

Tug-of-war over reproduction in a cooperatively breeding cichlid

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Abstract In group-living animals, dominants may suppress subordinate reproduction directly and indirectly, thereby skewing reproduction in their favour. In this study, we show experimentally that this ability ('power') is influenced by resource distribution and the body size difference between unrelated dominants and subordinates in the cichlid *Neolamprologus pulcher*. Reproduction was strongly skewed towards the dominant female, due to these females producing more and larger clutches and those clutches surviving egg eating better than those of subordinate females, but was not so when subordinates defended a patch. If breeding shelters were provided in two patches, subordinate females were more likely to exclusively defend a patch against the dominant female and breed, compared to when the same breeding resource was provided in one patch. Relatively large subordinate females were more likely to defend a patch and reproduce. Females also directly interfered with each other's reproduction by eating the competitors' eggs, at which dominants were more successful. Although dominant females benefited from subordinate females due to alloparental care and an increase in egg mass, they also showed costs due to reduced growth

in the presence of subordinates. The results support the view that the dominant's power to control subordinate reproduction determines reproductive partitioning, in agreement with the predictions from tug-of-war models of reproductive skew.

Keywords Cooperation · Cooperative breeding · Reproductive skew · Egg cannibalism · Growth · Status · Cichlidae

Introduction

Reproductive skew in animal societies is expected to depend on within-group relatedness, inbreeding avoidance, ecological constraints on independent breeding and the ability of dominants to control subordinate reproduction (Reeve et al. 1998; Johnstone 2000; Hamilton 2004; Adkins-Regan 2005; also called 'power,' Beekman et al. 2003). On the one hand, dominants may concede some reproduction to helpful subordinates, to assure that subordinates continue to provide alloparental care to the dominant's offspring or other benefits of grouping ('concession models,' Johnstone 2000). On the other hand, subordinates may refrain voluntarily from reproduction to avoid expulsion from the group ('restraint models,' Johnstone 2000). If dominants are not able to control subordinate reproduction, subordinate offspring may extract critical resources from the group like food and care at a penalty to the dominant's offspring. This may lead to active competition between dominants and subordinates over reproductive participation at the expense of total group productivity ('tug-of-war models,' Johnstone 2000). Experimental tests of factors affecting subordinate reproduction are scarce (Reeve and Keller 2001) and have focused on effects of

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relatedness (Langer et al. 2004), inbreeding avoidance (Faulkes and Bennett 2001) and dispersal opportunities (Heg et al. 2006a) on reproductive skew. No study has experimentally manipulated the ability of dominants to control subordinates ('power') and examined the resultant effects on skew.

The ability of dominants to, at least partly, control subordinate reproduction plays an important role in the assumptions of both concessions models (complete control) and tug-of-war models (partial control). Moreover, if subordinates can circumvent such control when dominant control is made more difficult to exert, this would strongly support the assumptions of tug-of-war models. If subordinates in all situations try to reproduce but are hindered at doing so by dominants, this would disfavour the assumptions of restraint models of reproductive skew.

We tested experimentally the effects of dominant control on reproductive skew and parental and alloparental care in the cichlid fish *Neolamprologus pulcher*, endemic to Lake Tanganyika. *N. pulcher* lives in cooperatively breeding groups consisting of a dominant breeding pair and up to 14 subordinate helpers (Balshine et al. 2001: 7% have only one helper). The majority of offspring and small subordinates have been produced by the current breeding pair (Dierkes et al. 2008), but frequent breeder exchange results in genetic relatedness of the helpers to the breeders falling sharply with helper age (Dierkes et al. 2005). Subordinate group members are also less related to the breeding male than to the breeding female due to extra-pair paternity (Dierkes et al. 2005). Previous work has shown that ecological constraints and predation risk may affect the incidence of subordinate dispersal and independent breeding (Heg et al. 2004a; Bergmüller et al. 2005). Groups may also contain multiple breeding females, and multiple breeding can be easily induced in artificial populations under laboratory conditions (Limberger 1983). Reproductive skew seems regulated by a tug-of-war over reproduction between the dominants and the subordinates, at least in males and within groups where subordinates and dominants are unrelated (e.g. large male subordinates are more likely to reproduce than small male subordinates, Heg et al. 2006a). Competition for the dominant breeding position is evident (Taborsky 1984; Balshine-Earn et al. 1998) and may be mediated by status and strategic adjustments in growth (Taborsky 1984; Heg et al. 2004b). *N. pulcher* is a substrate-breeding cichlid attaching their eggs secluded under rocks and in crevices (Taborsky and Limberger 1981) and under laboratory conditions can be induced to use flowerpot halves for spawning (Taborsky 1984).

