Gender Differences in the Costs that Subordinate Group Members Impose on Dominant Males in a Cooperative Breeder

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Abstract

In group-living species, a dominant male's ability to monopolize reproduction, and the cost of doing so, are expected to vary with a group's gender composition. We used spawning observations of a group-living cichlid, *Neolamprologus pulcher*, to test this expectation. We constructed groups that contained a dominant breeding pair and either two male subordinates, one male and one female subordinate or two female subordinates. Parasitic spawning by male subordinates was more common in groups with two male subordinates than in groups with one male and one female subordinate. Female subordinates were never observed laying eggs in dominant females' clutches, but three female subordinates laid independent clutches. During spawning, frequencies of dominant male aggression towards male and female subordinates were similar. Dominant males were less aggressive during non-reproductive periods. The declines were greater for female subordinates, such that, during non-reproductive periods, dominant males were more aggressive towards male subordinates. Aggression towards each subordinate was also affected by the second subordinate's gender; the direction of that effect differed for large and small subordinates. Male subordinates approached breeding shelters less often than female subordinates, and both male and female subordinates approached shelters more frequently when the second subordinate was male. Collectively, these patterns suggest: (1) that male subordinates impose higher costs on dominant males than female subordinates do and (2) that the presence of a second male subordinate imposes additional costs beyond those of the first male subordinate. We discuss the implications of these effects for dominant and subordinate group members.

Introduction

In group-living species, the costs and benefits of group membership can vary with group composition (Krause & Ruxton 2002). Such effects are most evident when reproduction occurs in a social context. In cooperatively breeding species, participation in reproduction is typically biased towards a socially dominant breeding pair (reviews in Stacey & Koenig 1990; Taborsky 1994; Emlen 1997; Solomon & French 1997; Reeve & Keller 2001; Koenig & Dickinson 2004). However, subordinate individuals do not necessarily forego current reproduction completely. Male subordinates may reproduce with a group's dominant (breeding) female, and genetic paternity analyses have confirmed that male subordinates sire young in various cooperatively breeding species (reviews in Cockburn 1998; Hughes 1998; Taborsky 2001). Likewise, female subordinates may produce their own offspring in addition to caring for those of

a dominant female (e.g. Richardson et al. 2002; Griffin et al. 2003; Heg et al. 2006). The extent to which reproduction within a group is monopolized by a dominant individual is referred to as the group's reproductive skew (Vehrencamp 1983).

Most studies of reproductive skew only consider dominant–subordinate interactions within a single gender (see discussions in Cockburn 2004, 2007; Magrath et al. 2004). Thus, the consequences of a dominant male's tolerance of a male subordinate are typically contrasted with the consequences of having no subordinate at all. Noë & Hammerstein (1994) set dominant–subordinate interactions within in a partner choice context. They argue that dominants should distinguish among subordinate partners and prefer those that give an honest signal of inferiority. However, the focus remains intra-sexual. A single-sex perspective may be appropriate in systems where only one subordinate gender helps but, in many systems, the more relevant contrast is between tolerating a male or female subordinate. For the dominant male in a mixed-sex group, the costs imposed by male and female subordinates are potentially very different. Reproduction by a female subordinate may increase the dominant male's fitness, because he will sire the subordinate's offspring. But the dominant male's reproductive success will decline if he shares paternity in a brood with a male subordinate. Furthermore, efforts to prevent a male subordinate from reproducing may themselves be costly. Thus, in a mixed-sex group, a subordinate's gender may be the most reliable indicator of the threat that the subordinate poses.

In this study, we highlight the importance of considering subordinates' genders when studying interactions between dominant and subordinate group members. We focus on differences in the costs that male and female subordinates impose on dominant males. Our study used aquarium observations of spawning *Neolamprologus pulcher*, a group-living, cooperatively breeding, cichlid fish endemic to Lake Tanganyika (Taborsky & Limberger 1981; Taborsky 1984 as *Lamprologus brichardi*; see Duftner et al. 2007 for taxonomic status). Free-living *N. pulcher* groups consist of a dominant breeding pair and, on average, 5–8 male and female subordinates of various sizes (Taborsky & Limberger 1981; Balshine et al. 2001). Smaller, juvenile subordinates are usually the recent offspring of the current dominant pair, whereas larger, sexually mature subordinates are often unrelated to one or both breeders, either because the subordinates are the offspring of breeders that have since been replaced by immigrants, or because

the subordinates themselves are immigrants (Stiver et al. 2004, 2006; Dierkes et al. 2005, 2008). Large male subordinates can be reproductively active, gaining some paternity in clutches spawned by dominant females (Dierkes et al. 1999; Heg et al. 2006, 2008; but see Fitzpatrick et al. 2006; Stiver et al. 2009). Subordinates of both sexes usually act as helpers (Taborsky & Limberger 1981; Taborsky 1984; Stiver et al. 2005; Bruintjes & Taborsky 2008; among others). Because we focused on differences in costs for breeders, we did not quantify subordinate helping behaviour in this study. Helping behaviour is clearly relevant to the consideration of benefits that offset those costs (see Discussion; see also Heg et al. 2008).

