it remains unclear why males participate in brood care.

Evidence from a field population suggests that both sexes of this species are constrained to monogamy because the male-biased sex ratio means there are few remating opportunities for males (Neat & Balshine-Earn 1999; Morley & Balshine 2003) and there is strong intrasexual competition for mates in both sexes (Morley & Balshine 2002). Earlier studies suggested that biparental care in *E. cyanostictus* is neither essential nor more efficient than uniparental care (Kuwamura et al. 1989; Morley 2000; Morley & Balshine 2002). However, it is unknown whether and how the absence of male care would affect the condition of offspring and brood-caring females. To test for this potential effect, we conducted an experiment where females were either assisted by males or forced to incubate alone. We tested whether male absence would influence female incubation duration, body condition and the duration of the interspawning intervals. We also compared the developmental stage, size and weight of young at release from parental care in biparental and uniparental treatments. If male desertion reduces offspring viability, this should influence the male's desertion decision. In addition, we assessed effects on the future reproduction of females, namely the quality of future clutches.

METHODS

Study Species

Eretmodus cyanostictus is endemic to Lake Tanganyika, Zambia, where it inhabits shallow rocky coastal zones around the lake (Kuwamura 1986; Kuwamura et al. 1989; Taylor et al. 2001). Pairs defend territories, which they leave only to chase away conspecific intruders (Morley 2000).

Experimental Conditions

We conducted the experiment from March 2002 to March 2003. Experimental fish were taken from a stock of adult fish kept at the University of Berne in several 500-litre tanks, consisting of fish imported from Lake Tanganyika and their first-generation offspring. Pair formation took place in the stock tanks. Experimental pairs were held in 100-litre compartments of a 200-litre tank. In a few cases, males started to attack their females (twice during female incubation, four times in the interclutch interval, see below). If a male continued to attack its mate and/or if a female showed first signs of injury (small lesions in dorsal or caudal fin) the experiment was immediately terminated, and the fish were transferred to their home tank. In the stock tanks, aggression ceased immediately. A layer of gravel (2 cm in diameter) and sand covered the bottom of each compartment and nine clay flowerpot halves and two PVC tubes (5 cm in diameter) were provided as shelters. Each compartment was equipped with an internal biological filter. Fish were kept at water temperatures of 26–27 °C and on a light:dark regime of 13:11 h to simulate natural light conditions at Lake Tanganyika. This study was done under licence from Kantonales Veterinäramt, Bern, Switzerland.

Experimental Design

The day after spawning, we alternately assigned 28 pairs to one of two treatments: (1) both parents incubating a clutch (pair treatment) or (2) females only incubating a clutch (single-female treatment). In the single-female treatment, a mesh partition was placed in the middle of the 100-litre compartment 2–5 days after spawning, which separated the female from the male and prevented the transfer of young between mates. It allowed visual contact and water exchange between the partners. All fish had access to an ad libitum food source (cubes containing Tetramin flake food mixed with agarose gel) for 30 min each day during the incubation period until young were released.

All fish were weighed ($\pm$0.01 g) with an electronic balance 1 day after spawning and on the day after the end of incubation. In the pair treatment, both fish were weighed on day 6 (as late as possible but before the shift of young from female to male to maximize the time between the first and second measurement and thereby to increase the accuracy of the weight change estimate for incubating females), that is, a mean $\pm$ SD of 2.1 $\pm$ 1.29 days before the shift of young, and the female was weighed again the day after the shift of young. We calculated body condition of fish as weight (g)/standard length (cm)^3 $\times$ 100 of single females, which is the most commonly used condition index in fish (Bolger & Connoly 1989). After release, we counted the young. Each young was weighed ($\pm$0.0001 g) with a Mettler (AE 100) high-precision balance (mean measurement error $\pm$ 0.95%, $N = 20$). For weighing, we placed the fish in a small petri dish on a moistened cotton pad, which removed excess water from its body surface. The standard length (SL) was measured ($\pm$0.01 cm, mean measurement error $\pm$ 0.36%) under a binocular microscope. Between and after the measurements, we released the young into a plastic dish with aquarium water. Fish resumed normal activity immediately after being released in their home tank.

