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Sex ratio and the sexual conflict about brood care in a biparental mouthbrooder

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Abstract The pay-off of deserting and leaving a mate to care for the offspring alone is generally assumed to depend mainly on the availability of alternative mating partners and on the potential spawning rate of males and females. *Eretmodus cyanostictus* is a monogamous mouthbrooding cichlid in which the clutch is successively incubated first by the female and then by the male. It has been suggested that parents are constrained to monogamy due to low remating probabilities for both sexes. We tested this hypothesis by varying the sex ratio experimentally. Mate desertion by either sex was not significantly higher when additional potential mates were present (males: 8.3%, females: 0%) than when there were no other same-sex conspecifics present (males: 0%, females: 0%). Males lost their mate to a male intruder during their incubation in 26.7% of cases. Pair members were more active and showed more aggression when same-sex conspecifics were present. Behavioural differences between treatments were strongest during the incubation period of a given sex. If no desertion takes place, sexual conflict may be expressed also on a second level, the amount of parental care each parent provides. Indeed, males took the offspring later when additional females were present, although male incubation time did not differ between treatments. A hitherto undescribed display behaviour of females was clear evidence of a conflict about the timing of shift of young. In conclusion, offering alternative mating opportunities did not strongly favour mate desertion in *E. cyanostictus*. It rather revealed a conflict between mates about when to shift the young.

Keywords Sex ratio · Sexual conflict · Brood care · Mouthbrooder · Cichlidae

Introduction

If engaging in parental care reduces the parent's future prospects for reproduction, a conflict between the two parents about the amount of parental care each parent provides should arise (Trivers 1972). The solution of this conflict should depend on the relative pay-offs of care and desertion, which often diverge substantially between the sexes (Trivers 1972; Clutton-Brock 1991), and on the decision of the partner (Maynard Smith 1977; Wade and Shuster 2002). Due to anisogamy, males are likely to gain more from deserting the brood in order to find additional mating opportunities than females do (Trivers 1972; Clutton-Brock 1991; but see Queller 1997; Wade and Shuster 2002). In addition, the benefits of desertion or care may depend on ecological factors (Emlen and Oring 1977). Theoretical models suggested that the availability of alternative mating opportunities is a key factor influencing the benefits of desertion (Maynard Smith 1977; Balshine-Earn and Earn 1998). Empirical studies in fish (e.g. Keenleyside 1983, 1985; Balshine-Earn and Earn 1998) and birds (e.g. Székely and Cuthill 2000) support this finding.

However, if caring of both parents greatly increases the survival chances of offspring, neither parent should desert (Maynard Smith 1977; Grafen and Sibly 1978; Clutton-Brock 1991). In this case, a conflict may arise about the amount of parental care each parent should provide. The outcome of this conflict is likely to be influenced by the operational sex ratio (OSR). The lower the costs of replacing the current mate, the higher the probability that an individual will exploit the parental investment of its mate and reduce its own investment (Lessells 1998). These costs are influenced by the availability of additional mates. It has been shown, for example, that male fairy martins reduced participation in

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incubation when the availability of fertile females increased (Magrath and Elgar 1997).

Eretmodus cyanostictus is one of the few mouth-brooding fish species that show biparental care and are socially monogamous (Keenleyside 1991). Evidence suggests that this species is also genetically monogamous (Taylor et al. 2003). Most mouthbrooders show female-only care and sequential polygamy (Oppenheimer 1970; Keenleyside 1991; Kuwamura 1997). A common explanation for the rarity of biparental mouthbrooding is that the mouth provides a safe incubation site for a small clutch to be protected by one parent alone (Oppenheimer 1970; Barlow 1984; Gross and Sargent 1985). Biparental care in mouthbrooders is expected to have few advantages unless (i) the size of the clutch is too large to fit into the mouth cavity of a single parent, or (ii) if both parents are needed for co-defence of the free-swimming fry after release (Perrone and Zaret 1979; Clutton-Brock 1991). Indeed, these two conditions hold for most of the biparental mouthbrooding species (e.g. Kuwamura 1986; Yanagisawa 1986; reviewed by Perrone and Zaret 1979; Clutton-Brock 1991).

In *E. cyanostictus*, the clutch is small enough to fit into a single mouth cavity and young are not defended after release (Kuwamura 1986; Kuwamura et al. 1989; Morley and Balshine 2002). Females incubate the young for about 8–12 days, and then males take over the clutch and incubate for another 10–16 days (Morley and Balshine 2002; Grüter and Taborsky 2004). While incubating, parents do not feed (Neat and Balshine-Earn 1999; Morley and Balshine 2003). Females may not be able to increase their reproductive rate greatly by deserting their mate, because they need at least 20 days to lay the next clutch after the end of their own incubation (Grüter and Taborsky 2004). It remains unclear, however, why males do not desert or expel their mates after spawning. In the field, solitary fish are frequently found (Neat and Balshine-Earn 1999). Partner-removal experiments revealed that fish of both sexes are replaced by new mates within 1 day in most cases (Morley and Balshine 2002). Hence males should be able to replace mates quickly. However, in an earlier study, we found that females without male assistance lost more weight and released smaller and less developed young (Grüter and Taborsky 2004). This suggests that male care is important to improve the survival prospects of young after release, which may be an important reason why males usually do not desert.

An alternative, though not a mutually exclusive hypothesis suggests that *E. cyanostictus* parents are constrained to biparental care and monogamy because there are few remating chances for males due to a male biased sex ratio (Neat and Balshine-Earn 1999; Morley and Balshine 2002, 2003). To test this hypothesis, we manipulated the sex ratio experienced by breeding pairs in the laboratory. Experimental changes of the OSR have been shown to induce or increase male and/or female desertion or polygyny in various cichlids (Keenleyside 1983, 1985; Balshine-Earn and Earn 1998; but see Rogers 1987; Wisenden 1994).

