

Asymmetric sexual conflict over parental care in a biparental cichlid

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Abstract Theoretical models predict that parents should adjust the amount of care both to their own and their partner's body condition. In most biparental species, parental duties are switched repeatedly allowing for repeated mutual adjustment of the amount of care. In the mouthbrooding cichlid *Eretmodus cyanostictus*, terms are switched only once with females taking the first share. The timing of the shift of the clutch between mates strongly determines both partners' brooding period and thereby their parental investment. Females signal their readiness to transfer the young several days before the male finally takes them, suggesting sexual conflict over the timing of the shift. In a lab experiment, we reduced the body condition of either the female or the male of a pair to test whether energy reserves affect the timing of the shift and whether female signalling behaviour depends on energetic state. Males with a lowered condition took the young later and incubated for a shorter period, which prolonged the incubation time of their female partners. When female condition was lowered, female and male incubation durations remained unchanged, although females signalled their readiness to shift more intensely. Our results suggest that males adjust their parental investment to own energy reserves but are unresponsive to their mate's condition. Females appear to carry the entire costs for the male's

adjustment of care. We propose that intrinsic asymmetries in the scope for mutual adjustment of parental investment and the costs of negotiation crucially influence solutions of the conflict between sexes over care.

Keywords Sexual conflict · Parental care · Negotiation games · Cichlids

Introduction

Differences in relative costs and benefits of parental investment between sexes can generate conflict about parental care (Trivers 1972; Parker et al. 2002; Houston et al. 2005). Asymmetries between sexes in the costs of care can be caused, among others, if parents differ in the amount of energy reserves they have available. Often, brood care is energetically demanding (Golet and Irons 1999; Horak et al. 1999), and it can reduce the residual reproductive value of a caring parent (Daan et al. 1990). Parents in poor condition may be forced to terminate brood care and to give up their brood (reviewed in Clutton-Brock 1991; Székely et al. 1996). Thus, parents are expected to adjust the amount of care to their own and their partners' body condition. If both parents care but one mate is forced to reduce its share, e.g. by experimentally lowered reserves or increased workload, the partner usually compensates for this reduction to some extent (e.g. *Aequidens paraguayensis*, Mrowka 1982; *Sturnus vulgaris*, Wright and Cuthill 1989; *Nectarinia osea*, Markman et al. 1995, 1996; *Parus major*, Sanz et al. 2000; *Charadrius alexandrinus*, Székely and Cuthill 2000; *Eretmodus cyanostictus*, Grüter and Taborsky 2004).

Game theoretical models suggest two avenues how the division of labour for the current brood can be determined in *developmental* time by negotiation. In 'competitive

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games', a parent should only partially compensate for a reduction in its partner's effort to prevent exploitation of its own effort by the partner. The equilibrium investment of both partners is then expected to be below the equilibrium of best responses in a game without prior negotiation (Houston and Davies 1985; McNamara et al. 1999). In 'cooperative games', partners bargain promises or threats about the investment they are willing to pay or to deny that are credible and fully binding. For example, the decision of a male to care for the brood may be influenced by honest signals of its female partner indicating that her body condition is too low to perform brood care alone (Barta et al. 2002; Houston et al. 2005).

In most biparental species, partners take turns in parental duties repeatedly. Parents incubate, defend or provision the young alternately, while their partners have the opportunity for recovery and self-maintenance (e.g. Székely and Cuthill 2000), and also to adjust the mutual investment during a potential negotiation process (McNamara et al. 1999, 2003). Only rarely do the parents care for the brood in non-overlapping terms with each parent providing care during a single term only. This pattern occurs in a number of mouthbrooding cichlids of the East African Lake Tanganyika (*Xenotilapia boulengeri*, *Tanganicodus irsacae* and *E. cyanostictus*; Kuwamura et al. 1989). For example, *E. cyanostictus* females incubate the young for 7–10 days before transferring them to the male that broods for another 12–16 days, after which, the young are independent. Mouthbrooding is energetically costly. No food is taken up during incubation, which results in substantial weight losses of male and female parents (Grüter and Taborsky 2004, 2005). Because of the peculiar sequence of care taking, female *E. cyanostictus* would only be able to reduce their share in brood care if males cooperate (i.e. take up the young), whereas they have no or little control over the duration of male care. Given the strong asymmetry in the potential to control decisions and given the fact that females can almost double the length of their incubation period if males are experimentally removed (Grüter and Taborsky 2004), it is surprising that males usually take the larger share of brood care in this species, and this may suggest a cooperative division of labour between partners.