The young were then transferred to an empty holding tank and the mesh partition was removed in the single-female treatment. Pair members of both treatments that had completed the first breeding cycle and had not divorced during this cycle (see below) were kept together until they spawned a second time. In the period between the release of young and the next spawning (nonincubation period) fish were fed with Tetramin flake food. They received a daily equivalent of 3.5% of pair total body mass, which approaches ad libitum food availability. After the second spawning, we coaxed the female into releasing the eggs by gently moving the fish up and down in a container

of water while holding it in a head-down position. Then, both parents were weighed again and eggs were counted and weighed.

In 13 of 15 trials of the pair treatment, young were successfully released. Two females aborted incubation because of continued male aggression. Of the 13 successful broods, one female did not transfer the young to the male and two females shifted their young only partly after 11 and 17 days, respectively. In the single-female treatment, 11 of 13 females completed incubation and released young. Two females aborted incubation and swallowed the eggs. Three pairs of the pair treatment and one pair of the single-female treatment divorced during the nonincubation period before the next spawning. One female of the single-female treatment died for unknown reasons after the release of young. Egg weights of successive clutches were obtained from six clutches in the pair treatment and from eight clutches in the single-female treatment.

Behavioural Observations

The length of the interspawning interval might have been influenced by the period of separation in the single-female treatment, as separation might alter the strength of the pair bond. Therefore we checked for behavioural differences between pairs of both treatments in the non-incubation period. We observed each fish for 10 min/day on at least 6 days, if possible (except when pairs spawned the next clutch earlier). Observations took place between 1300 and 1600 hours.

As a measure of activity we recorded the durations of two behavioural states, time swimming around (activity) and time under cover (hiding). We also recorded the frequencies of the following behavioural events in 10 min: feeding rate (number of bites on small food items in the sand or on surfaces), displays towards mate (the focal fish undulates its body; the intensity of this movement may vary considerably from bending to shaking of the body), and aggressive behaviour (chasing or biting the mate).

All behavioural observations were recorded with the OBSERVER 3.0 software (Noldus, Wageningen, The Netherlands).

Statistical Analysis

Statistical analyses were done with SPSS 10.0 (SPSS Inc., Chicago, U.S.A.). All tests are nonparametric because assumptions of parametric tests were not met. Test procedures are noted in the results. All tests are two tailed. Descriptive statistics are given as medians and quartiles (in brackets) throughout.

RESULTS

Incubation Duration

In the pair treatment, the incubation time of females (8 [7, 9] days, $N = 10$) was shorter than in males (13 [12.75, 15] days, $N = 10$; Wilcoxon signed-ranks test: $T = 8$, $P = 0.005$). In the single-female treatment, the females incubated about twice as long as in the pair treatment (single females: 18 days [17, 20]; pair females: 8 days [7, 9]; Mann–Whitney U test: $U = 0$, $N_1 = 11$, $N_2 = 10$, $P < 0.001$) but still less than the total incubation time of a pair ($U = 8.5$, $N_1 = 11$, $N_2 = 10$, $P < 0.001$; Fig. 1).

Weight Changes During Incubation

Initial body condition was not significantly different between females used in the pair treatment (3.36 [3.28, 3.69], $N = 8$) and those in the single-female treatment (3.32 [2.97, 3.72], $N = 9$; Mann–Whitney U test: $U = 28$, $P = 0.48$). Body condition of females in both treatments decreased during incubation (comparison before and after incubation; Wilcoxon test: single female: $T = 0$, $P = 0.008$; pair: $T = 0$, $P = 0.017$; Fig. 2a). During male incubation, female condition did not change significantly ($T = 16.0$, $P = 0.2$; Fig. 2a). Single females decreased more in condition during their incubation period than females in the pair treatment (1) until the shift of young (Mann–Whitney U test: $U = 13$, $N_1 = 9$, $N_2 = 8$, $P = 0.027$; Fig. 2a) and (2) until the end of male incubation ($U = 13$, $N_1 = 9$, $N_2 = 8$, $P = 0.027$; Fig. 2a). As a consequence, pair females were in better body condition than single females at release of young ($U = 17$, $N_1 = N_2 = 9$, $P = 0.022$). We tested whether single females may continue to incubate until their energy reserves fall below a certain minimum threshold, in which case the variance in female body condition at the onset of incubation should be higher than at the end. However, the variances did not differ significantly (Levene's test for equality of variances: $F = 0.055$, $N_1 = N_2 = 8$, $P = 0.82$).