To examine experimentally whether the ability of dominants to control subordinate reproduction plays a role in determining reproductive skew, we (1) varied the distribution of these suitable breeding shelters (by provid-

ing flowerpots grouped in either two patches of two pots or a single patch of four pots) and (2) varied the size difference between dominant and subordinate females, using unrelated non-breeding fish from our laboratory stock. We expected reproductive skew to decrease when flowerpots were distributed in two patches compared to one patch, particularly when the size difference was small. We further assessed whether dominants applied direct control by eating the subordinate's broods or vice versa (Ratnieks and Wenseleers 2005). Finally, we assessed how the presence of subordinates affects fitness components of the dominant females (through effects on reproduction, parental care and growth). If subordinate presence is beneficial (as suggested in previous experiments: Taborsky 1984; Brouwer et al. 2005), reproduction and/or growth should increase, and care should decrease for the dominant females. Dominant females may further increase growth to be able to control the subordinate females in the future, since dominance is usually size related in these cichlids (Taborsky 1984; Hamilton et al. 2005). However, these positive effects must outweigh the costs of applying control through costs of patrolling the territory and aggressive interactions.

Materials and methods

Experimental setup

Sixteen groups consisting of a breeding pair with one subordinate female helper (eight groups started with treatment 1 and the other eight groups with treatment 2, see "Experimental procedure") and eight single breeding pairs were created in one large octagonal ring tank (7,200-l, 60-cm height, 50-cm water column, 3-cm sand layer of 1-mm grain size, Fig. 1a). The ring tank was divided into eight sections, with each section containing three compartments (Fig. 1b). Fish could only interact with their neighbouring group within the same section. Four pot halves were placed in each compartment as breeding substrate. Cichlids spawn inside these pot halves, and females attach the eggs to the surface. Each compartment received ad libitum food (two feedings per day, 5 days TetraMin, 2 days fresh food with *Artemia* spp., *Daphnia* spp. and mosquito larvae each week), and excess food was removed the next morning. Water temperature (mean \pm SD=27.6 \pm 0.4°C) and illumination cycle (lights on from 08:00 to 21:00 hours) were kept constant in a climate-controlled room.

Experimental procedure

In each section, the two treatments and one single pair were established (Fig. 1b). Dominant males, dominant females

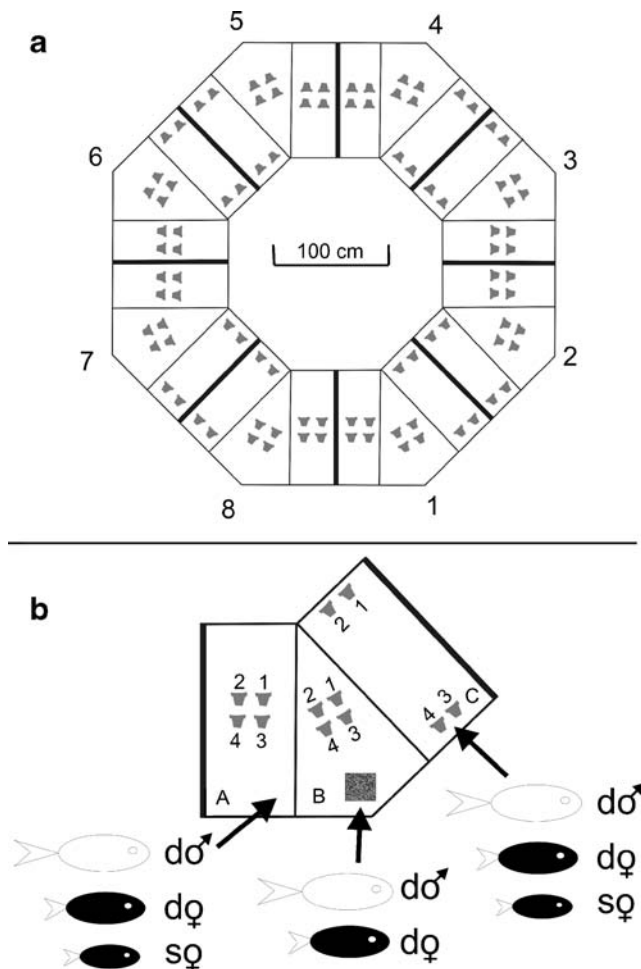


Fig. 1 Setup of the experiment. **a** Top view of the ring tank, showing the eight sections and the three compartments per section. All partitions were clear except the opaque partitions between the eight sections. **b** Detail of one section with the distribution of the four breeding shelters (flower pot halves, 1 to 4) in each compartment A, B and C. In all sections, the single breeding pair was settled in the middle compartment B. The two experimental treatments were established in the side compartments A and C, in this example, treatment 1 in A and treatment 2 in C. $d♂$: Dominant breeding male, $d♀$: dominant breeding female, $s♀$: subordinate female, **black square**: filter and air flow, **flower pot half**: used by the cichlids as breeding substrate