However, earlier observations on the behavioural interactions between pair members during incubation casts doubt on a cooperative share of duties in *E. cyanostictus* (Grüter and Taborsky 2005). Females signal their readiness to transfer the young to their partner repeatedly, several days before the shift takes place, by showing a peculiar display of behaviour. During this 'female-to-male shift display' or 'FMS display', females take a head-down position, open the mouth and shake the body for a short moment to several seconds. During the display, females sometimes drop a young, which they quickly catch before it

reaches the ground (see Grüter and Taborsky 2005 for a graphical illustration of this behaviour). The shift of duties between pair partners occurs when the male finally catches the dropped young and keeps it in its buccal cavity. Apparently, a behavioural negotiation process between partners takes place, where males do not respond immediately to the transfer signals of females. Nevertheless, females might gain partial control over the timing of the shift of young by varying the intensity of FMS displays.

To explore the roles and the potential for control of males and females in this negotiation process, we aimed to perturb the equilibrium division of labour experimentally. We achieved this by manipulating the energy reserves of breeders, as incubating parents continuously lose weight, and therefore, incubation duration should be critically limited by available reserves. We food-deprived either male or female of a pair independently from each other for a limited period of time to lower their body condition and recorded incubation durations, intensity of female signalling behaviour and potential fitness consequences of lowered condition on parents and offspring.

As a reaction to lowering the body condition, we expected females to attempt to transfer the clutch earlier than females in good condition by signalling their increased need by a higher rate of FMS displays. Accordingly, we expected males in low condition to take the young later and incubate shorter than when in good condition. Predictions about the responses of partners to their mates' lowered condition differ for cooperative and competitive games between partners. If the interactions we observe result from a cooperative adjustment of the level of effort, females should reduce the rate of FMS displays when male condition was experimentally lowered, thereby signalling their readiness to incubate for a longer period. When female condition had been reduced, males should readily respond to increased female signalling by taking the young earlier, and they should then incubate for a longer period. If partners engage in a competitive game over care, females should maintain their signalling rate even when male condition is reduced to prevent males from exploiting female effort. Similarly, when female condition is reduced, males should not or only hesitantly respond to their females' increased signalling effort.

Materials and methods

Experimental set-up

The experiments were conducted at the University of Bern using wild-caught fish and their first- and second-generation offspring. Before and after experiments, fish were kept in 250- to 450-l stock tanks, where they formed pairs and co-

defended all-purpose territories against conspecifics, similar as in the natural habitat of this species. All fish were kept at a water temperature of $27 \pm 1^\circ\text{C}$ and a light/dark cycle of 13:11 h with 10-min twilight at the beginning and end of the light phase to mimic the day lengths at Lake Tanganyika.

For the experiments, we divided six 200-l aquaria into 12 similar-sized 100-l compartments by transparent Plexiglas partitions. The compartments were equipped with a 3-cm layer of river sand and an internal biological filter. Eight flower pot halves, a polyvinyl chloride (PVC) tube, a PVC plate and coarse gravel provided shelters for adults and young. Each compartment was stocked with one *E. cyanostictus* pair that had been taken from the stock tanks (standard lengths [SL] and weights [mean \pm SD] of females, 7.03 ± 0.33 cm, 10.85 ± 1.54 g; males, 7.42 ± 0.25 cm, 12.34 ± 1.23 g). The transparent partitions between the compartments allowed visual contact between the two pairs of a tank but almost entirely prevented water flow and thereby the exchange of olfactory cues between them. This should help to stabilize the pair bonds before and between the actual experimental periods (Itzkowitz and Draud 1992), as from earlier observations, we knew that pairs divorce more likely when kept in complete isolation from conspecifics (Grüter and Steinegger, personal observations). However, as soon as one or both experimental pairs had spawned, an opaque PVC partition was placed between the compartments in addition to the transparent partition preventing further visual contact between pairs until incubation was terminated to avoid the influence of conspecifics on incubation durations (see Grüter and Taborsky 2005).