In males, initial body condition did not differ between treatments (single female: 3.29 [2.95, 3.6]; pair: 3.31 [2.99, 3.56]; Mann–Whitney U test: $U = 34$, $N_1 = 10$, $N_2 = 7$,

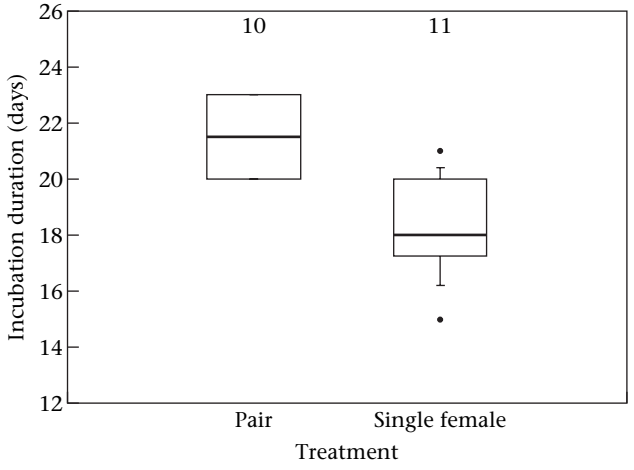

Figure 1. Total incubation duration of pairs and of females in the single-female treatment. The boxplots show medians, quartiles, 5th and 95th percentiles and minimum and maximum values outside of the percentiles (black dots). Sample sizes are given above the box plots.

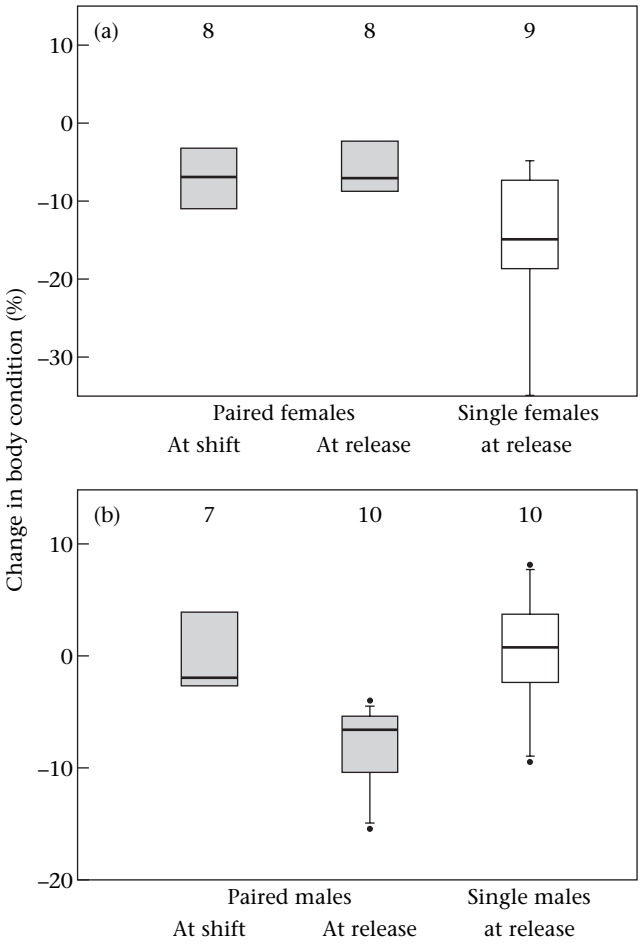

Figure 2. Change in (a) female and (b) male body condition relative to initial body condition; grey: pair treatment at shift of young to male and at release of young; white: single-female treatment. Boxplots as in Fig. 1.