and subordinate females were size matched between treatments within each section at the start of sequence 1. Subordinates were released first and 1 day later than the dominants (Heg et al. 2004b), which is the standard procedure to create groups of unrelated individuals in the laboratory (e.g. Taborsky 1984, Heg et al. 2004b, Bergmüller et al. 2005). In treatment 1 and the single pairs, the four pot halves were close together; in treatment 2, the four pot halves were divided into two patches (Fig. 1b, approximately 70 cm apart; see Heg et al. 2008: the average nearest neighbour distance is 90 cm in the field). Body size (SL mm) and body mass (mg) at the start of sequence 1 were (means \pm SD, sample size): dominant males (65.0 \pm

5.3 mm, 7,468 \pm 2,015 mg, $N=24$), dominant females (62.4 \pm 4.5 mm, 6,792 \pm 1,550 mg, $N=24$) and subordinate females (51.4 \pm 3.7 mm, 3,575 \pm 741 mg, $N=16$). After 30 days, all individuals were caught, and body measurements were taken again to determine growth, and all subordinates were removed. Dominants of each section were moved counter-clockwise two sections (e.g. section 1 to location 3); treatment 1 and 2 were swapped (i.e. dominants from compartment A were moved to C and vice versa) and stored in small cage nets. New subordinate females, matched in size to the previous helper in the group, were measured and released in each treatment compartment A and C; subordinates had the same size difference with the dominant females as during sequence 1 and were again similar in size within each section. We used new subordinate females to make sure their previous experience would not influence the results. One day later, the dominants were released from their cage nets (start of sequence 2). Again, after 30 days, all individuals were caught, and body measurements were taken to determine growth, and all subordinates were removed. One dominant female was dead because she jumped out of the ring tank just before the measurements were taken, resulting in one missing value. This female was replaced with a new dominant female of approximately the same size for sequence 3.

To test whether resource distribution in itself affected dominant breeding behaviour and growth without the presence of subordinates, we added a third sequence. Dominants of each section were again moved counter-clockwise two sections (e.g. section 1 from location 3 to location 5), and individuals from compartments A and C were swapped. In half of the A and C compartments, the pot distribution was changed, and in the other half, it remained the same compared to sequence 2 (start of sequence 3). No new subordinates were released, so all 24 pairs were now single breeding pairs. Note that the pot distribution of the single breeding pairs in compartments B were held constant during all three sequences, to test for sequence effects on reproduction and growth throughout the experiment. The single breeding pairs were also used as the control group to test for effects of the presence of subordinates on dominant growth and reproduction. After 30 days, all dominants were caught, and body measurements were taken to determine growth during sequence 3.

Reproduction and behavioural observations

Dominant and subordinate females showed their readiness to spawn several days before egg laying, by cleaning the breeding substrate and vigorously courting the breeder male. If both females spawned, this was usually on different days, except in two cases where the dominant and

subordinates females spawned simultaneously on the same day. Egg laying and egg eating were recorded by direct observations and video-recording of the compartments each day during all three sequences. Note that all broods were removed before hatching, so none of the compartments contained offspring, and egg loss could not be due to filial cannibalism. After spawning was completed, parental and alloparental care (frequency of cleaning and fanning eggs combined) was determined for the dominant and subordinate female simultaneously in treatments 1 and 2 during a 15-min observation using the software programme 'the Observer 3.0' (Noldus, Wageningen, The Netherlands) by Heg on the day of spawning. Frequency of care was determined for 96 of the 101 broods produced during sequence 1 and 2 of treatments 1 and 2 combined (71 broods of the dominant females, two not observed because body measurements had to be taken; 25 broods of the subordinate females, three not observed because they were completely consumed by the dominant female directly after spawning). In the evening, clutches were removed, eggs were counted (clutch size defined as the number of eggs surviving plus eaten), and eggs were gently dislodged from the pots into Petri dishes, up to 52 eggs per dish depending on the clutch size (1 to 11 dishes). Eggs with obvious abnormalities (clear cuticle or breakable) were collected and weighed separately and, since they were extraordinarily light, discarded from all analyses, leaving a total of 23,212 valid eggs. The total mass per dish was determined to the nearest 0.1 mg (Mettler AE100 balance) after 32 h drying in a stove at 70°C (measured once, dry eggs moved to a second dish and measured again and averaged to account for measurement errors; see also Taborsky et al. 2007). The two dishes were weighed empty to the nearest 0.1 mg. Average egg mass was calculated as the (total mass minus mass of empty dish)/number of eggs per dish. Within-clutch repeatability was very high (results not shown), so for convenience, only averages per brood are presented (average of up to 11 dishes). Territorial behaviour of all fish was recorded daily. If a subordinate female aggressively defended at least one breeding shelter against the breeder female during a sequence, she was considered territorial. Breeder males were invariably accepted in all shelters by all females.