Experimental pairs were checked daily for pairing and breeding status. If a pair member showed continued aggression against its mate or if a fish had signs of injury, we separated the pair members immediately. Before, between and after experiments, fish were fed twice per day. They were fed with TetraMin flake food (4 days a week), frozen zooplankton (2 days) and TetraPhyll flake food (1 day; both flake food types produced by Tetra, Blacksburg, VA).

Main experiment

Fifteen pairs were allocated successively to three treatments: (1) male and female body condition not manipulated during incubation (control treatment); (2) male body condition reduced before incubation (male treatment); (3) female body condition reduced before incubation (female treatment). To avoid biases due to sequence effects, we balanced the sequence of treatments each pair was exposed to.

Control treatment Male and female of a pair were separated daily for 90 min by a coarse plastic mesh during the entire female incubation period. During this time, the male was fed ad libitum with a food cube made of TetraMin, zooplankton

and agarose gel as carrier medium. At the end of the 90-min period, the remainders of the food cube were removed. Females were not offered food because they do not feed during incubation (Morley 2000; Grüter and Taborsky, personal observations). During male incubation, females were fed following the standard feeding regime (see above), whereas males do not feed when mouthbrooding.

Male treatment As in the control treatment, males and females were separated every day for 90 min by the plastic mesh during female incubation. However, in this treatment, no food was provided for the male. This treatment aimed to reduce the male's body condition before he started to incubate. The experimental starvation period of about 10 days (i.e. during the female incubation period) is not expected to harm the fish as (1) fish of this size can be easily kept without food for up to 30 days without negative effects on their health (e.g. incubating females of the cichlids *Tropheus moorii* and *Ctenochromis horei* starve deliberately for up to 6 and 4 weeks, respectively; Yanagisawa and Sato 1990; Taborsky and Foerster 2004), and (2) some *E. cyanostictus* starve naturally during incubation for maximum periods that can be longer than 10 days (Morley 2000). As in the control treatment, females were fed normally during male incubation.

Female treatment To lower the body condition of females before they start to incubate, we aimed to reduce their ration for approximately 10 days before spawning. In the laboratory, the period between the shift of young from females to males and next spawning is, on average, 20 days (Grüter and Taborsky 2004). Therefore, we starved females from the tenth day after the shift of a brood until the next spawning occurred, whereas males received a food cube every day during a 90-min period of separation from the female. However, as we did not know whether female starvation might inhibit oocyte maturation, we provided females with food ad libitum once every 5 days during the female treatment until spawning took place. All spawning occurred within 28 days after the onset of the female treatment. During female and male incubation, the set-up and feeding procedure were identical to the control treatment.

On the day the young were released by the male and were independent, we measured adult SL (nearest 0.5 mm) and weight (nearest 0.01 g). We counted the young, measured their SL (nearest 0.1 mm) and weighed them to the nearest 0.1 mg with a high-precision balance. For weighing, we placed each individual young in a small Petri dish containing a moistened cotton pad, which removed excess water from the body surface but prevented it from becoming dry. Then the young was placed back in a holding container. The difference between the dish with and without fish represents the wet weight of the young.

Afterwards, adults were placed back in their experimental compartment, and the young were transferred to a separate stock tank for juvenile fish.

When a pair had completed all three treatments, it was transferred back into its original stock tank. Pairs that divorced before completing all three treatments were moved to stock tanks containing juvenile fish. In most cases, the divorced partners re-mated soon again and were used again for the experiments.

Six pairs completed incubation successfully in all three treatments, one pair completed control and female treatment, six pairs completed only one treatment (three female treatments, two male treatments, one control) and two pairs did not breed successfully in any treatment. Brood failures were caused by male aggression (female abandoned eggs or had to be separated from male) or by male handicaps obliging the female to incubate alone (one male got blind, and one male had a deformed mouth).