$P = 0.96$). Neither the males of the single-female treatment (Wilcoxon test: $T = 24.0$, $N = 10$, $P = 0.72$) nor the males of the pair treatment ($T = 12.0$, $N = 7$, $P = 0.74$) showed a significant change in body condition during incubation of their mates (Fig. 2b). Body condition of mouthbrooding males of the pair treatment decreased during their incubation period ($T = 0$, $N = 10$, $P = 0.005$; Fig. 2b). Body condition of males at release of young did not differ between treatments (Mann–Whitney U test: $U = 32$, $N_1 = N_2 = 10$, $P = 0.19$).

Offspring Weight and Body Length

At the point of release, offspring of single females were smaller than offspring of females in the pair treatment (Mann–Whitney U test: $U = 15$, $N_1 = 11$, $N_2 = 10$, $P = 0.004$; Fig. 3). Offspring number (pair: 11.5 [9, 19], $N = 8$; single female: 15.5 [9, 18], $N = 8$; $U = 32$, $N_1 = N_2 = 8$, $P = 1.0$) and offspring weight (pair: 27.8 mg [24.9, 30.4], $N = 10$; single female: 26.5 mg [24.9, 30.1], $N = 11$; $U = 52$, $N_1 = N_2 = 10$, $P = 0.86$) did not differ between treatments. On average 62% of the

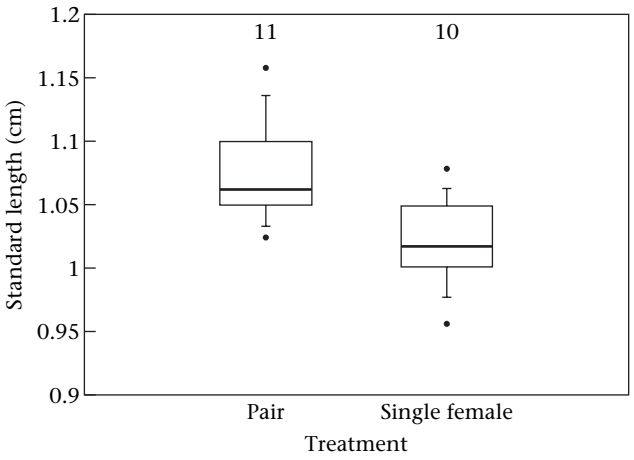

Figure 3. Standard length (SL) of offspring after release. Boxplots as in Fig. 1.

offspring of single-female clutches had not fully absorbed their yolk sac at the time of release (such young were found in six of eight analysed clutches), whereas this never happened in young released by males in the pair treatment (ratio of young with yolk remains and young without yolk remains per brood were compared; Mann–Whitney U test: $U = 8$, $N_1 = N_2 = 8$, $P = 0.01$).

Interspawning Interval and Egg Sizes

Interspawning intervals were 28% longer in the single-female treatment than in the pair treatment (Mann–Whitney U test: $U = 3$, $N_1 = 7$, $N_2 = 9$, $P = 0.001$; Fig. 4). The time from the end of female incubation until laying of the next clutch did not differ between treatments (pair: 20 days [18, 22]; single female: 20 days [16, 22.5] days; $U = 29.5$, $N_1 = 7$, $N_2 = 9$, $P = 0.837$). Female body condition at subsequent spawning did not differ between treatments (pair: 3.31 [3.17, 3.72]; single female: 3.35 [3.04, 3.66]; $U = 25$, $N_1 = 7$, $N_2 = 8$, $P = 0.78$).

There was no treatment effect on the number (pair: 20 [17.5, 27.8], $N = 6$; single female: 23 [18, 26.5], $N = 8$;

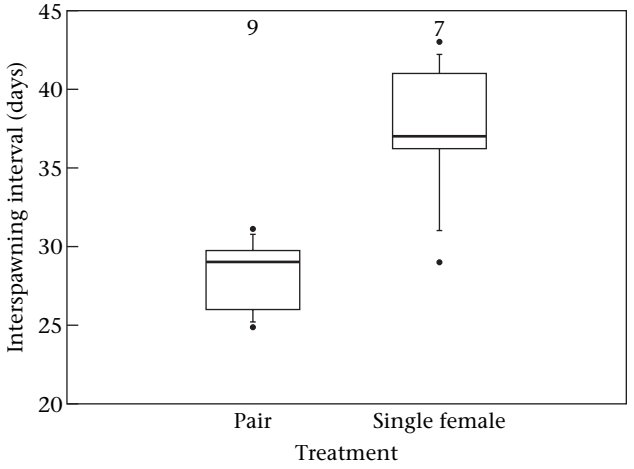

Figure 4. Interspawning interval in days. Boxplots as in Fig. 1.

