



International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report

IR-06-057

Asymmetric sexual conflict over parental care in a biparental cichlid

Marc Steinegger (marc.steinegger@esh.unibe.ch)
Barbara Taborsky (barbara.taborsky@esh.unibe.ch)

Approved by

Ulf Dieckmann
Program Leader, Evolution and Ecology Program

December 2006

Interim Reports on work of the International Institute for Applied Systems Analysis receive only limited review. Views or opinions expressed herein do not necessarily represent those of the Institute, its National Member Organizations, or other organizations supporting the work.

Contents

Abstract.....	2
Introduction	2
Methods	6
Results	10
Discussion.....	12
Acknowledgements	16
References	16
Tables	19
Figures	21

Asymmetric sexual conflict over parental care in a biparental cichlid

Marc Steinegger¹ & Barbara Taborsky^{1,2} (corresponding author)

¹Behavioural Ecology, Zoological Institute, University of Bern, Switzerland

²Evolution & Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, Austria

Correspondence:

Barbara Taborsky, Behavioural Ecology, Zoological Institute, University of Bern, Wohlenstrasse
50A, CH-3032 Hinterkappelen, Switzerland, e-mail: barbara.taborsky@esh.unibe.ch

Word count: 5170

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 partner's 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.

Key words: 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 & 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; Szekely 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 & Cuthill 1989; *Nectarinia osea*, Markman et al. 1995, 1996; *Parus major*, Sanz et al. 2000; *Charadrius alexandrinus*, Szekely & Cuthill 2000; *Eretmodus cyanostictus*, Grüter & 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 games' a parent should only partially compensate for a reduction of 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 & 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. Szekely & Cuthill 2000), but also to adjust the mutual investment during a potential negotiation process (McNamara et al. 1999, McNamara et al. 2003). Only

rarely 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 *Eretmodus 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 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 & 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), while 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 & Taborsky 2004), it is surprising that usually males 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 & Taborsky 2005). Females signal their readiness to transfer the young to their partner repeatedly already several days before the shift takes place by showing a peculiar display 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 & 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 of 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 in order 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.

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-litre 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 L:D cycle of 13:11h 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 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 (females: 6.3-7.3 cm standard length (SL), weight 8.35-12.64 g; males: 6.9-7.8 cm SL, weight: 10.28-14.45 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 & Draud 1992), as from earlier observations we knew that pairs divorce more likely when kept in complete isolation from conspecifics (C. Grüter and M. Steinegger, pers. obs.). 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 & 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 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, USA).

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). The sequence of the three treatments was randomly assigned to each pair.

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 & Taborsky pers. obs.). During male incubation, females were fed following the standard feeding regime (see above), while males do not feed when mouthbrooding.

Male-treatment: Like 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 (i) 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 moori* and *Ctenochromis horei* starve deliberately for up to six weeks

and four weeks, respectively, Yanagisawa and Sato 1990; Taborsky and Foerster 2004), and (ii) some *E. cyanostictus* starve naturally during incubation for maximum periods that can be longer than 10 days (Morely 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 & Taborsky 2004). Therefore we starved females from the 10th day after the shift of a brood until next spawning occurred, while 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 may 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 was identical to the control treatment.

On the day 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 spare 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 was used as 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 and six pairs completed only one treatment (three female treatments, two male treatments, one control). 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 end of female incubation and next spawning; see Grüter & 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 ($2.65 \text{ d} \pm 0.70 \text{ s.d.}$) 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 (cf. Morley 2000). Females started to release their eggs immediately, and the entire procedure takes between 10 and 20 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 & 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 (MS) 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 unless otherwise mentioned. In all tests our sample sizes were ≤ 12 . We used non-parametric tests throughout, 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 for descriptive statistics.

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), while 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 for SL, $R^2=0.41$, $N=15$, $P=0.01$). 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 (Tab. 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), while 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, $T=0$, $N=6$, $P=0.028$), while 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 (Tab. 2).