Each group in the study consisted of a dominant breeding pair, a large subordinate (male M or female F) and a small subordinate (male m or female f). The subordinates' genders were varied so that all four possible combinations were represented: large male and small male (Mm); large male and small female (Mf); large female and small male (Fm); and large female and small female (Ff). We have used these groups to address a range of questions: Heg et al. (2008) describe the patterns of genetic parentage for clutches laid during this study, and Mitchell et al. (2009) describe the effects of subordinate gender composition on dominant behaviour. The latter paper used preplanned focal individual observations conducted during non-reproductive periods. Here, we describe the results of observations that were made opportunistically at groups where we chanced to observe in-progress spawning. These observations are of particular interest because spawning is the context in which the cost of a male subordinate should be most evident.

We addressed four questions:

1. How common is parasitic spawning and does that frequency depend on the gender composition of the group? Prior to this study, the only direct observations of parasitic spawning in *N. pulcher* were anecdotal (Taborsky 1985; Dierkes et al. 1999). Direct observations are important for two reasons. First, the genetic paternity analyses that have been used to-date (Dierkes et al. 1999, 2008; Heg et al. 2006; Stiver et al. 2009) provide limited insight into behavioural interactions between dominants and subordinates. Second, because genetic analyses only detect successful fertilizations, they may underestimate the frequency with which subordinates spawn (Dierkes et al. 1999).

2. Are dominant males more aggressive towards male subordinates than towards female subordinates?

We predicted that dominant males would be more aggressive towards male subordinates, and especially towards large male subordinates (which gain more parentage than small subordinates, Heg et al. 2006), and that this tendency would be more pronounced during spawning.

3. Are male and female subordinates equally able to approach breeding shelters? The extent to which a subordinate restricts itself, or is restricted, to a peripheral location is an indirect measure of the aggression that it faces within its group. We predicted that male subordinates, especially large male subordinates, would be restricted to peripheral locations to a greater extent during spawning. Because subordinates may be subject to aggression from both members of a dominant breeding pair, we otherwise made no predictions regarding differences between male and female subordinates or regarding effects of the second subordinate's gender.

4. Are dominants males' interactions with one subordinate affected by the gender of the second subordinate? This study is the first to consider effects of gender composition, as distinct from effects of a focal individual's gender. We had no *a priori* expectations regarding effects of gender composition. However, subsequent parentage analyses revealed that dominant males lost more parentage to the large subordinate male if the small subordinate was also male (Heg et al. 2008). Therefore, *a posteriori*, we expected that dominant males had more difficulty controlling two male subordinates than a single male subordinate, at least during spawning. This pattern should be evident from the analyses of questions 1–3.

Although we have distinguished between large and small subordinates, we have intentionally limited our treatment of this aspect of the study. The effects of subordinates' sizes on interactions with dominants have already been subject to some study in this system (e.g. Skubic et al. 2004; Hamilton et al. 2005; Heg et al. 2006). Repeating those comparisons here would distract from the consideration of effects related to gender composition — effects that until now have been largely ignored and that were therefore the focus of this study.

We did not assess the costs that male and female subordinates may impose on dominant females. During our observations, interactions between dominant females and subordinates were too infrequent to allow meaningful comparisons. Interactions between dominant and subordinate females have been explored by Heg (2008) and Heg & Hamilton (2008).

Methods

The groups observed during this study were a subset of the groups used in a larger study of gender-specific queuing, growth and parentage in *N. pulcher* (e.g. Heg et al. 2008; Mitchell et al. 2009). Each group consisted of a dominant breeding pair (male and female), a large subordinate and a small subordinate. Within each group, the large subordinate was 10–20 mm smaller than the dominant female and the small subordinate was 5–10 mm smaller than the large subordinate. All fish were measured at the start of the experiment, sexed (using differences in the shape of the genital papilla) and marked by taking a short (2–4 spines) clip from the dorsal and/or anal fin to aid in individual identification. Fin clipping is a standard-marking technique in this species (e.g. Taborsky 1985; Heg et al. 2006) and had no adverse effects on the fish. The four fish comprising a group were released into a single compartment within a larger aquarium (see below). Subordinates were released directly into their compartments. Dominants were kept overnight in individual isolation nets within their compartments before being released. This method of experimentally creating *N. pulcher* groups with desired characteristics is well-established (Taborsky 1984). Groups in the larger study were organized in sets of four, with subordinates' genders varied and rank-specific sizes kept constant within each set. Because the spawning observations described in this study were collected opportunistically on a subset of those groups, it was not practical to consider possible effects of a subordinate's size independent of its gender and social rank. We have therefore ignored this aspect of the broader study's design. Among groups that were observed spawning, mean standard lengths for each social rank ($\pm$SE) were: dominant male: 67 ± 1.2 mm, dominant female: 62 ± 0.8 mm, large subordinate: 50 ± 0.3 mm and small subordinate: 41 ± 0.3 mm. Rank-specific lengths did not differ significantly among treatments (ANOVA: dominant male: $F_{3,26} = 0.76$, p = 0.53; dominant female: $F_{3,26} = 0.62$, p = 0.61; large subordinate: $F_{3,26} = 0.006$, p = 1; small subordinate: $F_{3,26} = 1.12$, p = 0.36). Length differences between adjacent-ranked group members were also consistent across treatments (dominant male − dominant female: $F_{3,26} = 0.50$, p = 0.69; dominant female − large subordinate: $F_{3,26} = 0.73$, p = 0.54; large subordinate − small subordinate: $F_{3,26} = 1.86$, p = 0.16). *Neolamprologus pulcher* typically mature at $\sim$35 mm (Taborsky 1985; Dierkes et al. 1999), so all subordinates were assumed to be

mature. Subordinates as large as 57 mm are observed in the field (Balshine et al. 2001). All fish were laboratory-reared descendents of fish caught near Mpulungu, Zambia, at the southern end of Lake Tanganyika, and had been housed in large aggregation aquaria without access to spawning substrate prior to this experiment. Aggregation aquaria housed fish of both sexes and of a range of size classes. The allocation of fish to experimental groups was randomized, so any effect of prior familiarity should not have biased our results.