Mann–Whitney U test: $U = 20.5$, $N_1 = 6$, $N_2 = 8$, $P = 0.66$) or weight (pair: 15.7 mg [14.5, 17.7], $N = 6$; single female: 15 mg [14.2, 16.3], $N = 8$; $U = 18$, $N_1 = 6$, $N_2 = 8$, $P = 0.49$) of eggs found in the next clutches produced after the experimental period.

Behavioural Observations

Activity levels, feeding rates and display rates during the nonincubation periods did not differ between pairs exposed to different treatments (Table 1).

DISCUSSION

If the survival chances of offspring can be raised significantly by shared parental care, biparental care is likely to evolve (Clutton-Brock 1991). In our experiment, offspring of unassisted *E. cyanostictus* females were smaller at release than offspring of females receiving help by their mate. Furthermore, 62% of young reared by females alone still had visible yolk sac remains at release and hence were at an earlier stage of development. Under natural conditions the survival prospects of smaller, less-developed young may be greatly reduced for several reasons. In fish, burst swimming speed increases with offspring size (Garenc et al. 1999). Both faster swimming speed and a larger body size per se are probably responsible for the observation that predation risk and the spectrum of predators of offspring decrease quickly with the latter's body size (Nagoshi 1987; Sogard 1997). In addition, larger juveniles tolerate physical extremes better than their smaller conspecifics (reviewed in Sogard 1997). We found no difference in weight of offspring between treatments. Thus, the smaller offspring of females of the single-female treatment may have had more reserves in relation to body length than the offspring released in the pair treatment. However, reserves partially stored in a yolk sac protruding from the belly may handicap the swimming abilities of young.

Females substantially prolonged their incubation period when rearing young without a male. However, they did not compensate fully for the missing incubation effort of their mate, probably because they were energetically limited. It is unclear which cue single females use to decide when to release the young. Our results did not support the hypothesis that single females stop incubating when their energy reserves fall below a threshold minimum.

Females almost never feed during incubation (C. Grüter, unpublished data). In the current study the body condition of females without male help declined on average by 14.9% during incubation. The female with the longest incubation time (21 days) lost 34.8% of her initial condition. In comparison, the condition of females with male help decreased by only 6.9% during incubation. As a consequence, females that received male help were in better condition at the release of young than unassisted females. Our results might have been confounded by the fact that females in the pair treatment were weighed twice as often as those in the single-female treatment. Owing to an additional handling stress, pair females may have lost extra weight until the end of a breeding cycle. However, in that case the existing differences in weight loss between treatments would have been reduced and hence should have influenced our results in a conservative direction.

Interspawning intervals of females were extended by 28% in the single-female treatment. The partial separation of partners in the singe-female treatment obviously did not affect intrapair behaviour after the separation (cf. Table 1) and therefore is unlikely to be responsible for the difference in interspawning intervals. Rather, this difference could be a consequence of the extended starvation period of single females that caused a decrease in body weight and hence a lower body condition by the end of incubation. In other fish species, a reduced body condition may impair both the survival and the reproductive rate of females (e.g. Smith & Wootton 1994, 1995a, b; Balshine-Earn 1995).

However, despite the lower body condition of singly caring *E. cyanostictus* females after incubation, neither the interval between the end of female incubation and the next spawning (ca. 20 days) nor female body condition after the next spawning differed between treatments. Similarly, females needed about 3 weeks to respawn when their eggs were removed immediately after spawning (C. Grüter, unpublished data). Apparently, the period between the end of female incubation and the next

Table 1. Comparison of behaviours between the two treatments during the nonincubation period (Mann–Whitney *U* tests)