If a male's decision whether to desert or to join in brood care depends mainly on OSR, males should abandon their mates after spawning when additional females are present. Likewise, in the presence of additional males, females may decide to switch mates after transferring their young in order to obtain better-quality partners or territories. Still, we would expect a weaker tendency of desertion in females than in males due to the limited possibility of females to enhance their reproductive rate by pairing up with a new mate.

If a fish faces the risk of losing its mate to an intruder, it may intensify mate-guarding behaviour. For example, sex-specific aggressive behaviour may serve mate guarding and can help to promote monogamy, as has been shown in fish (e.g. Reavis and Barlow 1998; Kokita 2002; Harding et al. 2003), shrimps (e.g. Rahman et al. 2003) and birds (reviewed in Slagsvold and Lifjeld 1994). During incubation, when a fish is obviously not ready to spawn, the risk of being deserted by its mate should be higher than in non-incubation periods. At the same time, the need for support by a partner, e.g. in territory defence, should be highest during incubation. Pair members should hence be more alert towards intruders when incubating. Therefore, we compared the level of sex-specific aggression, courtship, and general activity between set-ups with different sex ratios, and we did this also for periods with and without incubation.

If desertion does not occur, a conflict over the relative amount of parental care each parent provides may arise, which is expected to depend on the availability of alternative mating opportunities (Lessells 1998). Since in *E. cyanostictus* the amount of parental care is equivalent to the incubation duration, the timing of the shift of young from female to male is of special importance in this context. When additional females are present, males are expected to postpone the transfer of young, while in the presence of additional males, females should try to advance the transfer of young. In this context, we observed a female display behaviour that has not been described before and which indicates a sexual conflict over the timing of fry transfer. We further tested for potential energetic costs for mouthbrooding females and males depending on sex ratio. Finally, since sexual conflict about parental care may impose costs on offspring (Royle et al. 2002), we compared sizes and weights of offspring at independence between the set-ups with different sex-ratios.

Methods

Study species

E. cyanostictus (Cichlidae) is endemic to Lake Tanganyika. It inhabits the shallow rocky coasts of the lake (Kuwamura 1986; Kuwamura et al. 1989), where it feeds on epilithic algae (Yamaoka 1997). Pairs aggressively defend all-purpose territories of a diameter of 1–2 m against the adjacent neighbouring pairs and floaters. Pair members raise their young in these territories and almost exclusively feed there. They leave their territories only rarely for short

excursions. Males are larger, more active and more aggressive against intruders, while females feed and hide more than males (Morley 2000). *E. cyanostictus* breeds year round and there are no marked peaks of reproductive activity over the course of the year.

Experimental conditions

We conducted our experiments between March 2002 and March 2003. Experimental fish were taken from a stock of adult fish kept at the University of Berne, consisting of imported fish from Lake Tanganyika, Zambia, and from the first-generation offspring bred in our laboratory. Experimental fish were held in 200-l tanks. A layer of sand covered the bottom of each aquarium. Sixteen flower-pot halves, two PVC tubes (5 cm in diameter) and ten PVC plates (40×20 cm) were provided as shelters. Several patches of gravel (about 20 pieces/patch) were distributed over the tank bottom to provide shelter for the offspring after release by the parents. The tanks were equipped with internal biological filters. Fish were kept at a water temperature of 26–27°C and a 13 h:11 h L:D cycle. They were fed to satiation with Tetramin flake food once a day in the morning.

Experimental design

Thirty-seven different pairs were alternately assigned to one of three treatments (see below). There was no difference in standard length of pair males or pair females between treatments [males: ANOVA: $F_{2,37}=0.061$, $P=0.94$, range: 5.9–7.4 cm standard length (SL); females: ANOVA: $F_{2,37}=0.16$, $P=0.85$, range: 4.9–6.9 cm SL].

Fish were kept in the experimental tanks for one full reproductive cycle. A pair and two additional unpaired fish were transferred from our stock tanks to the experimental tank before spawning and stayed there until the pair finished incubation. We use the simplified term “intruders” to denote the two unpaired fish that were introduced with the pair. For the three treatments, experimental tanks were stocked with the following combinations of fish:

- “Male treatment”: a pair and two male intruders (3 males:1 female sex ratio). In 7 of 12 cases, 1 of the 2 intruders was larger than the pair male.
- “Equal treatment”: a pair with a male and a female intruder (2:2 sex ratio), which were chosen to be as similar as possible to the size of the respective sex in the paired fish. While the 2 males never differed by more than 0.3 cm in SL, this occurred twice in the 12 cases for females.
- “Female treatment”: a pair and two female intruders (1:3 sex ratio). In 10 of 13 cases, 1 of the 2 intruders was larger than the pair female.

All fish were weighed on day 1 after spawning and the day after the end of total incubation. The pair was weighed again on day 6, i.e. shortly before the shift of young. The female and the two intruders were weighed the day after the shift of young. After release from incubation, young were weighed to the nearest 0.0001 g (mean measurement error: $\pm 0.95\%$, $N=20$) using a high-precision balance, and their standard length (SL) was measured to the nearest 0.1 mm (mean measurement error: $\pm 0.36\%$, $N=20$) under a binocular. Numbers of young were not comparable because apparently the adult fish consumed some of them. The incubation periods of females and males, as well as total incubation time of the pair, were recorded.