Groups were maintained in adjacent 125 l compartments within three 1000 l aquaria (see Heg et al. 2008). Compartments were 65 cm high, with 65 × 32.5 cm bases. The floor of each compartment was covered with ∼6 cm of sand. Each compartment contained two clay flower pot halves that were used by the fish as shelters and for breeding. Each compartment also contained a translucent tube, suspended near the surface, which was used by subordinates as a refuge from dominant aggression, and a suspended filter, which was also used as a refuge by subordinates. The availability of refugia near the surface ensured that subordinates always had a means of avoiding interactions with dominants. Compartments were separated by alternating clear and opaque partitions, such that each group could see one adjacent group from the same set of four. The compositions of neighbouring groups were randomized. Water temperature was maintained at 27.5 ± 1°C. The light regime was a 13:11 h light:-dark cycle. Groups were fed daily with commercial flake food. The amount of food was tailored to the sizes of the fish in each group (2.5% of the group's combined mass/d).

As noted above, spawning observations were opportunistic. Compartments were checked each morning for the presence of eggs, which were typically laid on the inner surface of the shelter, and for spawning activity. Spawning females repeatedly turned upside down and pressed their genital papilla against the inner surface of the breeding shelter. Spawning males approached the clutch (either entering the breeding shelter or at the entrance to it) and made a distinctive lateral roll, bringing the genital papilla up towards the clutch. When an in-progress spawning was detected, i.e. if eggs were visible in a breeding shelter and the breeding pair were actively spawning, an observation was initiated. All clutches were removed on the day-of-laying by replacing the flowerpots on which they had been laid. A part of each clutch was incubated artificially in a separate aquarium until hatching. The hatched offspring were

then used in genetic parentage analyses. Unfortunately, there was little overlap between the clutches that we observed being spawned and those that we successfully hatched. Results of the genetic parentage analyses are presented elsewhere (Heg et al. 2008). A second observation was conducted at least 3 d following the observed spawning and at least 2 d prior to any subsequent spawning. We refer to the latter observation as non-reproductive. Each observation lasted 10 min. During each observation, we noted all aggressive interactions between breeders and subordinates in successive 30 s intervals, along with the location of each fish. During spawning observations, we also recorded subordinate participation in spawning. Spawning by subordinates was identified in the same way as that of the dominant male and female. If the dominant female and male did not spawn during an observation period then the observation was excluded from analyses. For some groups, more than one in-progress spawning was detected. To simplify analyses, we considered only the first in-progress spawning detected for each group. The only subordinates that we observed participating in a subsequent spawning had also spawned parasitically during the first observed spawning, so this approach did not affect our results. Groups' gender compositions were known to the observer. Because dominant male aggression was unambiguous, it is unlikely that the observer's knowledge affected the results.

The frequency of dominant male aggression towards subordinates was quantified by counting the number of 30 s intervals during which aggressive interactions were observed (see Hamilton et al. 2005 for descriptions of aggressive behaviours). This count is a simple and easily-interpreted means of quantifying a dominant male's efforts to restrict the activity of its subordinates. For our purposes, it is a more meaningful index than a count of the total number of interactions because the latter measure weights a series of brief interactions more heavily than a single, prolonged interaction. We did not distinguish between 'overt' and 'restrained' aggression (sensu Taborsky 1984) in our analyses because a dominant's decision to escalate an aggressive interaction could not always be distinguished from a subordinate's decision to flee before escalation occurred. We also quantified the frequency with which subordinates approached the breeding shelters in their compartments. Subordinates seeking to avoid aggression from dominants consistently did so by limiting their use of the bottom of the compartment, near the breeding shelters. Therefore, we used the number of

30 s intervals during which a subordinate fish entered the lower third of its compartment as our index. Note that, because we removed entire clutches and the laying substrate, it is unlikely that dominants attributed a clutch's disappearance to their subordinates, i.e. that clutch removal influenced dominant male aggression. The number of clutches removed prior to the observed spawning did not differ among treatment groups (Poisson regression, LR $\chi^2_3 < 0.01$, p = 0.98). Therefore, any effect of clutch removal should not have biased our results.

Statistical Analyses

Variation in dominant male aggression towards subordinates and in subordinates' approaches to breeding shelters were analysed with generalized linear mixed models (GLMM, Faraway 2006) using the lmer function (Bates 2007) in R (version 2.5.1; R Development Core Team 2007). During a 10 min observation period, a dominant male could interact with a subordinate, and a subordinate could enter the lower third of its compartment, during up to 20 intervals. Counts for aggressive interactions never approached 20; only a single observation exceeded 12. Therefore, we opted to fit dominant male aggression using quasi-Poisson models. Counts of intervals during which subordinates visited the lower third of their compartments did reach 20, and were fit using quasi-binomial models. Models of this sort do not lend themselves to standard likelihood-ratio effect tests. Instead, we assessed the importance of the fixed effects in each model using a Markov Chain Monte Carlo simulation procedure (function mcmcsamp) to generate highest posterior density credible intervals, analogous to 95% confidence limits, for each fixed effect. For ease of interpretation, we used the same simulations to generate p-values for the fixed effects: as the proportion of the simulated effect estimates that exceeded the actual estimate.