	Treatment			
	Pair	Single female	*U*	*P*
Activity (% of time not hiding)				
Males	15.59 [6.4, 34.9] (6)	11.85 [5.8, 40.7] (7)	17.0	0.63
Females	15.49 [13.1, 59.9] (6)	17.09 [0.9, 59.2] (7)	21.0	1.00
Feeding (bites/10 min)				
Males	1.5 [0, 8.5] (6)	0 [0, 3.5] (7)	18.0	0.73
Females	4.75 [0, 5] (6)	5 [0.5, 7.5](7)	16.0	0.53
Displays/10 min				
Males	1.5 [0.4, 2.3] (6)	2 [0, 4] (7)	17.0	0.63
Females	4.5 [2.5, 8.8] (6)	4 [0.5, 11] (7)	19.5	0.84

Medians are given with quartiles in brackets and sample sizes in parentheses.

spawning is not influenced by the incubation duration itself or by female body condition after incubation. Similar results have been reported for other mouthbrooding cichlids (*Oreochromis mossambicus*: Smith & Haley 1988; *Ctenochromis horei*: Taborsky & Foerster 2004). In *O. mossambicus*, oocyte growth and, correspondingly, the production of ovarian steroid hormones were arrested after the first few days of brood care until mouthbrooding ended (Smith & Haley 1988). The distributions of oocytes in ovaries of wild-caught *E. cyanostictus* suggest that a similar mechanism may act in this species (Morley & Balshine 2003). Hence, we conclude that the extension of the interspawning interval in *E. cyanostictus* females caring alone is due only to the additional days of incubation.

Mouthbrooding and, consequently, starvation decreased subsequent fecundity of females in the Galilee St Peter's fish, *Sarotherodon galilaeus* (Balshine-Earn 1995). In our study, the duration of female incubation did not influence egg number or egg weight of the next clutch. Apparently, the reduced body condition of females in the single-female treatment after incubation, that is, at the time when oocyte growth is thought to resume, did not affect these variables. Egg weight and clutch size may be influenced by female body condition mainly closely before and at spawning (Taborsky & Foerster 2004), when we found no difference in body condition of females between treatments.

A possible incentive for an *E. cyanostictus* male to desert his mate and brood could be to avoid the weight loss associated with incubation. However, in our study, males prevented from assisting their mates did not have significantly better body condition at release of the young than brood-caring males, suggesting that this cost is not important. It seems more likely that the benefits of desertion may be low for males under natural conditions, because of a male-biased sex ratio and high intrasexual competition for mates and territories (Neat & Balshine-Earn 1999; Morley & Balshine 2002, 2003).

It has been suggested that biparental care is neither essential nor more effective than uniparental care in *E. cyanostictus*, and that factors other than the need for biparental care must be maintaining the evolutionary stability of the mating system (Kuwamura et al. 1989; Morley 2000; Morley & Balshine 2002). Contrary to this, our results indicate that the costs of male desertion are high because of decreased survival prospects of young, and that therefore male care is essential for breeding success in this species. The need for male brood care may favour the maintenance of long-term monogamy in *E. cyanostictus*. In our experiments, a female took about 20 days from the end of her incubation period to the next spawning, regardless of whether she had to incubate alone or whether the male took over the second half of incubation. Hence a male taking over the clutch for 2 weeks has to wait only a week until his female is ready to spawn again. In contrast, if benefits of male care were low and females incubated alone, males could instead search for a new female that is ready to spawn. This strategy may be risky, however, especially if populations have a male-biased operational sex ratio (cf. Neat & Balshine-Earn 1999; Morley & Balshine 2003).

Acknowledgments

We thank Michael Taborsky, Francis Neat and an anonymous referee for valuable comments on the manuscript. We are very grateful to Rolf Eggler and Peter Stettler for aquarium maintenance, logistic and technical support. B.T. was financed by the Austrian Science Fund (FWF P14327-B06).

References

Balshine-Earn, S. 1995. The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. *Animal Behaviour*, **50**, 1–7.

Barlow, G. W. 1984. Patterns of monogamy among teleost fishes. *Archiv für Fischereiwissenschaft*, **35**, 75–123.

Bolger, T. & Connoly, P. L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology*, **34**, 171–182.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Garenc, C., Couture, P., Laflamme, M.-A. & Guderley, H. 1999. Metabolic correlates of burst swimming capacity of juvenile and adult threespine stickleback (*Gasterosteus aculeatus*). *Journal of Comparative Physiology B*, **169**, 113–122.