Statistical analyses

Data on reproductive skew, clutch size, egg mass and growth were analysed with general linear mixed models (GLMM, REML procedure, for dominants) or general linear models (GLM, for subordinates) in SPSS 11.0, correcting for sequence and individual identity within section as random effects were appropriate (note that individual subordinates were used only once, i.e. during

one sequence only). Data on the number of broods were analysed with GLMM or GLM including a log link. Reproductive skew (the total number of surviving eggs produced by the subordinate divided by the total number of surviving eggs produced by the dominant plus the subordinate per sequence) and egg eating (number of eggs eaten divided by the clutch size) with GLMM or GLM including a logit link in R1.0.8, correcting for sequence and individual identity within the section as random effects were appropriate (Crawley 2002). Binomial reproductive skew was calculated following Nonacs (2000) and ranges between -0.5 (more equal than expected from random distribution), 0 (random) and 0.5 (maximum skew), based on the total numbers of surviving eggs per sequence. Parental care and alloparental care were analysed with non-parametric statistics in SPSS 11.0. All other analyses were conducted in SPSS 11.0.

Results

Reproductive skew

As expected, subordinate females were more likely to defend an exclusive patch in treatment 2 (5 out of 16 groups) compared to treatment 1 (1 out of 16 groups, $\chi^2=3.60$, one-tailed $p=0.029$, logistic regression), particularly so when the size difference with the dominant female was small (Fig. 2a, $\chi^2=3.06$, one-tailed $p=0.04$, logistic regression). Whether the subordinate female was able to secure one or more pots had immediate effects on her productivity. Reproductive skew was close to zero (reproduction evenly shared) between the dominant females and the territorial subordinates (Fig. 2b). In contrast, reproduction was highly skewed towards the dominant females if subordinates were not able to control an exclusive breeding patch (Fig. 2b). The proportion of eggs produced by the subordinate of the total group productivity was significantly affected by whether she was territorial (GLMM corrected for the effects of sequence, section and group within section, $t_{13}=3.15$, $p=0.008$), and when corrected for this effect, treatment ($t_{13}=-0.79$, $p=0.44$) and the difference in size were not significant ($t_{13}=-0.47$, $p=0.65$).

Reproductive success and female status

In the presence of a female subordinate, dominant females increased their average egg mass compared to single breeding pairs, whereas there were no effects on the number of broods and clutch sizes (Table 1). The treatments did not affect any of the reproductive parameters of the dominant females, including the percentage of eggs lost due to egg eating (Table 1). In contrast, differences between the

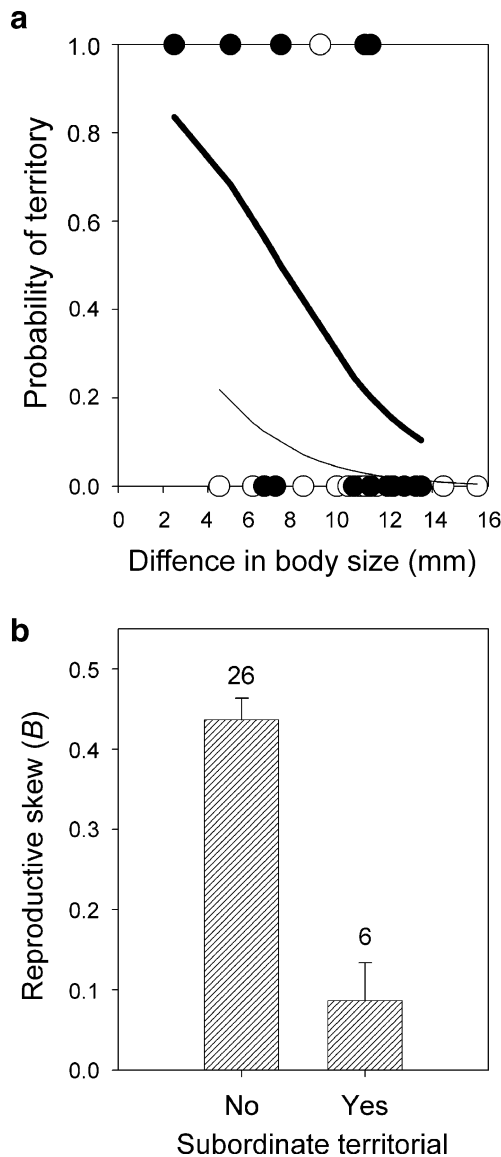


Fig. 2 Multiple breeding and reproductive skew in cichlid groups. **a** Subordinate females were more likely to secure a territory in treatment 2 (black circles) compared to treatment 1 (white circles) and when the size difference with the dominant female was small (SL dominant female – SL subordinate female, lines from logistic regression in text). **b** Reproductive skew was high in groups without a territorial subordinate (No), compared to groups where the subordinate was territorial (Yes)