Given our sample size, it was not possible to assess differences between large and small subordinates and differences between spawning and non-reproductive observation periods within a single analysis. Instead, we opted to run two pairs of GLMM. To compare counts between spawning and non-reproductive periods, we constructed separate GLMM for the large and small subordinate. Fixed effects in these analyses were the genders of the subordinates, the observation period (spawning or non-reproductive) and the three pair-wise interactions between

these effects. The structure of the data was such that the three-way interaction could not be included. The groups themselves were included as a random effect. To compare counts for the two subordinates, we ran separate GLMM for the two observation periods. Fixed effects in these analyses were focal subordinate size (large or small) and gender, the gender of the second subordinate and the pair-wise interactions. The groups were again included as a random effect. Note that our primary interests were in effects of the two subordinates' genders, which were included as predictors in all analyses. In each case, a reduced model was arrived at through stepwise removal of non-significant (p > 0.1) terms. Marginally non-significant effects (0.10 > p > 0.05) were retained. The effect of group composition on the likelihood of parasitic spawning was assessed using Fisher's Exact Test.

Results

Spawning Activity by Subordinate Group Members

Observations of in-progress spawning were conducted at 30 groups. Parasitic spawning by subordinate males was observed in six of the 21 groups at which at least one male subordinate was present (Table 1). Among groups, parasitic spawning by a male subordinate was significantly more likely where both subordinates were male (five of eight Mm groups) than where one subordinate was male and the other female (one of 13 Fm or Mf groups; two tailed Fisher's Exact Test, p = 0.01). There was also some indication that individual male subordinates were more likely to spawn parasitically when the second subordinate in the group was male (six of 16 males) than when the second subordinate was

Table 1: Occurrence of parasitic spawning, defined as subordinate participation in spawning with the opposite-sex dominant of the breeding pair for each treatment (sex of large subordinate and sex of small subordinate)

| | Size of the subordinate spawning | | | | |
Treatment	Large	Small	Large and small	None spawning	n
Male, male (Mm)	2	2	1	3	8
Male, female (Mf)	0	0	0	5	5
Female, male (Fm)	0	1	0	7	8
Female, female (Ff)	0	0	0	9	9

Sample size is the total number of groups at which an in-progress spawning was observed.

female (one of 13 males). Statistically, this trend was suggestive, but non-significant (two tailed Fisher's Exact Test, p = 0.09). Both large (three of 13) and small (three of 16) male subordinates were observed spawning parasitically.

Two large female subordinates (one each in Ff and Fm groups) and one small female subordinate (in a Mf group) were observed laying eggs. These events were not concurrent with clutches laid by the breeding female. Two of these clutches had disappeared within hours of being laid; we presume that the eggs were eaten. Female subordinates were never observed contributing eggs to clutches laid by dominant females, although one clutch with mixed maternity was detected by parentage analyses (Heg et al. 2008).

Dominant Male Aggression Towards Subordinates

The frequency of dominant male aggression towards subordinates varied with the sizes and genders of both subordinates, and between spawning and non-reproductive observation periods as follows.

Overall, dominant males were more aggressive towards male subordinates than towards female subordinates and were more aggressive during spawning than during non-reproductive periods (Fig. 1, Table 2). However, the exact level of aggression towards each subordinate was also influenced by the sex of the other subordinate and by pair-wise interactions between subordinates' sexes and the observation period. In general, during non-reproductive periods, dominant males adjusted their behaviour depending on the sexes of their subordinates

whereas, during spawning, they were relatively insensitive to group composition. For example, female large subordinates were only attacked during spawning whereas male large subordinates were attacked during both observation periods (Fig. 1a, focal gender × period effect in Table 2a), and were attacked more often when the small subordinate was also male (Fig. 1a, non-focal gender effect in Table 2a).

For small subordinates (Fig. 1b), the sex effect was less clear-cut (p = 0.07; Table 2a). Dominant male aggression towards small subordinates was much more sensitive to the observation period (more frequent during spawning), the gender of the large subordinate (more frequent when male) and the interaction between the latter and period (more frequent during the non-reproductive period when the large subordinate was male than when the large subordinate was female; Fig. 1b, Table 2a).

When the observation periods were analysed separately, the subordinate's size was the only significant predictor of the number of attacks that it received during spawning (large > small; Fig. 1, Table 2b). In contrast, during the non-reproductive period, dominant male aggression depended on subordinate size (large > small) and sex (male > female), modified by the sex of the other subordinate in the group (Table 2b).