Behavioural observations

We observed the four fish in each experiment at least four times between spawning and fry transfer and six times between fry transfer and release whenever possible [total duration of observa-

tion/fish before shift: 47.6 min \pm 13.9 (mean \pm SD); after shift: 61.7 min \pm 15.8]. The observations were done between 1300 and 1600 hours and took 10 min each. The four fish were recorded simultaneously. All behavioural observations were recorded with the OBSERVER 3.0 program (Noldus, Wageningen, the Netherlands).

During the 10-min observations, we recorded two states continuously, the time fish were swimming around (“active”) and time under cover (“hiding”). Additionally, we recorded the frequencies of the following behavioural events per 10 min: “feeding” (number of bites of small food items on surfaces or on the sand), “courtship display” (the focal fish undulates its whole body with varying intensity from bending to shaking of the body), and aggressive behaviours, which consisted of “bite” (aggressive biting of another fish), “chase” (chasing another fish) and “weak aggression” (swimming towards another fish until it escapes, but not chasing it). For all social behaviours, it was recorded towards which other fish they were directed. For a more detailed description of the behaviours, see Morley (2000: Appendix C).

Aggressive displays and courtship displays towards conspecifics look almost identical to the observer (Morley 2000). However, these two behavioural categories can be distinguished from each other when taking behavioural sequences into account. Aggressive displays mostly appear in combination with other aggressive behaviours as bites, weak aggression, chases or mouth fights. So all displays that were followed by another aggressive behaviour were excluded from the category “courtship display”.

During data recording, we distinguished between large and small intruders as larger intruders may pose a higher threat to pair fish. Pair fish may therefore behave differently towards intruders of different sizes. However, due to the high aggression of pair fish towards intruders, the values of the different behaviours were zero [except for activity of large (0.09; 0–1.5) and small (0; 0–1.3) intruders] and did not differ between treatments or between large and small intruders. Also the aggression towards large and small intruders did not differ (Wilcoxon signed-rank tests; pair males: $z=-1.875$, $N=25$, $P=0.061$; pair females, $z=-0.55$, $N=25$, $P=0.58$). Therefore it is unlikely that differences in intruder size notably influenced the behaviour of pair fish during the experiment, and we do not distinguish between intruder sizes from now on.

There was a clear dominance relationship between fish. A “dominant” fish could initiate aggression towards a subdominant fish and chase it, but never the other way round. In some cases, pair males lost their dominance status to a male intruder after the latter won a fight. In these cases, intruder males became aggressive towards pair males.

Female-to-male shift display

Before the shift of young from an incubating female to her male actually took place, females showed a distinctive display behaviour that we interpret as an attempt of the female to transfer the young to the male (“female-to-male-shift display” or FMS-display). Here we describe this display for the first time. Furthermore, we measured the frequency and number of FMS-displays using of video recording. We recorded the tank every hour for 5 min 45 s starting at 0930 hours until 1930 hours (11×5 min 45 s; total 63.25 min per day). Video recording started on day 4 after spawning and ended after the shift of young from the female to the male.

Statistical analysis

For most analyses, we used non-parametric statistics, as for our small sample sizes we cannot adequately test for deviations from normality. Parametric statistics were only used when comparing size measurements (body lengths and weights), which can be generally assumed to be normally distributed in fish. Offspring body measurements were analysed using general linear mixed models (GLMM) in SPSS 10.0. SPSS uses the restricted maximum-likelihood method (REML) to decompose the variances and derive

Table 1 Comparison of behaviours between males and females (Wilcoxon matched-pairs signed-rank tests)

		Pair male	Pair female	<i>z</i>	<i>P</i> (<i>N</i>)
Aggressive behaviours/10 min		2.5 [1.3–6]	0 [0–1]	–3.30	0.001 (25)
Activity in %	Total	40.4 [25.4–61]	26.3 [13.5–48.7]	–1.59	0.118 (26)
	Before shift	37.6 [23.1–53]	13.4 [4.4–37.8]	–2.70	0.007 (26)
Courtship/10 min		2.8 [1–4]	4 [3–6]	–3.93	0.007 (24)
Feeding rate		3.5 [1.5–10.1]	16 [10.6–28.9]	–3.39	0.001 (24)

parameter estimates. Using REML GLMMs, we estimated the variance due to one random effect—brood, and one fixed effect—treatment. All tests are two-tailed. Descriptive statistics are given as medians and interquartile ranges (in square brackets) unless otherwise stated. Statistical analysis of data was performed using SPSS 10.0.

Results

Influence of sex ratio on the probability of mate change

In 2 out of 24 cases (8.3%) where males had access to additional females, the pair male expelled his mate after spawning and formed a new pair with another female (1 case in female treatment, 1 case in equal treatment). The occurrence of mate change by males was not different from zero (two treatments with additional females present compared with the male treatment, where no mate change could take place; *G*-test, $G=1.24$, $P>0.1$)

Females never actively expelled or deserted their mates. However, four pair males lost their dominance status (26.7%) and were evicted by intruder males, which paired up with the pair female in three of four cases. The occurrence of mate change in females due to male eviction did not differ from zero (two treatments with additional males present compared with the female treatment; *G*-test, $G=3.36$, $P=0.06$).

Influence of sex ratio on sex-specific aggression, courtship and activity

Aggression rates between members of a pair were almost non-existent [median of all treatments: 0; (0–0)]. Overall, pair females were less aggressive against intruders, showed more courtship displays towards the mate and had a higher feeding activity compared to pair males, but overall activity did not differ between pair members (Table 1).