Effect of food deprivation on female condition and egg production

In an additional series of experiments, we tested for a potential effect of food deprivation on female clutch size, egg mass and interspawning interval (defined here as interval between the end of female incubation and the next spawning; see Grüter and Taborsky 2004). Ten pairs were exposed to a female treatment (female body condition reduced) and a control treatment (no manipulations of condition) in random order. Experimental set-up and procedure until spawning were identical to the main experiment, but in these experiments, we removed the eggs from females shortly ($2.65 \text{ days} \pm 0.70 \text{ SD}$) after spawning. Females were coaxed to release their eggs in a plastic dish with water by holding the fish almost in a head-down position and dipping their head in and out the water one or two times (Morley 2000; Grüter and Taborsky 2004). Females started to release their eggs immediately, and the entire procedure takes between 5 and 10 s depending on clutch size. We measured female SL and weight as described above and weighed each individual egg. To take the fresh weight of an egg, we placed it on a piece of aluminium foil, dried its surface gently with a piece of tissue, waited for 3 min to let the remaining water evaporate and then weighed it to the nearest 0.1 mg with a high-precision balance. Subsequently, each egg was dried at 75°C for 24 h and weighed again.

Video analyses

According to Grüter and Taborsky (2005), the FMS display is not shown before day 4 after spawning. Therefore, we

took real-time video recordings during the daily 13-h light period from day 4 after spawning until all young had been shifted to the male. Indeed, in our experiments, the earliest FMS displays occurred on day 5 after spawning, but most females started even later (see “Results”). One pair shifted the young already on day 4 during the first treatment, and therefore, this pair was filmed from day 1 after spawning in the two subsequent treatments. No FMS display was shown in this pair during these trials. The recordings suggest that the male aggressively forced the female to shift the young. The recordings of pairs successfully breeding in all three treatments were analyzed in real time to count the number of FMS displays. To avoid observer bias, videotapes were analyzed in a random order while the observer (M.S.) was blind with regard to treatment and date.

Statistical analysis

Statistical analysis was carried out using SPSS 12.0. All statistical tests are two-tailed. For sample sizes below ten, we used non-parametric tests, as we cannot test reliably for a deviation from a normal distribution of data for such small sample sizes. Medians and quartiles (in square brackets) are given as descriptive statistics for these data.