Gross, M. R. & Sargent, R. C. 1985. The evolution of male and female parental care in fishes. *American Zoologist*, **25**, 807–822.

Keenleyside, M. H. A. 1991. *Cichlid Fishes: Behaviour, Ecology and Evolution*. London: Chapman & Hall.

Kuwamura, T. 1986. Parental care and mating systems of cichlid fishes in lake Tanganyika: a preliminary field survey. *Journal of Ethology*, **4**, 129–146.

Kuwamura, T. 1997. The evolution of parental care and mating systems among Tanganyikan cichlids. In: *Fish Communities in Lake Tanganyika* (Ed. by H. Kawanabe, M. Hori & N. Nagoshi), pp. 57–86. Kyoto: Kyoto University Press.

Kuwamura, T., Nagoshi, M. & Sato, T. 1989. Female-to-male shift of mouthbrooding in a cichlid fish, *Tanganicodus irsacae*, with notes on breeding habits of two related species in Lake Tanganyika. *Environmental Biology of Fishes*, **24**, 187–198.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.

Morley, J. I. 2000. Intraspecific competition and monogamy in the cichlid fish, *Eretmodus cyanostictus*. Ph.D. thesis, University of Cambridge.

Morley, J. I. & Balshine, S. 2002. Faithful fish: territory and mate defence favour monogamy in an African cichlid fish. *Behavioral Ecology and Sociobiology*, **52**, 326–331.

Morley, J. I. & Balshine, S. 2003. Reproductive biology of *Eretmodus cyanostictus*, a cichlid fish from Lake Tanganyika. *Environmental Biology of Fishes*, **66**, 169–179.

Nagoshi, M. 1987. Survival of broods under parental care and parental roles of the cichlid fish, *Lamprologus toae*, in Lake Tanganyika. *Japanese Journal of Ichthyology*, **34**, 71–75.

Neat, F. C. & Balshine-Earn, S. 1999. A field survey of the breeding habits of *Eretmodus cyanostictus*, a biparental mouthbrooding cichlid in Lake Tanganyika. *Environmental Biology of Fishes*, **55**, 333–338.

Oppenheimer, J. R. 1970. Mouthbreeding in fishes. *Animal Behaviour*, **18**, 493–503.

Oring, L. W. 1982. Avian mating systems. In: *Avian Biology* (Ed. by D. S. Fayner, J. R. King & K. C. Parkes), pp. 1–92. New York: Academic Press.

Perrone, M. & Zaret, T. M. 1979. Parental care patterns of fishes. *American Naturalist*, **113**, 351–361.

Smith, C. J. & Haley, S. R. 1988. Steroid profiles of the female tilapia, *Oreochromis mossambicus*, and correlation with oocyte growth and mouthbrooding behavior. *General and Comparative Endocrinology*, **69**, 88–98.

Smith, C. & Wootton, R. J. 1994. The cost of parental care in *Haplochromis argens* (Cichlidae). *Environmental Biology of Fishes*, **40**, 99–104.

Smith, C. & Wootton, R. J. 1995a. The cost of parental care in teleost fishes. *Reviews in Fish Biology and Fisheries*, **5**, 7–22.

Smith, C. & Wootton, R. J. 1995b. Experimental analysis of some factors affecting parental expenditure and investment in *Cichlasoma nigrofasciatum* (Cichlidae). *Environmental Biology of Fishes*, **42**, 289–302.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science*, **60**, 1129–1157.

Taborsky, B. & Foerster, K. 2004. Female mouthbrooders adjust incubation duration to perceived risk of predation. *Animal Behaviour*.

Taylor, M. I., Rueber, L. & Verheyen, E. 2001. Microsatellites reveal high levels of population substructuring in the species-poor Eretmodine cichlid lineage from Lake Tanganyika. *Proceedings of the Royal Society of London, Series B*, **268**, 803–808.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Westneat, D. F. & Sargent, R. C. 1996. Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends in Ecology and Evolution*, **11**, 87–91.

Yanagisawa, Y. 1986. Parental care in a monogamous mouthbrooding cichlid *Xenotilapia flavipinnis* in lake Tanganyika. *Japanese Journal of Ichthyology*, **33**, 249–261.