Discussion

As expected, *Eretmodus 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 of lower body condition are an increased risk of predation and a higher probability of catching diseases (reviewed in Smith & Wootton 1995). The reduction of male incubation period occurred by young being shifted *later* than in controls, resulting 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. (i) 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. (ii) The fitness consequences of starvation may differ qualitatively between sexes and a reduction of care may only be observed in the more strongly affected sex. This was suggested for great tits, *Parus major*, in which brood care seems

to affect male 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, while 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 inter-spawn 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. (iii) 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 (McCormick & Hoey 2004, Schürch & Taborsky 2005) of offspring. 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 & Taborsky in prep.). This may be crucial for a quick transfer of young, as in the natural habitat numerous potential egg and larvae predators are around (B. Taborsky, pers. obs.) 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 incubate always longer than females and remain faithful even if alternative mating partners are presented in excess (Grüter & Taborsky 2005). If males could indeed decide to a large extent about *both* partner's 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. (i) *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. (ii) Barta et al. (2002) had also predicted that under certain conditions females may

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 in order to prevent females from lethal exhaustion and/or to reduce the risk for young. However, our results do not support this hypothesis, as males did not respond to higher FMS-display rates. (iii) 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 & 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 (B. Taborsky, unpubl. data). (iv) 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 & 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. (1989). (i) In *E. cyanostictus*, most likely the negotiation process is costly, and (ii) 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.

Acknowledgements

We thank Michael Taborsky and Christoph Grüter for helpful discussions throughout this study, Rolf Eggler for logistic and technical support and Dolores Schütz for assistance with the experiments. The experiments were conducted under the license of the Veterinary Office of Kanton Bern, Switzerland (license no. 31/05). BT acknowledges financial support by the Forschungsstiftung, University of Bern (48/2003).

References

- 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
- Daan S, Dijkstra C, Tinbergen JM (1990) Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour* 114:83-116
- Golet GH, Irons DB (1999) Raising young reduces body condition and fat stores in black-legged kittiwakes. *Oecologia* 120:530-538
- Grüter C, Taborsky B (2004) Mouthbrooding and biparental care: an unexpected combination, but male brood care pays. *Anim Behav* 68:1283-1289
- Grüter C, Taborsky B (2005) Sex ratio and the sexual conflict about brood care in a biparental mouthbrooder. *Behav Ecol Sociobiol* 58: 44-52
- Horak PS, Jenni-Eiermann S, Ots I (1999) Do great tits starve to reproduce? *Oecologia* 119:293-299
- Houston AI, Davies NB (1985) The evolution of cooperation and life history in the dunnock *Prunella modularis*. In: Sibly RM, Smith RH (eds) *Behavioural ecology*. Blackwell Scientific, Oxford, pp 471–487
- Houston AI, Székely T, McNamara JM (2005) Conflict between parents over care. *Trends Ecol Evol* 20:33-38
- Izkowitz M, Draud MJ (1992) Conspecific intruders influence pair formation in a monogamous fish. *Behav Proc* 28:59-64
- 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. *Env Biol Fishes* 24:187-198