The activity of males differed between treatments (Kruskal-Wallis ANOVA, $\chi^2=11.465$, $N=8,8,8$, $P=0.003$; Fig. 1a), due to differential activity during male incubation. During this period, males were more active (Mann-Whitney *U*-test, $U=13$, $N=16,8$, $P=0.001$; Fig. 1a) but not more aggressive against intruders (Mann-Whitney *U*-test, $U=35$, $N=16,8$, $P=0.081$; Fig. 1b) in those treatments where at least one male intruder was present as compared to the treatment with females only.

In contrast, activity of females differed between treatments only during female incubation (Kruskal-

Wallis ANOVA, $\chi^2=9.214$, $N=9,9,8$, $P=0.01$; Fig. 2a). When additional females were present, females were more active (Mann-Whitney *U*-Test, $U=24$, $N=9,17$, $P=0.004$; Fig. 2a). Also, overall aggression of females towards intruders differed between treatments (Kruskal-Wallis ANOVA, $\chi^2=8.872$, $N=9,8,8$, $P=0.012$). These differences were strongest during the female incubation period (Kruskal-Wallis ANOVA, $\chi^2=11.31$, $N=9,9,8$, $P=0.003$; Fig. 2b; male incubation: $\chi^2=5.99$, $N=8,8,8$, $P=0.05$), when females showed more aggression when at least one female intruder was present (Mann-Whitney *U*-test, $U=36$; $N=9,17$, $P=0.01$; Fig. 2b).

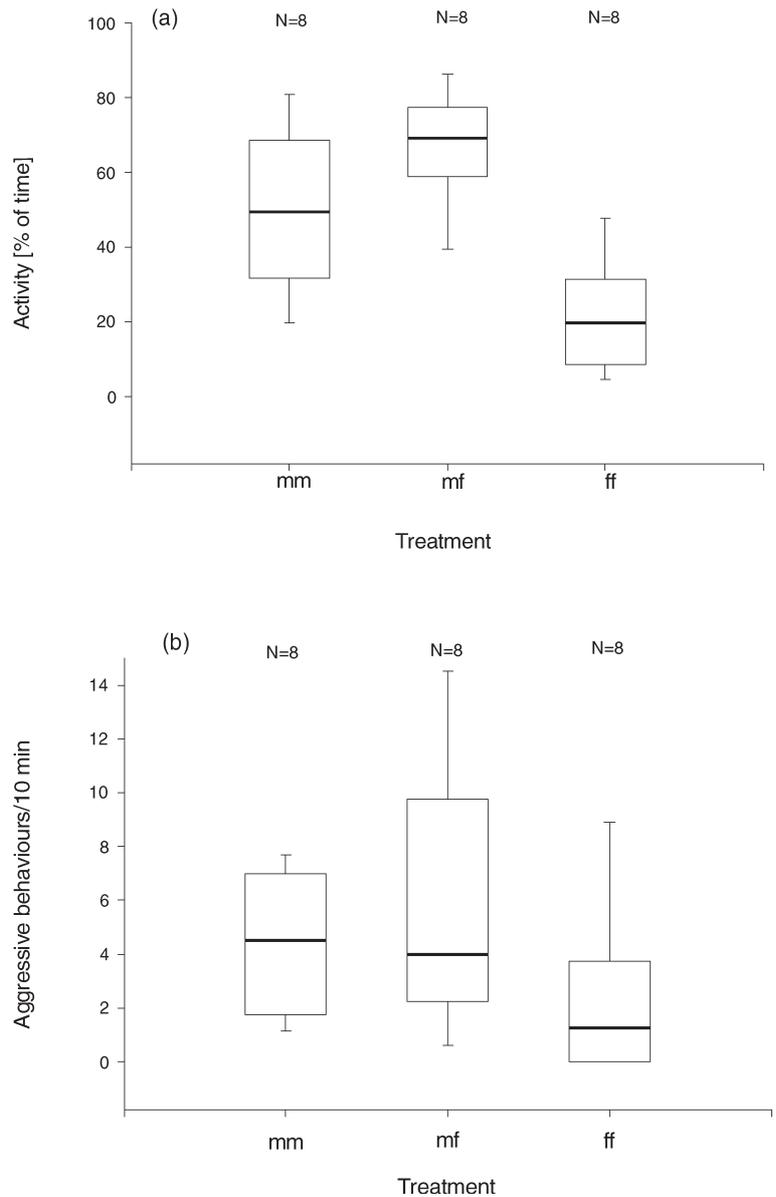
Influence of sex ratio on sexual conflict about parental investment

The probability of finishing incubation did not differ between treatments in females (in total 70% finished incubation, *G*-test, $G=0.72$, $P>0.1$) or in males (85% finished incubation, *G*-test, $G=3.04$, $P>0.1$). The main reasons for failure of incubation were swallowing of eggs or young and eviction or death of a partner.

Incubation duration of females differed between treatments (Kruskal-Wallis, $\chi^2=6.8$, $N=9,9,8$, $P=0.033$; Fig. 3). Females incubated 2 days longer when additional females were present than when no female intruder was present (Mann-Whitney *U*-test: $U=29.5$, $N=9, 17$, $P=0.009$; Fig. 5). Male incubation duration was on average 13 days (11–14.5) and did not differ between treatments (Kruskal-Wallis ANOVA, $\chi^2=3.79$, $N=7,7,7$, $P=0.15$). Total incubation time was on average 21 days (20–23.5) and did not differ between treatments (Kruskal-Wallis ANOVA, $\chi^2=3.519$, $N=7,7,7$, $P=0.17$).