dominant and subordinate female in reproduction were pronounced, suggesting dominant suppression of subordinate reproduction. Dominant females produced twice as many clutches of larger sizes compared to subordinates (Table 1). Clutch size showed a steep increase with female body mass in dominants, whereas this was not the case in subordinates (Fig. 3a, GLMM clutch size: effect of status, $F_{1, 35.5}=11.1$, $p=0.002$; body mass, $F_{1, 22.6}=10.2$, $p=0.004$; status \times body mass, $F_{1, 34.9}=9.2$, $p=0.005$). The average mass of an egg increased slightly with female

body mass in dominants, whereas it depended on the interaction with female body mass (Fig. 3b, GLMM egg mass: effect of status, $F_{1, 28.0}=5.1$, $p=0.032$; body mass, $F_{1, 21.7}=1.3$, $p=0.27$; status \times body mass: $F_{1, 28.1}=6.0$, $p=0.020$).

Reproductive suppression of subordinate females

No effects on reproduction of the two treatments were detected in subordinate females (Table 1). However, we found evidence for direct dominant suppression of subordinate reproduction. A larger proportion of the subordinate's broods were consumed by the dominant females, compared to the proportion of the dominant's broods consumed by the subordinate females (Table 1), and again there were no effects of the treatments. Two results show that reproductive suppression by the breeder female was only possible and successful if the subordinate female was not able to secure an own territory to breed in. First, territorial subordinate females produced significantly more broods than other subordinate females (means \pm SEM=2.17 \pm

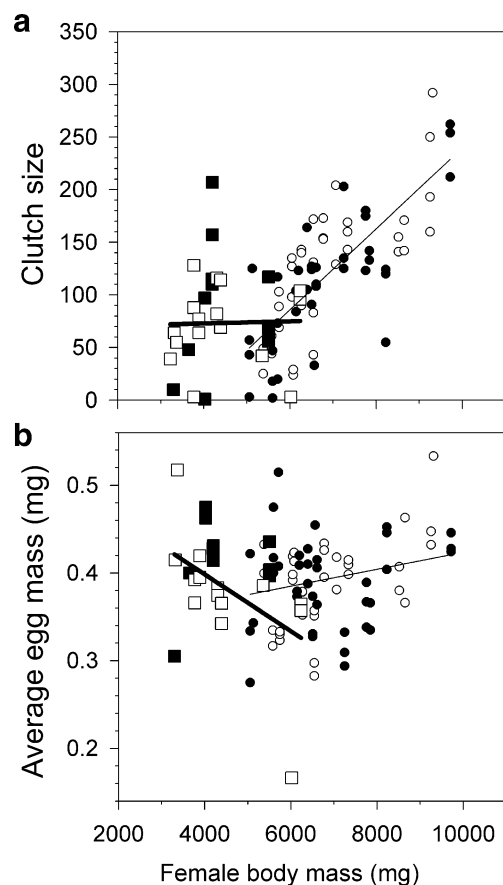


Fig. 3 Clutch size and egg mass of dominant and subordinate females. **a** Clutch size and **b** egg mass depended on status (dominants: circles, subordinates: squares), female body mass and their interaction but not on the treatments (treatment 1: white, treatment 2: black). Depicted are regression lines from two GLMMs on clutch size and average egg mass, respectively

Table 1 Reproduction of dominant and subordinate females in *Neolamprologus pulcher* depending on the treatments

Status, treatment	Number of broods	Clutch size ^a	Egg mass ^a (mg)	Percent eggs eaten
Dominant females				
Treatment 1	2.19±0.28 (16)	126.9±10.5 (35)	0.3888±0.0087 (34)	0.2±0.2 (35)
Treatment 2	2.50±0.24 (16)	113.6±10.1 (38)	0.3891±0.0086 (37)	2.6±2.6 (38)
Single pairs ^b	2.40±0.19 (40)	152.3±5.5 (93)	0.3828±0.0058 (93)	–
RD ^c	0.92	0.37	0.47	0.42
HP ^c	0.35	0.49	0.039	–
RD×HP ^c	0.60	0.58	0.18	–
Subordinate females				
Treatment 1	0.69±0.25 (16)	89.6±18.5 (11)	0.4163±0.0133 (11)	9.1±9.1 (11)
Treatment 2	1.00±0.26 (16)	67.5±9.6 (17)	0.3746±0.0196 (14)	23.5±10.6 (17)
RD ^c	0.33	0.41	0.64	0.93
Effect of status ^d	<0.001	0.002	0.032	0.003

In treatment 1, the four pots were close together; in treatment 2, the pots were divided into two patches with two pots each. Depicted are means±SEM with sample sizes in brackets.