- Markman S, YomTov Y, Wright J (1995) Male parental care in the orange-tufted sunbird - behavioral adjustments in provisioning and nest guarding effort. *Anim Behav* 50:655–669
- Markman S, YomTov Y, Wright J (1996) The effect of male removal on female parental care in the orange-tufted sunbird. *Anim Behav* 52:437–444
- McCormick MI, Hoey AS (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. *Oikos*. 106:225-242
- McNamara JM, Gasson CE, Houston AI (1999) Incorporating rules for responding into evolutionary games. *Nature* 401:368-371
- McNamara JM, Houston AI, Barta Z, Osorno J-L (2003) Should young ever be better off with one parent than with two? *Behavioral Ecology* 14:301-310
- Mock DW & Fujioka M (1990) Monogamy and long-term pair bonding in vertebrates. *Trends Ecol Evol* 5:39–43
- Morley JI (2000) Intraspecific competition and monogamy in the cichlid fish, *Eretmodus cyanostictus*. PhD Thesis, University of Cambridge, Cambridge UK
- Morley JI, Balshine S (2002) Faithful fish: territory and mate defence favour monogamy in an african cichlid fish. *Behav Ecol Sociobiol* 52:326-331
- Mrowka W (1982) Effect of removal on the parental care behaviour of the biparental cichlid *Aequidens paraguayensis*. *Anim Behav* 30:295-297
- Parker GA, Royle NJ, Hartley IR (2002) Intrafamilial conflict and parental investment: a synthesis. *Phil Trans R Soc Lond B* 357:295-307
- Sanz JJ, Kranenbarg S, Tinbergen JM (2000) Differential response by males and females to manipulation of partner contribution in the great tit *Parus major*. *J Anim Ecol* 69:74–84
- Schürch R, Taborsky B (2005) The functional significance of buccal feeding in the mouthbrooding cichlid *Tropheus moorii*. *Behaviour* 142:265-281
- Smith C, Wootton RJ (1995) The cost of parental care in teleost fishes. *Rev Fish Biol Fisher* 5:7-22
- Steinegger M (2005) Sexual conflict over parental care and the function of female display behaviour in the biparental cichlid *Eretmodus cyanostictus*. Masters Thesis, University of Bern, Bern, Switzerland
- 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
- Székely T, Webb JN, Houston AI, McNamara JM (1996) An evolutionary approach to offspring desertion in birds. In: Nolan V, Jr, Ketterson ED (eds) *Current Ornithology*. Vol 13, Plenum, New York
- Tabosky B, Foerster K (2004) Female mouthbrooders adjust incubation duration to perceived risk of predation. *Anim Behav* 68:1275-1281

- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the Descent of Man. Aldine, Chicago, pp 136-179
- Wright J, Cuthill I (1989) Manipulation of sex-differences in parental care. Behav Ecol Sociobiol 25:171-181
- Yanagisawa Y, Sato T (1990) Active browsing by mouthbrooding females of *Tropheus duboisi* and *Tropheus moorii* (Cichlidae) to feed the young and/or themselves. Env Biol Fish 27:43–50

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

3

	Control treatment	Female treatment	<i>T</i>	<i>P</i>	<i>N</i>	Male treatment	<i>T</i>	<i>P</i>	<i>N</i>
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

4

5 **Table 2** Comparison of interspawning interval, clutch size, fresh weight and dry weight between
6 control and female treatment (Wilcoxon matched-pairs signed-ranks tests).