Subordinates' Approaches to Breeding Shelters

As with patterns of dominant male aggression, the frequencies with which subordinates entered the lower third of their compartment varied with the genders
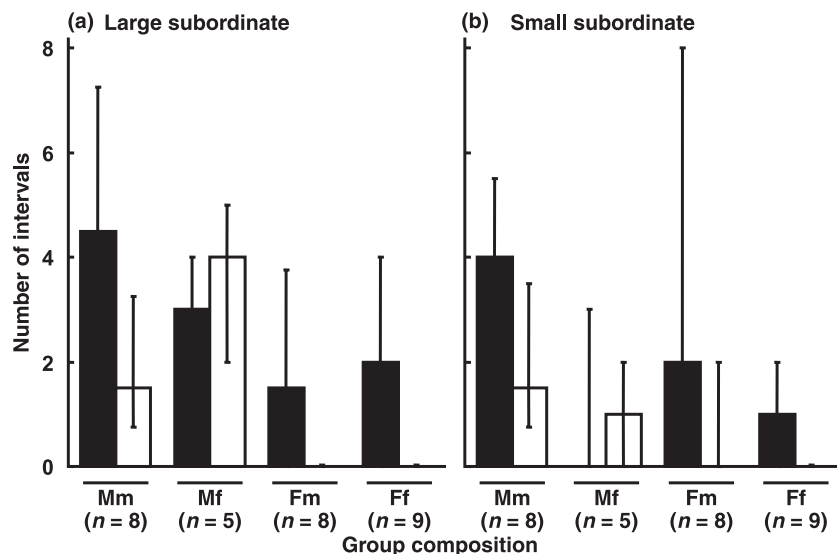

Fig. 1: Number of 30 s intervals (median ± interquartile range) during which dominant breeding males interacted aggressively with their subordinates during 10 min spawning (solid bars) and non-reproductive (hollow bars) observation periods for the four different subordinate gender combinations (Large, small subordinate sex). Panel a: aggression towards large subordinates; panel b: aggression towards small subordinates.

Table 2: Results of generalized linear mixed model analyses of differences in the number of observation intervals during which dominant males interacted aggressively with their subordinates as a function of each focal subordinate's gender

Focal size		Large subordinate			Small subordinate		
Factor	df	Coefficient	HPD interval	p-Value	Coefficient	HPD interval	p-Value
(a) Separate models for large and small subordinates							
Intercept	1	−0.54	−1.55–0.16	0.14	−1.33	−2.26 to −0.36	0.004
Focal gender	1	1.85	0.93–2.91	<0.001	0.85	−0.14–1.66	0.07
Non-focal gender	1	−0.96	−2.10 to −0.11	0.08	1.07	0.06–2.19	0.04
Period	1	1.12	0.51–1.91	<0.001	1.63	0.97–2.27	<0.001
Focal gender × period	1	−1.26	−2.11 to −0.45	0.002		ns	
Non-focal gender × period	1	1.15	0.045–2.18	0.009	−1.04	−1.85 to −0.33	0.009

Period		Spawning			Non-reproductive		
Factor	df	Coefficient	HPD interval	p-Value	Coefficient	HPD interval	p-Value
(b) Separate models for spawning and non-reproductive observation periods							
Intercept	1	0.67	0.24–1.06	0.001	−2.10	−3.67 to −0.75	<0.001
Focal gender	1		ns		1.67	0.91–2.66	<0.001
Non-focal gender	1		ns		1.19	0.32–2.62	0.05
Focal size	1	0.58	0.20–0.98	0.004	1.06	−0.25–2.43	0.05
Non-focal gender × focal size	1		ns		−1.61	−3.00 to −0.53	0.006

In Part a, results for large and small subordinates were analysed separately and the observation period (spawning or non-reproductive) was included as a third predictor. In Part b, results for each observation period were analysed separately and the size of the focal subordinate was included as a third predictor. See Table 1 for sample sizes.

Coefficients for the effects of each subordinate's gender (male or female) use female as the reference factor level, i.e. the coefficients indicate the changes in frequency for a male subordinate relative to a female subordinate. In Part a, coefficients for effects of the observation period (spawning or non-reproductive) use the non-reproductive period as the reference factor level. In Part b, coefficients for the effects of the focal subordinate's size (large or small) use the small subordinate as the reference factor level. Analyses used Poisson models, so coefficients fit the log-transformed number of observation intervals. Highest posterior density (HPD) credible intervals are analogous to 95% confidence intervals. Pair-wise interactions that are not presented or that are presented as 'ns' were non-significant ($p > 0.1$) and were not included in the reduced model.

of both subordinates and between spawning and non-reproductive observation periods (Fig. 2).

Female large subordinates used the lower third of their compartment more than male large subordinates did, and large subordinates of both sexes used the lower third of their compartment more often in groups where the small subordinate was male (Fig. 2a: Mm and Fm treatments; Table 3a). These effects were consistent between the two observation periods. The structure of the data was such that the interaction between the genders of the large and small subordinate could not be evaluated.

Patterns of space use by small subordinates were more complex, but the overall trends were the same (Fig. 2b). Males used the lower third of their compartment less often than females did, and there was a marginally non-significant tendency for small subordinates of both sexes to use the lower third of their compartment more often in groups where the large subordinate was male (Fig. 2b: Mm and Mf treatments; Table 3a). In contrast to large subordinates, patterns of space use by small subordi-

nates did differ between the two observation periods. The effect of a small subordinate's own sex was significantly greater during the non-reproductive period, while the effect of the large subordinate's sex was most pronounced during spawning (Table 3a).