^a GLMM, corrected for the effects of female body mass (all $df=1$), on clutch size: dominant females, $p<0.001$; subordinate females, $p=0.85$; on egg mass: dominant females, $p=0.43$, subordinate females, $p=0.096$

^b $N=16$ pairs during sequence 1 and 2 plus $N=24$ pairs during sequence 3

^c GLMM or GLM statistical effect of resource distribution (RD, $df=1$) and for the dominant females also presence of helpers (HP, $df=1$), and their interaction (RD×HP, $df=1$)

^d GLMM statistical effect of status ($df=1$, dominant or subordinate), excluding the single breeding pair females

0.17, $N=6$ vs $0.54±0.17$, $N=26$, Mann–Whitney U test, $U=13$, $p=0.001$) and did not differ in these respects from their dominant female group members ($1.83±0.48$, with $N=6$ groups, and Wilcoxon's test $z=-0.71$, $p=0.48$). Second, only one of the territorial subordinate's broods lost eggs due to dominant female egg eating (out of 13 broods or 3 eggs of 969 eggs), compared to 4 out of 15 broods (or 145 eggs of 1,164 eggs, $G_1=159.4$, $p<0.001$) in other subordinate females.

Benefits to breeder females of having a female subordinate

Dominant females may benefit from the presence of subordinates due to alloparental care (Fig. 4a). Indeed, the frequency of the dominant female parental care was negatively correlated with the frequency of subordinate alloparental care ($N=71$ dominant broods, Pearson's $r=-0.36$, $p=0.002$) but not vice versa ($N=25$ subordinate broods, $r=-0.04$, $p=0.84$). This shows that breeder females need to provide less care if their subordinate female is helpful. One of our intriguing results is that dominant females apparently were willing to reciprocate this subordinate support, by showing alloparental care of non-territorial subordinate broods (Fig. 4b). However, both females showed significantly larger investment in own broods (comparing parental vs alloparental care, both $p<<0.001$, Fig. 4). Notably, subordinate females showed virtually no alloparental care when they were territorial (i.e. defended one or more pots for breeding against the dominant), whereas otherwise parental and alloparental care did not depend on the treatments (Fig. 4).

Dominant females did not produce more or larger broods in the presence of subordinates but did increase their average egg mass compared to when they were breeding as a single breeding pair (Table 1).

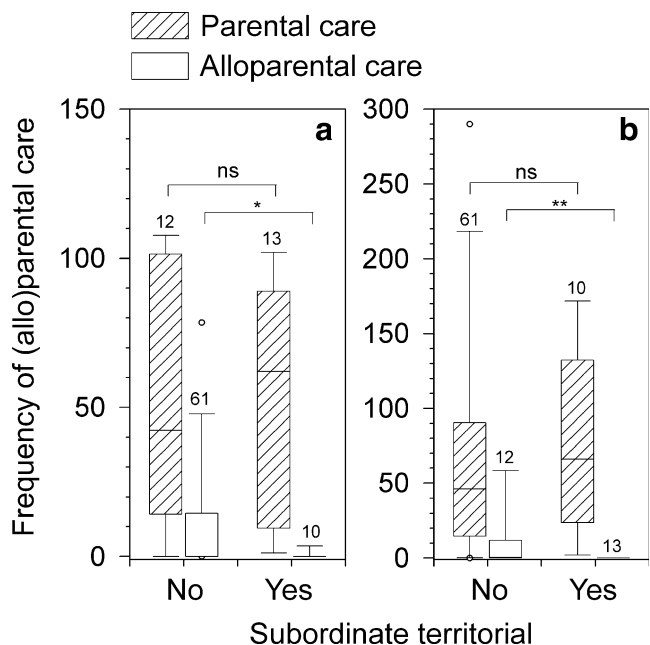


Fig. 4 Parental and alloparental direct brood care by females. Frequency of alloparental care but not parental care by **a** subordinate females and **b** dominant females depended on whether the subordinate was territorial (*Yes*) or not (*No*). Depicted are box plots (medians with boxes 90% and whiskers 95% intervals) with sample sizes (number of broods) on top of the boxes. Significant differences are indicated in the graph (one-tailed Mann–Whitney U tests based on Monte Carlo simulation)