The differences of female incubation times between treatments may potentially be fully controlled by a male's decision when to take the young. Indeed, we detected a specific display behaviour indicating that females try to shift the young earlier than males actually take the brood. Between day 4 and day 7 after spawning, incubating females started to show the “female-to-male shift display” when being approached by the pair male. A displaying female took a head-down position, opened her mouth and started to shake her body, remaining in this position from a short moment to several seconds. The female sometimes dropped a young while she was in the display position (Fig. 4). If the male did not take it up, the female caught the young before it touched the bottom. When the shift of young finally took place, males suddenly started to catch young dropped by the female. The number of FMS-dis-

Fig. 1 a Activity and **b** aggressive behaviours of males *after* the shift of young from females to males (*mm* male treatment, *mf* equal treatment, *ff* female treatment). Boxplots represent medians, quartiles and the 5th and 95th percentiles.



plays recorded during incubation did not differ between treatments despite the differences in female incubation times (Kruskal-Wallis ANOVA, $\chi^2=1.196$, $N=7,7,8$, $P=0.55$; Fig. 5).

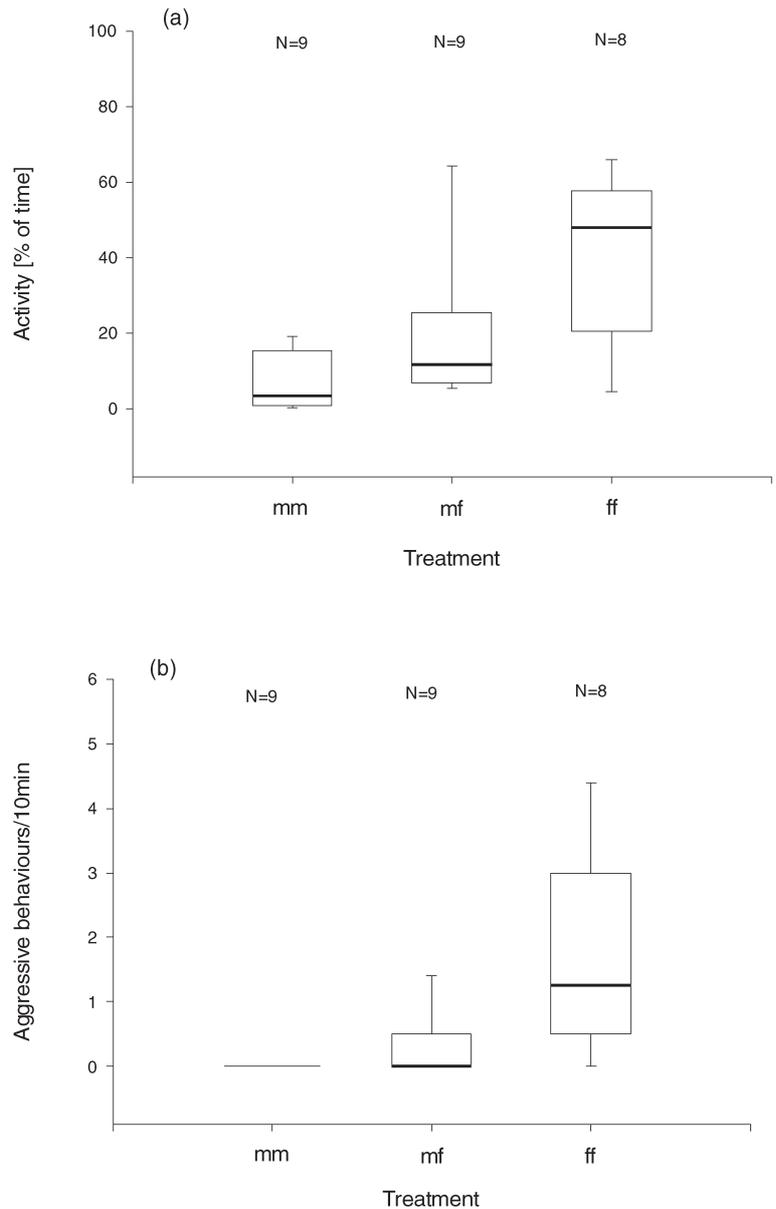
Differences in weight changes between treatments may reflect costs and benefits for the two sexes about the actual timing of shift. The weight gain of males before the shift of young differed between treatments (Kruskal-Wallis ANOVA, $\chi^2=6.628$, $N=7,8,7$, $P=0.036$). Males gained more weight in the two treatments where additional females were present (Mann-Whitney U -test: $U=18$, $N=7,15$, $P=0.014$). Male body mass gain correlated positively with female incubation duration (Pearson correlation, $r=0.69$, $P<0.001$; Fig. 6). Females lost on average 7.5% [=median; (4.8–9.7%)] of body mass during incubation, but weight loss did not differ between treatments (Kruskal-Wallis ANOVA, $\chi^2=1.1$, $N=8,8,7$, $P=0.58$). The number of FMS-displays shown by a female

correlated negatively with her weight loss during incubation (Spearman's $\rho=0.46$, $N=20$, $P=0.041$).

During male incubation, males lost on average 8.4% [=median; (3–12.2%)] of their mass while females gained 11.1% [=median; (4.4–18.6%)]. Weight changes during female incubation did not differ between treatments, neither in males nor in females (Kruskal-Wallis ANOVAs; males: $\chi^2=2.37$, $N=7,6,6$, $P=0.31$; females: $\chi^2=1.23$, $N=6,6,7$, $P=0.54$).

Standard lengths of offspring after release (young nested within brood: REML GLMM: $F_{2,16.28}=1.03$, $P=0.38$), as well as offspring weights (young nested within brood: REML GLMM: $F_{2,15.88}=1.26$, $P=0.31$), did not differ between treatments.

Fig. 2 a Activity and **b** aggressive behaviours of females *before* the shift of young from females to males. Boxplots as in Fig. 1.