Results

Main experiment

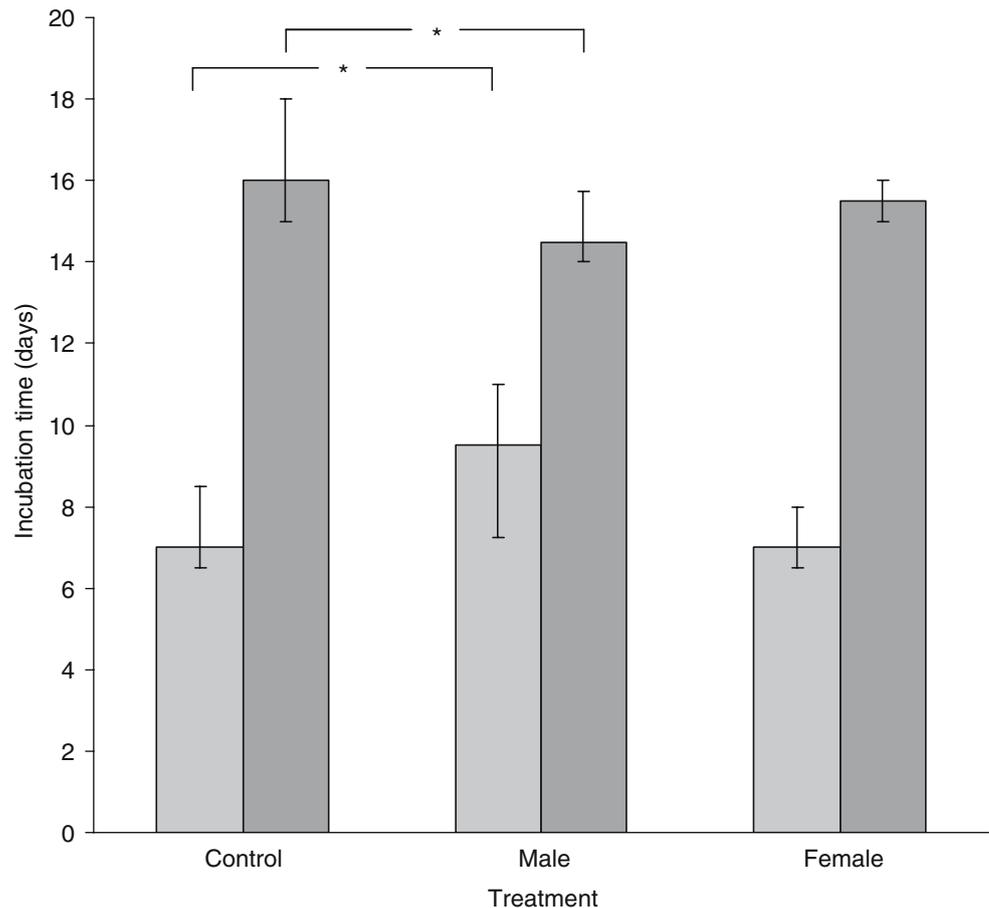
When males were food-deprived, females incubated on average 2.5 days longer than in control treatments (Wilcoxon matched-pairs signed ranks test, $T=0$, $N=6$, $P=0.043$; Fig. 1), whereas males incubated on average 1.5 days shorter (Wilcoxon test, $T=0$, $N=6$, $P=0.043$) compared to controls. At the end of incubation, males were on average 3.3% lighter after a male treatment (11.26 g [11.16, 12.45]) than after a control treatment (12.18 g [11.52, 13.10]), but this difference was not significant (Wilcoxon test, $T=1$, $N=5$, $P=0.08$).

In contrast, in the female treatment, neither female nor male incubation times differed significantly from the control treatment (female incubation time, $T=4$, $N=7$, $P=0.72$; male incubation time, $T=0$, $N=6$, $P=0.11$; Wilcoxon tests; Fig. 1).

Total incubation time did not differ between treatments (female treatment, 23 days [22, 24]; male treatment, 23.5 days [22.25, 25.5]; control, 24 days [21.5, 25]; $N=6$ in all cases; female treatment vs control, $T=4$, $P=0.17$; male treatment vs control, $T=2$, $P=0.14$; Wilcoxon tests).

As expected, independent young were larger when they had been incubated for longer periods (regression analysis, $SL=0.13 \text{ incubation time} + 7.77$, $R^2=0.41$, $N=15$, $P=0.01$).

Fig. 1 Female (light grey bars) and male (dark grey bars) incubation time during control, male and female treatments. Medians and quartiles are shown. * $P < 0.05$



This corresponds to an estimated growth increment of 0.13 mm for each extra day of incubation assuming an approximately linear growth of larvae. Clutch sizes and offspring lengths and weights did not differ when comparing female and male treatments with the control treatment, respectively (Table 1).

Usually, females started to show FMS displays from day 7 (=median; quartiles, 6, 8 days; minimum, 5 days) after spawning. During controls, a maximum total number of 188 displays was observed (daily maximum, 166 displays), whereas the highest total display frequency (372 times) occurred in a female treatment (daily maximum in female treatments, 214 displays). In female treatments, FMS displays were shown at a significantly higher daily rate (Wilcoxon test, $T=0$, $N=6$, $P=0.028$; Fig. 2) and in higher total numbers during female

incubation (Wilcoxon test, $T=0$, $N=6$, $P=0.028$), whereas neither the daily rate (Wilcoxon test, $T=1$, $N=5$, $P=0.14$; Fig. 2) nor the total frequency of displays (Wilcoxon test, $T=4$, $N=5$, $P=0.72$) differed between male treatments and controls.