Costs to breeder females of having a female subordinate

We found evidence for a cost of the subordinate's presence on the dominant females, presumably due to the costs of direct and indirect control of subordinate reproduction. Growth of breeder females was reduced when living with subordinate females, whereas no such effects were apparent in breeder males (Fig. 5, see also Appendix). There were no effects of the treatments on the growth of the subordinate females and the dominant females and males (see also Appendix), and we also detected no effects of the size

difference with the breeder female nor did we detect subordinate breeding or territoriality, on dominant and subordinate growth (results not shown).

Discussion

Our study shows that the power of dominants to control subordinate reproduction may influence reproductive skew in cooperative breeders (CB) in at least two mechanistic ways. First, they may prevent the subordinate female from laying a clutch, and second, they may eat part or whole of the subordinate's clutch ('egg eating'). As predicted, (1) this power is highest when the breeding resources are close together, i.e. when the expected costs of control are low. These results are in line with other studies on multiple breeding in cooperative cichlids, both from the field and the laboratory (Limberger 1983; Schradin and Lamprecht 2000; Heg et al. 2005). Territorial subordinates produced an equivalent number of broods as dominants did, and their eggs were less likely to get eaten compared to subordinates who could not secure an own breeding spot. It is interesting to note that similar results have been obtained in some tests of the 'polygyny threshold model' (PTM), where primary females were less likely to prevent secondary females from settling when the breeding resources were widely spaced (Sandell and Smith 1996). However, in contrast to the PTM where primary females have nothing to gain from the presence of secondary females (rather paternal care may be lost to secondary broods, e.g. Heg and van Treuren 1998), we show that dominant females gain subordinate alloparental female care if they can prevent them from establishing an own territory. Mixed mating systems where PTM may grade into CB have also been reported (Heg and van Treuren 1998). (2) Dominant control was more successful if the size difference between the dominant and the subordinate was large. Effects of the same-sex size difference on reproductive skew in communally and cooperatively breeding groups have been mixed, with some reporting effects and others reporting no effects (Scott 1997; Awata et al. 2006; Heg et al. 2006b).

Our experiment shows that size differences, evictions from the group (Balshine-Earn et al. 1998) and breeding resource distribution may have to be taken into account simultaneously in future studies addressing natural patterns of reproductive skew (assuming evictions and breeding resource monopolisation are costly to the dominants). Our results show direct and indirect dominant suppression of subordinate reproduction, but this suppression appears not completely successful, and subordinates can circumvent suppression by attempting to defend an exclusive breeding patch. These findings suggest a tug-of-war over reproduction in female cichlids, similarly as reported for male

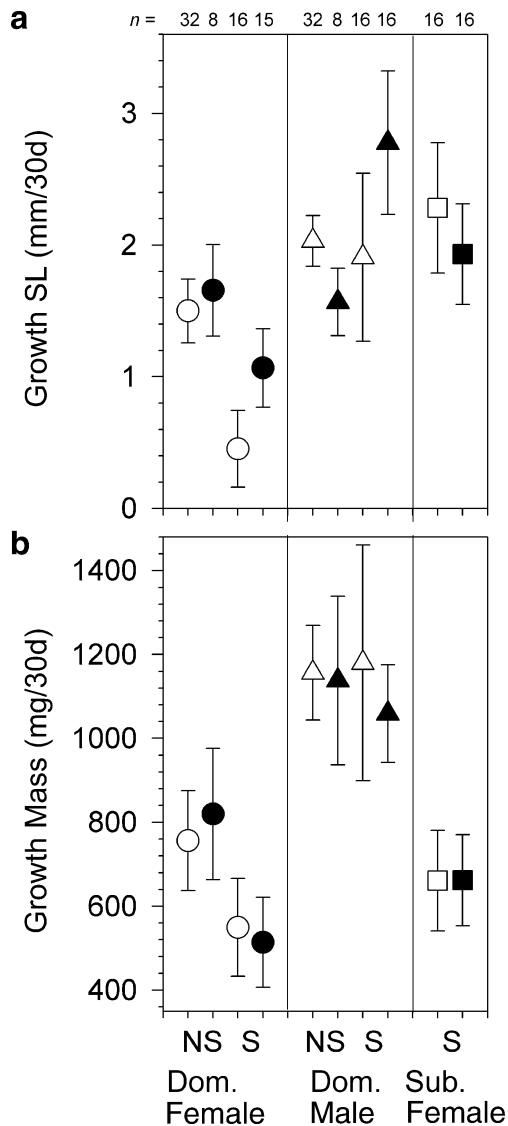


Fig. 5 Growth of dominants and subordinates. Dominant females grew more slowly in **a** standard length and **b** body mass when living in groups with a subordinate female (S) compared to when living only with a breeder male (NS). No such effects were detected in dominant males, and there were no effects of the resource distribution on growth of dominants and subordinates. Depicted are means \pm SEM with sample sizes on top of the bars. White, treatment 1 and single breeding pairs with pots together; black, treatment 2 and single breeding pairs with pots separate. See for statistics Appendix