Discussion

The outcome of a sexual conflict about the amount of parental care strongly depends on the different relative pay-offs of care or desertion for males and females (Trivers 1972; Clutton-Brock 1991). Often males can increase their reproductive rate by deserting their mate and the current brood and by seeking additional mating opportunities, while females usually cannot increase their reproductive rate by multiple matings (Trivers 1972; Clutton-Brock 1991).

In *E. cyanostictus*, it has been suggested that parental desertion is unlikely due to intra-sexual aggression and low availability of alternative mating partners for males due to a male-biased sex-ratio (Neat and Balshine-Earn 1999; Morley and Balshine 2002). We investigated how variation in the availability of potential alternative mates

influences the probability of switching mates and the readiness to care for the offspring. Experimental changes in mate availability have been shown to favour polygyny or desertion by either sex in other cichlids (Keenleyside 1983,1985; Balshine-Earn and Earn 1998).

In our study, males changed mates during female incubation in 8.3% of all cases, which is a low proportion given that female intruders were often larger than their mate and closer to spawning condition. The expelled females continued to incubate and released few small young. One male that abandoned his current incubating female and mated with a small female intruder switched back to the original mate during incubation of the new mate. Several reasons may explain why males did not change mates more often. Grüter and Taborsky (2004) showed that the consequences of male absence can be severe for offspring and female condition, both of which

Fig. 3 Incubation duration of females in days. Boxplots as in Fig. 1.

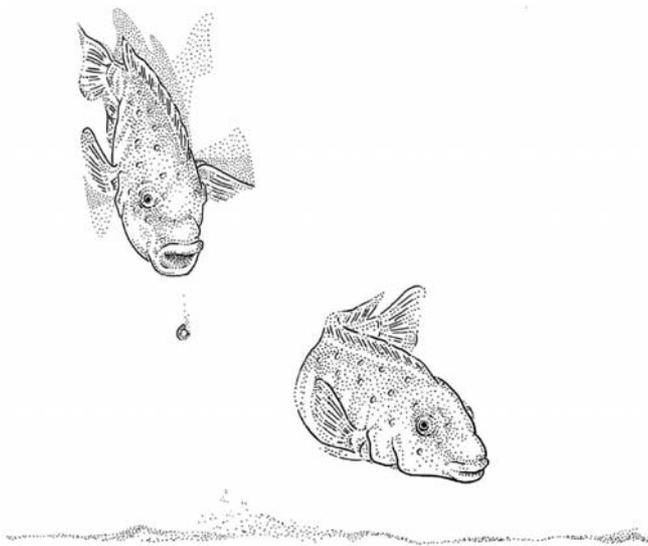
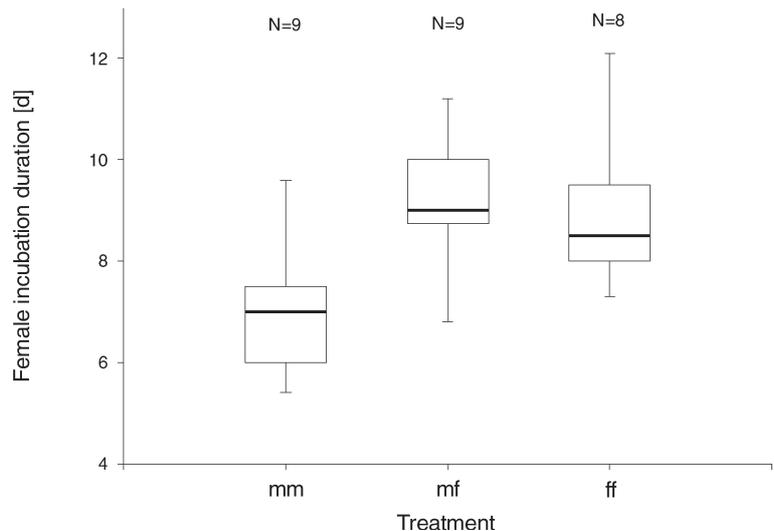


Fig. 4 An FMS-display: a female in a head-down position shakes her body until a young drops out of her mouth. The male does not take the young and turns off (drawing by Nadja Stadelmann).

may lead to reduced offspring survival. Thus, selection may favour biparental care in *E. cyanostictus* and constrain the flexibility of the mating system (see also Rogers 1987; Wisenden 1994).

Sex-specific aggression, especially in females, may be another reason for rare partner desertion, and has been shown to stabilise or increase monogamy in other fish (e.g. Reavis and Barlow 1998; Kokita 2002; Harding et al. 2003), shrimps (e.g. Rahman et al. 2003) and birds (reviewed in Slagsvold and Lifjeld 1994). When at least one intruder female was present, females were more active and aggressive, as compared to the male-only treatment. Correspondingly, males were more active in the treatments with male intruders present, but only when incubating themselves. In general, differences in aggressive behaviour and activity between treatments were most apparent or strongest during a parent's own incubation

period. During female incubation, females are more in danger of being deserted or expelled, while during male incubation, the risk of a male losing its mate and territory to an intruder should be highest. Indeed, this happened in 26.7% of the cases where at least one additional male intruder was present, which may indicate an important cost of incubation for males. Males with a clutch in their mouths are likely to have difficulties in mouth fights and aggressive biting, and thus have a reduced ability to defend their mate and territory, while incubating females are defended by their larger mates. Behavioural shifts during incubation seem to be a reaction to these increased risks.