Analysing the observation periods separately, small subordinates tended to use the lower third of their compartment to a greater extent than did large subordinates (Fig. 2b, Table 3b). Because small subordinates altered their pattern of space use between observation periods, whereas large subordinates did not, the size-dependent difference in space use was more pronounced during non-reproductive periods; during spawning, this difference was only evident in the Mm and Mf treatments. As with patterns of dominant male aggression, a subordinate's size had less effect on its location than its gender did. Thus, in groups with one male and one female subordinate (Mf and Fm), the female made greater use of the lower third of its compartment than the male did, regardless of the two subordinates' relative sizes.
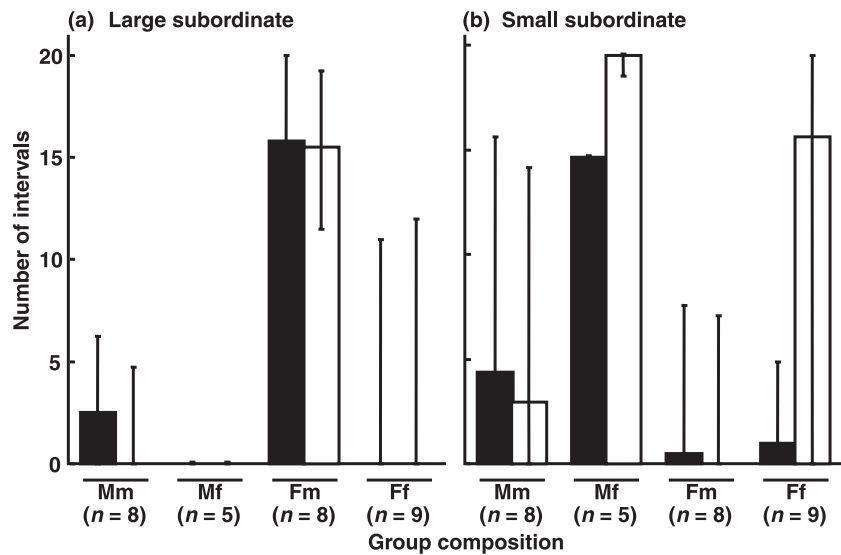
(a) Large subordinate   **(b) Small subordinate**

Fig. 2: Number of 30 s intervals (median ± interquartile range) during which subordinates entered the lower third of their group's compartment during 10 min spawning (solid bars) and non-reproductive (hollow bars) observation periods for the four different subordinate gender combinations (large and small subordinate sex). Panel a: large subordinates; panel b: small subordinates.

Discussion

Our results suggest that, for the dominant male in a *N. pulcher* group, male subordinates impose higher costs than female subordinates. We observed parasitic spawning in over one quarter of the groups (six of 21) where at least one male subordinate was present and in over half the groups (five of eight) where both subordinates were male. Both large and small male subordinates spawned. These observations provide a behavioural context for previous studies demonstrating that subordinates can gain paternity in dominant females' clutches (Dierkes et al. 1999; Heg et al. 2006, 2008). Genetic parentage analyses carried out in conjunction with this study also detected mixed paternity, and confirmed our finding that the likelihood of extra-pair paternity increases when two male subordinates are present (Heg et al. 2008). Because there was little overlap between the spawnings that we directly observed and the clutches for which we could determine genetic parentage, we cannot connect parasitic spawning and paternity on a clutch-by-clutch level.

In addition to spawning parasitically, male subordinates influenced dominant male behaviour. During non-reproductive periods, dominant males were more aggressive towards male subordinates. This difference is consistent with the pattern of dominant male aggression described by Mitchell et al. (2009) using separate observations. Male subordinates were also restricted to peripheral positions to a greater extent than female subordinates, an effect that we attribute to the threat of dominant male aggression.

For a dominant male, aggressive interactions constitute an additional cost of a male subordinate, beyond that of lost paternity. While those interactions may not involve much risk of injury, they are energetically expensive (Grantner & Taborsky 1998). In the field, aggressive interactions with subordinates would also limit a dominant male's ability to detect predators of eggs, of juvenile offspring and of the male himself. Our results differ from those of Taborsky (1985), who detected no gender-specific responses to subordinates. Taborsky's (1985) study population was from the north end of Lake Tanganyika. Many subordinates in the northern population leave their groups for large, non-breeding aggregations after reaching maturity. Therefore, it is not clear whether the same patterns of dominant male aggression should be expected.

Interactions between dominant males and each of their subordinates were also sensitive to the gender of the second subordinate in a group. During non-reproductive periods, dominant males were less aggressive towards large subordinates in groups where the small subordinate was male (Mm and Fm treatments), and were more aggressive towards small subordinates in groups where the large subordinate was male (Mm and Mf treatments). Also, during both observation periods, all subordinates were less restricted to peripheral positions in groups where the second subordinate was male. Most importantly, dominant males experienced a higher risk of parasitic spawning when both their subordinates were male. There was some indication that the increased risk was partially because of an increase in the

Table 3: Results of generalized linear mixed model analyses of differences in the number of observation intervals during which subordinates entered the lower third of their compartment as a function of each subordinate's gender

Focal size		Large subordinate			Small subordinate		
Factor	df	Coefficient	HPD interval	p-Value	Coefficient	HPD interval	p-Value
(b) Separate models for large and small subordinates							
Intercept	1	−4.14	−6.60 to −1.48	0.01	0.89	−1.66–3.83	0.38
Focal gender	1	−5.89	−10.84 to −1.80	<0.001	−4.59	−8.05 to −0.65	0.03
Non-focal gender	1	6.04	2.66–12.32	0.009	2.91	−0.95–5.82	0.20
Period	1		ns		−3.93	−4.92 to −3.18	<0.001
Focal gender × period	1		ns		2.43	1.51–3.35	<0.001
Non-focal gender × period	1		ns		0.98	0.16–2.28	0.06