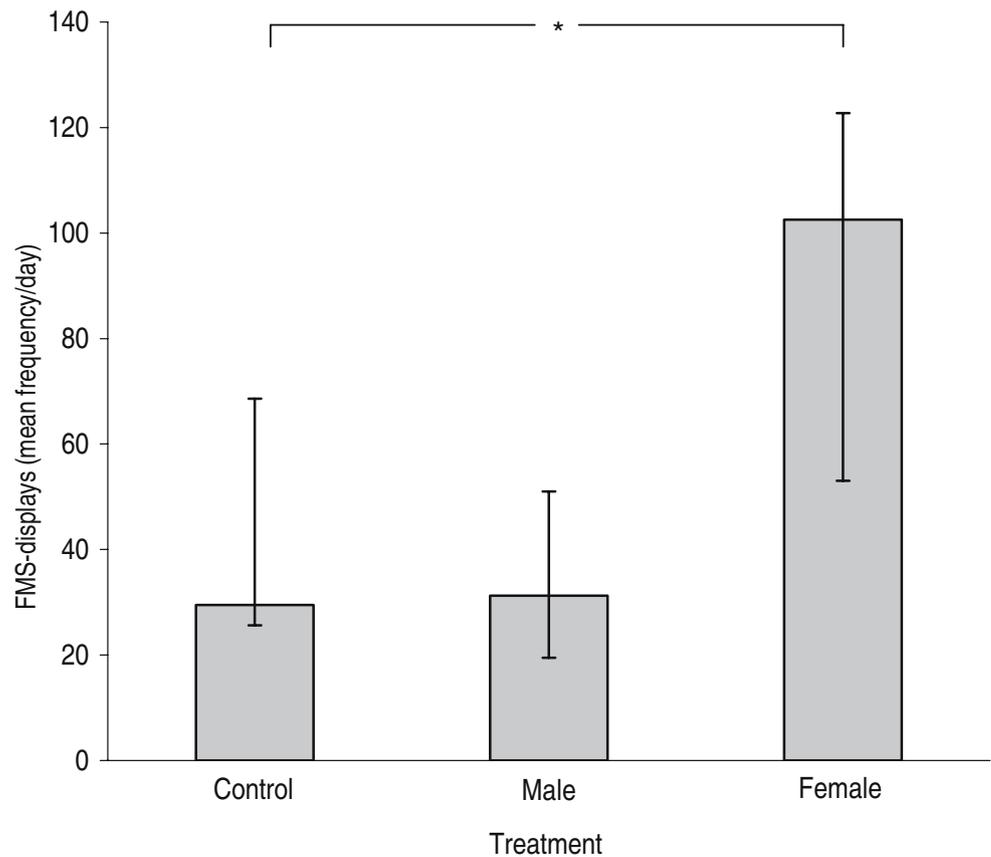
Effect of food deprivation on female condition and egg production

On the day after spawning, females were on average 3.9% lighter when having been in a female treatment during the previous breeding cycle than when having been in a control treatment before (Wilcoxon test, $T=1$, $N=8$, $P=0.017$; Fig. 3). Interspawning intervals, clutch sizes and fresh- and dry-egg weights were not significantly affected by the female treatment (Table 2).

Table 1 Comparison of clutch size, offspring size (SL) and offspring weight after release between the control vs female and male treatment, respectively (Wilcoxon matched-pairs signed-ranks tests)

	Control treatment	Female treatment	T	P	N	Male treatment	T	P	N
Clutch size	13 [4.75, 16.75]	9.5 [6.25, 12.75]	6	0.69	6	5.5 [3.25, 16.75]	7.5	1	6
SL (mm)	10.64 [10.23, 11.30]	10.51 [10.39, 11.30]	5	0.25	6	10.59 [10.27, 11.32]	3	0.22	6
Weight (mg)	25.9 [24.5, 27.6]	25.7 [24.0, 30.7]	9	0.75	6	28.4 [25.9, 31.0]	6	0.35	6

Fig. 2 FMS display rate in the control, male and female treatments. Medians and quartiles are shown. $*P < 0.05$



Discussion

As expected, *E. cyanostictus* males incubated the clutch for shorter periods when their body condition had been reduced experimentally, suggesting that they adjusted parental investment to their body reserves (see Barta et al. 2002). In general, potential costs of being in a lower body condition are an increased risk of predation and a higher probability of catching diseases (reviewed in Smith and Wootton 1995). The reduction in male incubation period, occurred by young being shifted *later* than in controls, resulted in longer female incubation. Thereby, the *total* brood-care period remained unchanged, and consequently, we did not detect any adverse effects on offspring fitness.