When pairs remained stable over the total incubation period, a sexual conflict became apparent about the timing of the shift of young from females to males, which ultimately determined the amount of parental care performed by females. We interpret the described "female-to-male shift display" as an explicit sign of conflict between males and females. In extreme cases, a female had to display more than 1,000 times for up to 7 days (estimate based on counts of video recordings) until the male took over the young. This behaviour may be energetically costly and it may increase the probability of attracting predators. Contrary to our expectation, we found that females who showed the FMS-display more often lost *less* body mass during incubation. This may indicate that displaying does not afford an enhanced amount of energy. Alternatively, females that lose body mass more slowly during incubation for some other reason may be able to also afford a higher investment in FMS-displays. We did not detect any differences in the frequency of displays between treatments, which may be due to small sample size and a very strong inter-individual variance in display frequency. The influence of body condition and the roles of the sexes for the outcome of this conflict is currently being investigated.

When at least one additional female was present, males took over the offspring 2 days later than in the absence of additional females. This corresponds to an extension of 28.6% of female incubation time as compared to the male

Fig. 5 Total number of FMS-displays of females towards their mates until the shift of young from female to male occurred. Boxplots as in Fig. 1.

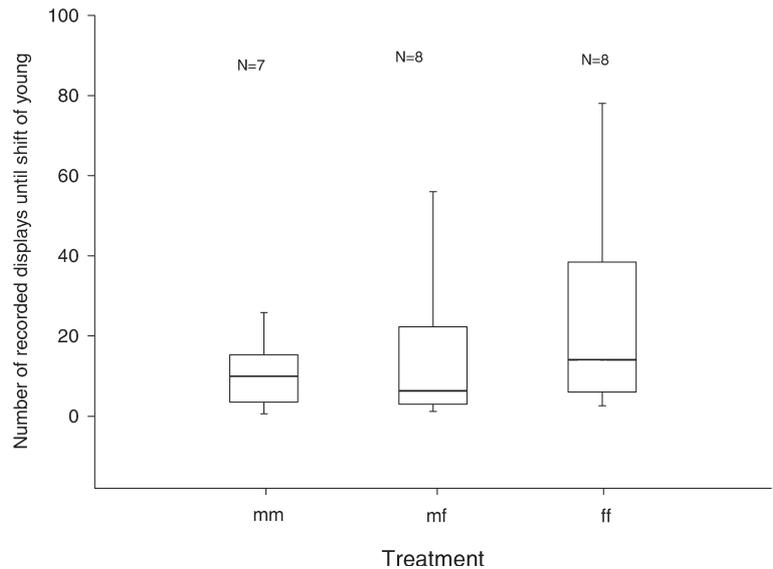
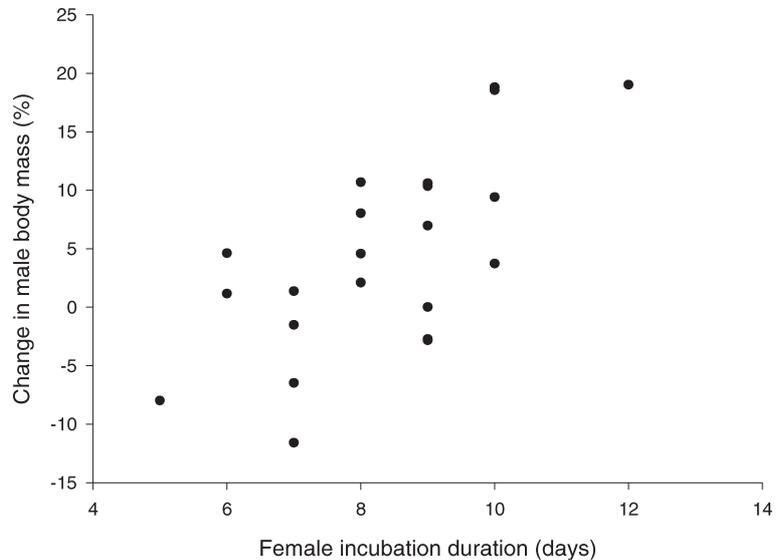


Fig. 6 Relationship between the duration of female incubation and the change in male body mass before the shift of young.



treatment. During this period, males probably build up reserves before the starvation period during male incubation, which is reflected by the positive relationship between female incubation time and the increase in male body mass during this period. These results are in accordance with the prediction that a male should exploit his partner's investment more strongly when the costs of replacing it are low in the face of alternative mating opportunities being readily available (see Lessells 1998). However, males did not seem to reduce their incubation period when females had incubated longer.

Females lost 7.5% of their weight during incubation. Although females incubated longer in the presence of additional females, female weight loss did not differ significantly between treatments. As the variation between individuals was large, our sample size was probably too small to detect any differences. Body size and mass of young also did not differ between treatments. As the total incubation times did not differ between treat-

ments, offspring may be relatively unaffected by the apparent conflict between the sexes.

In conclusion, our results show that there is a sexual conflict about the *quantity* of parental care in *E. cyanostictus*. The FMS-display allows pair partners to negotiate actively about their share in broodcare. However, males appear to be in a superior position to decide about the duration of female *and* male incubation. This is markedly different from the usual pattern of biparental care, where males and females take turns in incubation or provisioning of young repeatedly (e.g. Clutton-Brock 1991). In those species, both parents would have the chance to reduce their own workload, leaving a greater share of work for the partner, which should eventually lead to the evolution of a stable equilibrium (e.g. Barta et al. 2002). In contrast, it is as yet unclear how stability of the relative shares of male and female incubation can be achieved in *E. cyanostictus*.