Period		Spawning			Non-reproductive		
Factor	df	Coefficient	HPD interval	p-Value	Coefficient	HPD interval	p-Value
(b) Separate models for spawning and non-reproductive periods							
Intercept	1	−1.87	−3.49 to −0.38	0.01	0.38	−1.45–2.44	0.64
Focal gender	1	−2.30	−3.66 to −0.79	0.002	−2.81	−4.41 to −1.51	<0.001
Non-focal gender	1	3.05	1.80–4.59	<0.001	2.46	0.73–3.74	<0.001
Focal size	1	0.12	−0.66–0.35	0.60	−2.02	−2.45 to −1.63	<0.001
Focal gender × focal size	1	−0.99	−1.78 to −0.36	0.006		ns	

In Part a, results for large and small subordinates were analysed separately and the observation period (spawning or non-reproductive) was included as a third predictor. In Part b, results for each observation period were analysed separately and the size of the focal subordinate was included as a third predictor. See Table 1 for sample sizes.

Coefficients for the effects of each subordinate's gender (male or female) use female as the reference factor level, i.e. the coefficients indicate the changes in frequency for a male subordinate relative to a female subordinate. In Part a, coefficients for effects of the observation period (spawning or non-reproductive) use the non-reproductive period as the reference factor level. In Part b, coefficients for the effects of the focal subordinate's size (large or small) use the small subordinate as the reference factor level. Analyses used binomial models, so coefficients fit the logit-transformed number of observation intervals. Highest posterior density (HPD) credible intervals are analogous to 95% confidence intervals. Pair-wise interactions that are not presented or that are presented as 'ns' were non-significant (p > 0.1) and were not included in the reduced model.

likelihood of each individual subordinate spawning when the second subordinate was male rather than female. We discuss this possibility below. From a dominant male's perspective, the outcome is that two male subordinates are more costly than a single male subordinate. Our study is the first to consider this aspect of group composition in a cooperative breeder. Variation in the gender composition of *N. pulcher* groups may be particularly important in field populations, where groups are larger and will frequently include more than one mature male subordinate (Balshine et al. 2001).

Although differences in male aggression between spawning and non-reproductive observation periods and towards male and female subordinates matched our expectations, interactions between these effects did not. We had expected that increased aggression during spawning would be directed primarily towards (large) male subordinates. Instead, we found that male subordinates experienced more aggression than females during non-reproductive observations, but that no difference was evident during spawning.

Both male and female small subordinates spent less time in the lower third of their compartment during spawning, and the difference between these males and females was less pronounced during spawning. During spawning, dominant males were more aggressive towards large than small subordinates, but contrary to our expectation, this difference was not restricted to male subordinates. Distinguishing between male and female subordinates may be difficult (Taborsky 1985), and indiscriminate aggression during spawning may be more efficient than delaying each response while assessing the threat posed. However, subordinates in each group were familiar to the dominant male and differed markedly in size, so dominant males are expected to have recognized them. Alternatively, the aggressive responses of dominant males to female subordinates may be adaptive, perhaps limiting the risk that the dominant female is interrupted during spawning or that eggs are eaten by subordinates (von Siemens 1990; Heg & Hamilton 2008; Heg et al. 2008). Neither explanation is consistent with our interpretation of

aggression as an efficient means by which dominant males prevent male subordinates from spawning. Nevertheless, regardless of which subordinate is the recipient of dominant male aggression, the outcome is that dominant males invest more in aggressive interactions in groups where male subordinates were present.

Whether the cost of a male subordinate leads to a preference for female subordinates should depend on the benefits that male and female subordinates provide. Gender differences in helping behaviour have been described in various cooperatively breeding species (e.g. Clutton-Brock et al. 2002; Stiver et al. 2005; Woxvold et al. 2006; and references therein). The implications of those differences for dominant members of family groups have been discussed in the context of sex ratio manipulation (review in Komdeur 2004). Under some circumstances, breeding pairs are expected to overproduce the offspring gender that repays some of its production cost (Emlen et al. 1986). Extending this logic to *N. pulcher*, in which dominant breeding pairs may have unrelated subordinates of both sexes, we would predict either that male subordinates provide more help than female subordinates (to compensate for the cost difference) or, if male subordinates do not provide greater benefits, that dominant males prefer female subordinates. Helping behaviour in *N. pulcher* has been well-studied (e.g. Taborsky & Limberger 1981; Taborsky 1984; Stiver et al. 2005; Bruintjes & Taborsky 2008). Male and female subordinates perform the same suite of helping behaviours, and there is no indication that male subordinates help more than females: male subordinates make fewer breeding shelter visits than female subordinates (Stiver et al. 2005), show less alloparental direct brood care (Heg et al. 2008) and frequencies of territory maintenance and defence behaviours do not differ between the sexes (Stiver et al. 2005; Bruintjes & Taborsky 2008). Furthermore, female subordinates may also provide dominant males with spawning opportunities (Heg 2008; Heg & Hamilton 2008; Heg et al. 2008) — a benefit that male subordinates cannot provide. If higher costs of male subordinates are not offset by greater benefits, then do dominant males prefer female subordinates? Female-biased sex ratios have been found within *N. pulcher* groups from a northern population, where large subordinates may join aggregations of non-breeders (Taborsky 1985). Sex ratios are not female-biased in a southern population, where those aggregations do not occur (Balshine et al. 2001), even though dispersal in the southern population does appear to be

male-biased (Stiver et al. 2006). Dispersal could result from eviction (Dierkes et al. 1999), but could also reflect decisions made by subordinates without any coercion. Desjardins et al. (2008) observed that dominant males responded more aggressively to simulated intrusions of breeder-sized males, i.e. to potential usurpers, than to breeder-sized females. An equivalent comparison of responses to smaller intruders, i.e. to potential new subordinates, would be informative. The same arguments apply when considering a second subordinate. If two male subordinates are more costly than a single male subordinate, then the costs and benefits associated with a second subordinate may depend, not only on the second subordinate's gender, but also on the gender of the first subordinate. Thus, studies of trade-offs related to group membership need to consider both a focal individual's gender and also the gender composition of a group.