cichlids (Heg et al. 2006a). In contrast, not only subordinate but also dominant females were willing to provide alloparental care. This shows that at least in female cichlids, where reproduction cannot be directly lost due to competition as in males, a certain level of reproduction may be conceded and supported, as long as subordinate females provide alloparental care or are in another way helpful to the dominant females (Heg et al. 2004a; Brouwer et al. 2005). It appears that the cichlid social system retains the possibility of cooperation between females, despite a tug-of-war over reproduction amongst them. This may also explain why female cooperatively breeding cichlids are sometimes willing to share one breeding patch with another breeding female (e.g. Heg et al. 2005), although on average, the between-group distance in our main study population is 90 cm (Heg et al. 2008). Previous studies have found positive effects of the presence of helpers of various sizes and sexes on the breeder's survival (Heg et al. 2004a), egg production (Taborsky 1984) and offspring survival (Brouwer et al. 2005) and negative effects on average egg mass (Taborsky et al. 2007). Our study shows that the presence of a single, large female helper has a slightly, non-significant negative effect on clutch size and significantly increases egg mass (Table 1).

The results suggest that the costs and benefits ('helper effect') of the helpers to the breeders may depend on helper sex and size and may depend on the size and distribution of the breeding resources, warranting closer experimentation. A single female subordinate seems to increase the current reproductive value of the dominant female through an increase in egg mass and alloparental care, but it remains unclear whether these outweigh the costs in reduced residual reproductive value dominant females incur due to a reduced growth (e.g. lower increase in future clutch sizes, see Fig. 3a). The results further show that the power to control subordinate reproduction plays a critical role in cichlid female reproduction. It remains to be tested whether male cichlid reproduction is also affected by the dominant's male power to control spawning by subordinate males. Awata et al. (2006) showed that both types of males may substantially invest in their reproductive capacity, with male dominants increasing their testes size in the presence of a male helper in *Julidochromis ornatus*. Hypothetically, the dominant male's ability to exclude subordinates physically from the site of spawning may be a direct method of male control.

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Appendix

Table 2 Growth of dominant males, dominant females and subordinate females

Factor	Growth SL (mm)/ 30 days				Growth body mass (mg)/ 30 days			
	<i>F</i>	<i>df</i>	Error <i>df</i>	<i>p</i> value	<i>F</i>	<i>df</i>	Error <i>df</i>	<i>p</i> value
Dominant males ^a								
Intercept	10.69	1	67.0	0.002	13.80	1	20.6	0.001
RD	0.49	1	67.0	0.487	0.110	1	65.8	0.741
HP	1.06	1	67.0	0.308	0.032	1	5.8	0.863
RD×HP	1.38	1	67.0	0.244	0.057	1	63.4	0.813
Body size ^b	6.28	1	67.0	0.015	1.097	1	24.7	0.305
Dominant females ^a								
Intercept	1.99	1	66.0	0.164	2.54	1	33.4	0.121
RD	2.62	1	66.0	0.110	0.31	1	66.0	0.580
HP	11.37	1	36.1	0.002	5.71	1	35.6	0.022
RD×HP	0.016	1	66.0	0.898	0.65	1	66.0	0.422
Body size ^b	0.78	1	64.2	0.380	0.15	1	65.0	0.703
Subordinate females ^c								
Intercept	0.65	1	21	0.428	0.018	1	21	0.895
RD	0.34	1	21	0.566	0.000	1	21	0.994
Body size ^b	0.41	1	21	0.528	0.003	1	21	0.953

Results are presented for six separate analyses for growth in SL and body mass, depending on resource distribution (RD), helper presence (HP) and RD×HP (the latter two effects for dominants only), and corrected for body size at the start of each sequence.

^a GLMM corrected for random sequence and individual identity within section effects.

^b Growth in SL corrected for SL at the start of each sequence and Growth in body mass corrected for body mass at start of each sequence.

^c GLM corrected for random sequence and section effects. Note that subordinate females were used only once during the whole experiment, and therefore no correction for random individual identity effects were necessary.

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