7

	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

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27 **Figure Legends**

28

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

31

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

34

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

36

37

38

39

40

41

42

43

44

45

46

47

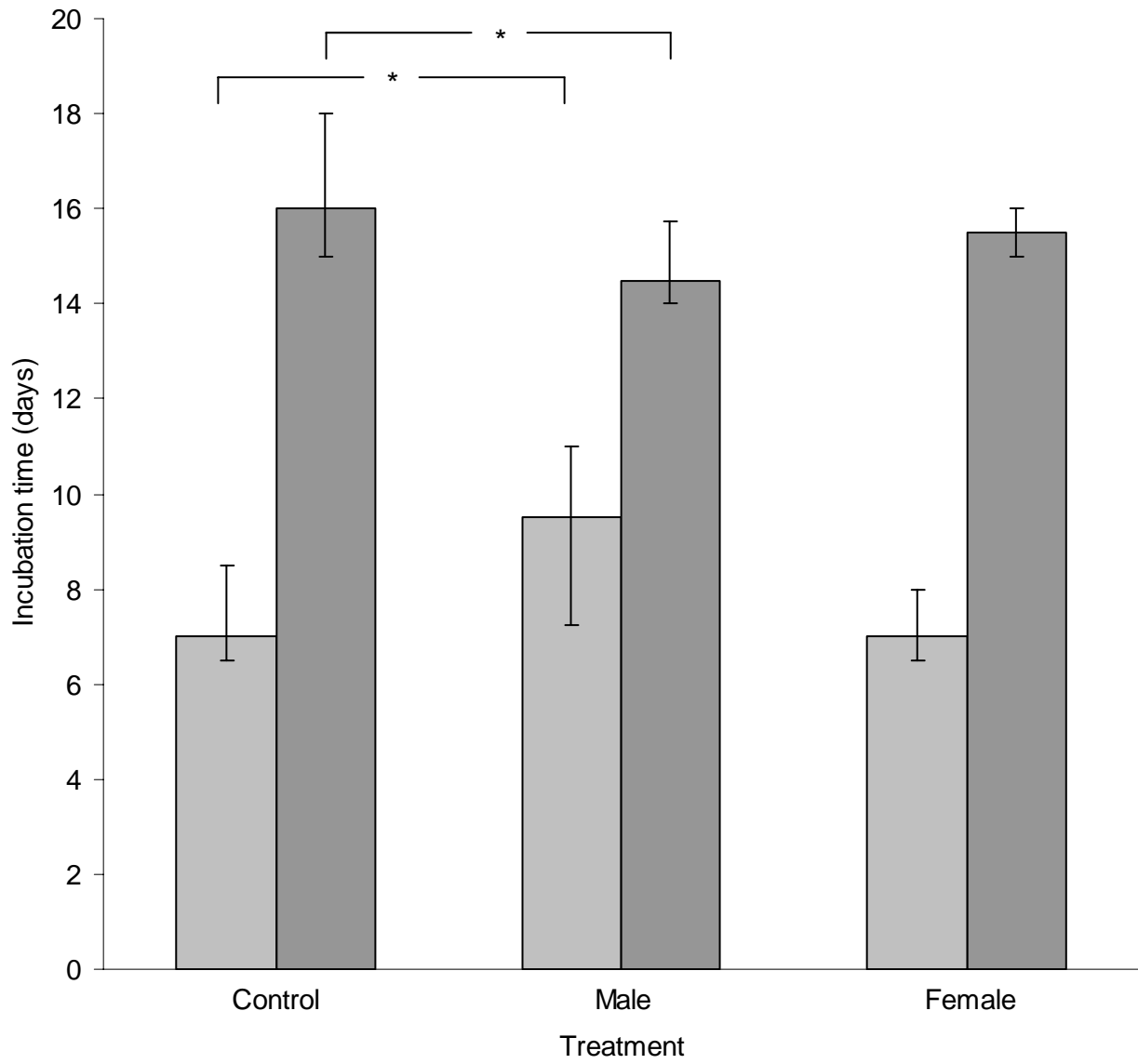
48

49

50

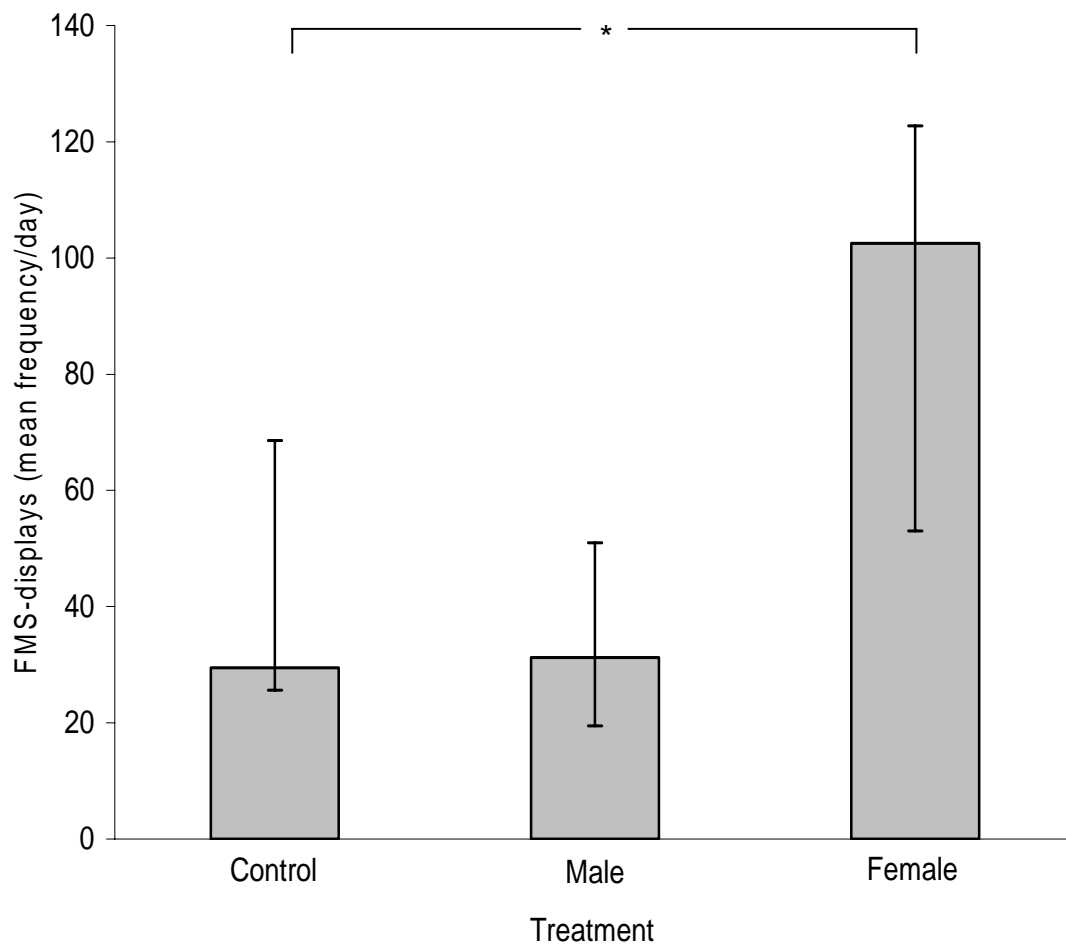
51

52



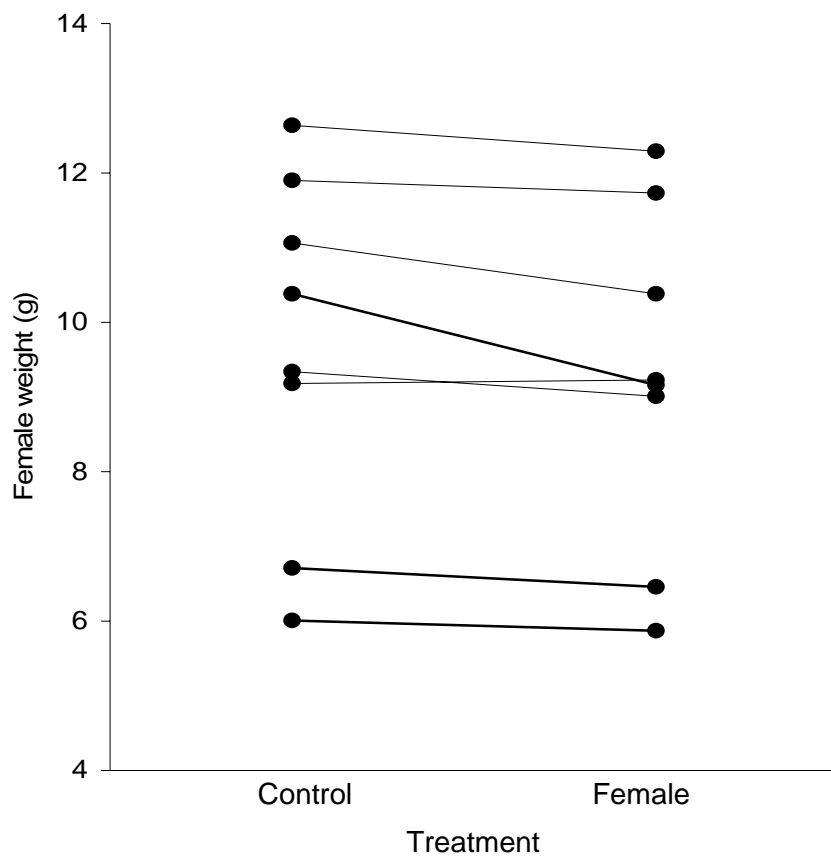
53
54
55
56
57
58
59
60
61
62

Fig. 1, Steinegger & Taborsky



63
64
65
66
67
68
69
70
71
72

Fig. 2, Steinegger & Taborsky



73
74

75

76

77

78

79

80

81

82

83

84

85

Fig. 3, Steinegger & Taborsky