Contrary to our expectation, we found no effect of food deprivation on the female incubation period. There are several possible explanations why male, but not female, incubation was affected by food deprivation. (1) Males may be more sensitive to a lowering of energy reserves before incubation because males incubate for a longer period than females and therefore any additional energetic costs might be more detrimental for them. However, our results render this possibility unlikely, as the relative weight differences of fish after the control treatment and after a starvation treatment was similar in males and females. (2) The fitness consequences of starvation may differ qualitatively between

sexes, and a reduction in care may only be observed in the more strongly affected sex. This was suggested for great tits, *P. major*, in which brood care seems to affect male

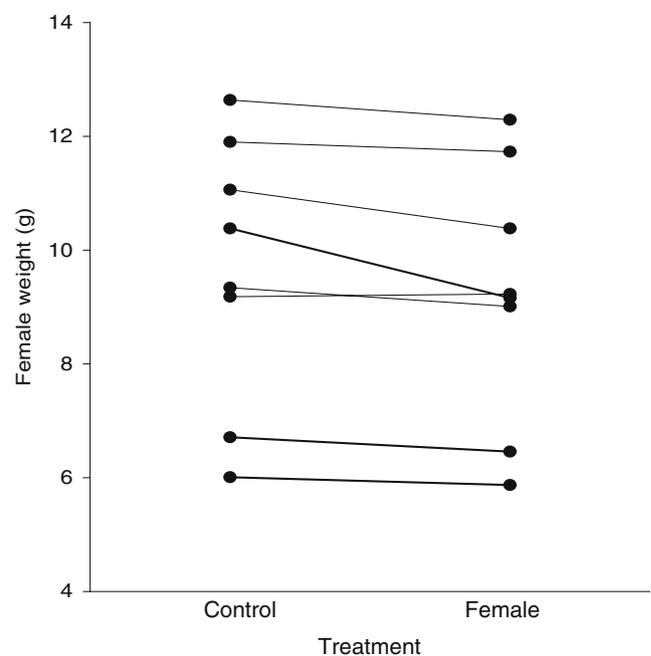


Fig. 3 Weight of females after spawning following a control treatment or a female treatment

Table 2 Comparison of inter-spawning interval, clutch size, fresh weight and dry weight between control and female treatment (Wilcoxon matched-pairs signed-ranks tests)

	Control	Female treatment	<i>T</i>	<i>P</i>	<i>N</i>
Interspawning interval	24.5 [21.2, 30.2]	25.0 [22.0, 30.5]	29.5	0.46	12
Clutch size	27 [24, 36]	32 [30, 36]	6.5	0.2	8
Fresh weight (mg)	14.3 [12.8, 16.0]	14.0 [13.0, 14.8]	14.0	0.58	8
Dry weight (mg)	7.6 [7.0, 8.0]	7.0 [6.8, 8.3]	10.0	0.26	8

survival more strongly than female survival (Sanz et al. 2000). In these birds, males reduced care after being experimentally handicapped by feather clipping, and females fully compensated for reduced male care, whereas males did not increase care after females had been handicapped. In *E. cyanostictus* females, food limitation during a reproductive event is likely to affect future reproductive output under natural conditions, although we did not find evidence for this under lab conditions; neither interspawn intervals nor number or weight of eggs were affected by the female treatment. Under natural conditions, males with a reduced condition may be less able to defend the pair territory, which may result in territory loss, as in *E. cyanostictus*, males take the more active role in defence (Morley and Balshine 2002). Hence, although the potential costs for males and females are not directly comparable, male costs may be regarded to be more severe, as a loss of the territory during incubation may result not only in the loss of the current brood but also of a secure place for both partners to produce future clutches. (3) Females may be coerced to incubate for the same duration as in control trials if males do not respond to the reduced condition of their mate and refuse to take the young earlier. Our results suggest that this may indeed be the case. Females with an experimentally reduced condition showed the FMS displays more often than controls, probably to signal their higher need to shift the young, but apparently this did not motivate males to take the clutch earlier.