Regarding the *maintenance* of biparental care, mechanisms preventing the opportunity of mate switching may play an important role, such as sex-specific aggression and mate-guarding. In contrast to its influence on the quantity of brood care, the decision of partners whether to care or not does not appear to depend strongly on the availability of alternative mating partners in *E. cyanostictus*. Male incubation appears to enhance the survival of young greatly (Grüter and Taborsky 2004), and may hence be favoured over desertion via natural selection. Future field work should reveal whether additional ecological factors like the distribution of food and suitable territories may influence the propensity for desertion, and whether replacements of pair fish by intruders play a significant role in the mating system under natural conditions.

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References

- Balshine-Earn S, Earn DJD (1998) On the evolutionary pathway of parental care in mouth-brooding cichlid fish. *Proc R Soc Lond B* 265:2217–2222
- Barlow GW (1984) Patterns of monogamy among teleost fishes. *Arch Fischereiwiss* 35:75–123
- Barta Z, Houston AI, McNamara JM, Székely T (2002) Sexual conflict about parental care: The role of reserves. *Am Nat* 159:687–705
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–232
- Grafen A and Sibly R (1978) Model of mate desertion. *Anim Behav* 26:645–652
- Gross MR, Sargent RC (1985) The evolution of male and female parental care in fishes. *Am Zool* 25:807–822
- Grüter C, Taborsky B (2004) Mouthbrooding and biparental care: an unexpected combination, but male brood care pays. *Anim Behav* 68:1283–1289
- Harding JA, Almany GR, Houck LD, Hixon MA (2003) Experimental analysis of monogamy in the Caribbean cleaner goby, *Gobiosoma evelynae*. *Anim Behav* 65:865–874
- Keenleyside MHA (1983) Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim Behav* 31:683–688
- Keenleyside MHA (1985) Bigamy and mate choice in the biparental cichlid fish *Cichlasoma nigrofasciatum*. *Behav Ecol Sociobiol* 17:285–290
- Keenleyside MHA (1991) Cichlid fishes—behaviour, ecology and evolution. Chapman & Hall, London
- Kokita T (2002) The role of female behaviour in maintaining monogamy of a coral-reef filefish. *Ethology* 108:157–168
- Kuwamura T (1986) Parental care and mating systems of cichlid fishes in lake Tanganyika: a preliminary field survey. *J Ethol* 4:129–146
- Kuwamura T (1997) The evolution of parental care and mating systems among Tanganyikan cichlids. In: Kawanabe H, Hori M, Nagoshi N (eds) Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto, pp 57–86
- 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. *Environ Biol Fish* 24:187–198
- Lessells CM (1998) Sexual conflict in animals. In: Keller L (ed) Levels of selection. Princeton University Press, Princeton, pp 74–99
- Magrath MJL, Elgar MA (1997) Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proc R Soc Lond B* 264:1731–1736
- Maynard Smith J (1977) Parental investment: a prospective analysis. *Anim Behav* 25:1–9
- Morley JI (2000) Intraspecific competition and monogamy in the cichlid fish, *Eretmodus cyanostictus*. PhD Thesis, University of Cambridge
- Morley JI, Balshine S (2002) Faithful fish: territory and mate defence favour monogamy in an african cichlid fish. *Behav Ecol Sociobiol* 52:326–331
- Morley JI, Balshine S (2003) Reproductive biology of *Eretmodus cyanostictus*, a cichlid fish from Lake Tanganyika. *Environ Biol Fish* 66:169–179
- Neat TB, Balshine-Earn S (1999) A field survey of the breeding habits of *Eretmodus cyanostictus*, a biparental mouthbrooding cichlid in lake Tanganyika. *Environ Biol Fish* 55:333–338
- Oppenheimer JR (1970) Mouthbreeding in fishes. *Anim Behav* 18:493–503
- Perrone M, Zaret TM (1979) Parental care patterns of fishes. *Am Nat* 113:351–361
- Queller DC (1997) Why do females care more than males? *Proc R Soc Lond B* 264:1555–1557
- Rahman N, Dunham DW, Govind CK (2003) Social monogamy in the big-clawed snapping shrimp, *Alpheus heterochelis*. *Ethology* 109:1–17
- Reavis RH, Barlow GW (1998) Why is the coral-reef fish *Valenciennea strigata* (Gobiidae) monogamous? *Behav Ecol Sociobiol* 43:229–237
- Rogers W (1987) Sex ratio, monogamy and breeding success in the Midas cichlid (*Cichlasoma citrinellum*). *Behav Ecol Sociobiol* 21:47–51
- Royle NJ, Hartley IR, Parker GA (2002) Sexual conflict reduces offspring fitness in zebra finches. *Nature* 416:733–736
- Slagsvold T, Lifjeld JT (1994) Polygyny in birds: the role of competition between females for male parental care. *Am Nat* 143:59–94
- Székely T, Cuthill IC (2000) Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. *Proc R Soc Lond B* 267:2087–2092
- Taylor MI, Morley JI, Rico C, Balshine S (2003) Evidence for genetic monogamy and female-biased dispersal in the biparental mouthbrooding cichlid *Eretmodus cyanostictus* from Lake Tanganyika. *Mol Ecol* 12:3173–3177
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Heinemann, London, pp 136–179
- Wade MJ, Shuster SM (2002) The evolution of parental care in the context of sexual selection: a critical reassessment of parental investment theory. *Am Nat* 160:285–292
- Wisenden BD (1994) Factors affecting mate desertion by males in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Behav Ecol* 5:439–447
- Yamaoka K (1997) Trophic ecomorphology of tanganyikan cichlids. In: Kawanabe H, Hori M, Nagoshi N (ed) Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto, pp 25–56
- Yanagisawa Y (1986) Parental care in a monogamous mouthbrooding cichlid *Xenotilapia flavipinnis* in lake Tanganyika. *Jpn J Ichthyol* 33:249–261