Similarly, it is possible that males with reduced condition coerced females to incubate longer in male treatments by not taking the young in time. Alternatively, compensation for reduced paternal care may have been a strategic decision of females in order not to compromise growth (Grüter and Taborsky 2004, this study) and thereby survival chances of offspring (McCormick and Hoey 2004; Schürch and Taborsky 2005). If this was true, we had expected that females signal their readiness to incubate longer by reducing the rate of FMS displays. However, the frequency of FMS displays did not differ between male and control treatment, suggesting that females may have compensated forcibly.

Based on these results, it is difficult to judge the role of FMS displays in the negotiation about the amount of parental care, as we did not find an effect of female signalling on male incubation duration or of male condition on signalling frequency. However, the latter test had low

power because of a very small sample size. In addition to the presumed role in negotiation, the display seems to be involved in the agreement between partners about the place of the shift (Steinegger and Taborsky, unpublished data). This may be crucial for a quick transfer of young, as in the natural habitat, numerous potential egg and larvae predators are abundant (Taborsky, personal observations), and the risky time outside the parental buccal cavities should be minimized.

In summary, our results suggest that *E. cyanostictus* males do adjust their parental investment to their own energy reserves, the costs for this adjustment being carried entirely by the female. Both sexes appeared to be largely unresponsive to the energetic state of the partner, which renders cooperative bargaining over duties, unlikely in this species, and suggests the existence of strong sexual conflict over parental care (see Houston et al. 2005). Still, *E. cyanostictus* males always incubate young longer than females and remain faithful even if alternative mating partners are presented in excess (Grüter and Taborsky 2005). If males could indeed decide to a large extent about *both* partners' investment, why do they not exploit their mate's effort more strongly or even desert mouthbrooding females to seek alternative matings?

Several circumstances may limit the males' potential to exploit their mate's effort. (1) *E. cyanostictus* females experimentally forced to incubate alone release smaller, less-developed young with reduced survival chances than after biparental care (Grüter and Taborsky 2004). This is in accordance with the predictions of a model by Barta et al. (2002) that biparental care can only be evolutionary stable, if none of the partners has enough reserves to care for the young alone. (2) Barta et al. (2002) had also predicted that under certain conditions, females might impose a handicap on themselves by reducing their energy reserves deliberately below a level at which they cannot raise offspring alone, thereby forcing males to provide brood care. The FMS display could be regarded as a possible candidate for such a self-inflicted handicap, as it can be assumed to be costly both energetically and in terms of predation risk for mother and young. Females might show the display frequently to force males to take over the clutch soon to prevent females from lethal exhaustion and/or to reduce the risk for the young. However, our results do not support this hypothesis, as males did not respond to higher FMS display rates. (3) The amount of conflict over care may be reduced

if mates have common interests, for example, when mates remain mated monogamously over several breeding seasons. In this case, mates should have an interest to maintain their partners in good condition to enhance their survival and fecundity during following breeding events (reviewed in Mock and Fujioka 1990; see also Houston et al. 2005). Field data suggest that in a high proportion, pairs stay together for successive broods, but that monogamy is not lifelong (Taborsky, unpublished data). (4) Finally, a deserting male may have a low chance to occupy a new territory or to find unmated females due to a male-biased sex ratio (Morley and Balshine 2002).

E. cyanostictus is one of the few biparental species where brood care is performed strictly in non-overlapping periods with only one shift of parental duties from the female to the male. The peculiar female display behaviour may make this species an ideal model for direct observations and manipulations of the process of negotiation over parental care (McNamara et al. 1999). There are two qualitative differences from the assumptions made in the model by McNamara et al. (1999). (1) In *E. cyanostictus*, most likely, the negotiation process is costly, and (2) the options of partners during negotiation are intrinsically highly asymmetric. Besides differences in quality between partners as considered by McNamara et al. (1999), we propose to include costs of negotiation and the role of intrinsic asymmetries in the scope to respond to partners in future theoretical work on the negotiation about the amount of care between mates.

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