Our results suggest the potential for complex effects of gender on interactions between subordinates. Same-sex subordinates are typically regarded as competitors for future reproductive opportunities. However, subordinates can also benefit from one another's presence. Both subordinates were less restricted to peripheral positions when one of the subordinates was male, and large subordinates experienced less dominant male aggression in groups with a small male subordinate (although the reverse was true for small subordinates in groups with a large male subordinate). An intriguing observation was the tendency (albeit non-significant: p = 0.09) for parasitic spawning to increase disproportionately when both subordinates were male. Patterns of subordinate male paternity show the same effect: male large subordinates significantly increased their parentage when a male small subordinate was present compared with when a female small subordinate was present (comparing treatment Mm with Mf; Heg et al. 2008). A plausible interpretation is that a dominant male's efforts to police the behaviour of one subordinate limit his ability to police a second (Noë 2007). Dubois et al. (2004) have modelled a similar process in a social foraging context, referring to it as 'distraction sneaking'. We saw no indication that male subordinates were coordinating their behaviour to facilitate parasitic spawning or to reduce dominant male aggression. However, our observations were not designed to detect such effects.

Dominant females were rarely aggressive during our observations, so we could not contrast their responses to male and female subordinates. It is not clear whether or how those responses should differ.

Dominant female *N. pulcher* do respond behaviourally to the sexes of their subordinates (Mitchell et al. 2009) and lay larger clutches when male subordinates are present (Heg et al. 2006; Hamilton & Heg 2007). The cost associated with a reproductively active female subordinate depends, in part, on whether the two females' clutches and broods compete for depreciable parental or alloparental care. Assessing that possibility would require field estimates of hatching success and juvenile survival for offspring of cohabiting females. Differences in the costs and benefits of subordinates for dominant males and females are worth exploring, as they may be an important source of conflict within a group (Cockburn 2007).

In discussing this study's implications, we have noted that the costs (and benefits) of male and female subordinates may differ for free-living vs. aquarium-housed groups. We would expect such differences to be quantitative rather than qualitative. For example, if *N. pulcher* avoid mating with close relatives then our results may overestimate the occurrence of parasitic spawning, because subordinates in our groups were always unrelated to dominants, whereas dominants and subordinates in free-living groups will sometimes be related (Dierkes et al. 2005). Alternatively, the risk of parasitic spawning may be greater for free-living dominant males if potential parasites are more difficult to monitor in a more complex environment. In either case, a difference between male and female subordinates remains, because a male subordinate can pose a threat to a dominant male whereas a female subordinate cannot. Fitzpatrick et al. (2006) reported that male subordinates in free-living *N. pulcher* groups have smaller gonads (both absolutely and relatively) than dominant males. They argued that male subordinates are reproductively suppressed and that subordinate male paternity may be an aquarium artefact. However, Fitzpatrick et al. (2006) also found that the sperm of dominants and large subordinates were physiologically equivalent, and the fact that male subordinates had testes of a considerable size, even if smaller than those of dominant males, suggests that those subordinates had some reproductive potential. This interpretation is further corroborated by a significant correlation between a dominant's relative testis mass (GSI) and the number of male subordinates present in the group, and by the absence of any such relationship with the number of female subordinates present (Fitzpatrick et al. 2006). Mixed paternity in free-living groups has been reported by Dierkes et al. (2008) (five of 12

groups) and Stiver et al. (2009) (three of five groups). Dierkes et al. could not identify the extra-pair sires and speculated that they were subordinates that had since been evicted. Stiver et al. identified dominant males at neighbouring groups as the extra-pair sires at two groups and proposed that neighbours, rather than resident subordinates, are the primary threat to a dominant male's paternity. However, regardless of the relative threat posed by neighbours and resident subordinates, the qualitative difference between male and female subordinates remains. Free-living male subordinates are producing sperm (Fitzpatrick et al. 2006), and the fact that male subordinates have the behavioural repertoire needed to spawn parasitically in aquaria (Taborsky 1985; Dierkes et al. 1999; this study) certainly suggests the potential for parasitic spawning in free-living groups as well (see also Dierkes et al. 2008). Moreover, as our results illustrate, male subordinates can be costly for dominant males, even if the subordinates rarely succeed in fertilizing eggs, because dominant males are more aggressive when male subordinates are present. High levels of within-group aggression are not an aquarium artefact: aggressive interactions are also frequent in free-living groups and are not restricted to periods during which dominance relationships are being established (Werner et al. 2003; Fitzpatrick et al. 2008). See also Taborsky (1984) for a comparison of results obtained in the field and under semi-natural laboratory conditions in this species.

Gender may be a particularly important aspect of group composition in group-living fish, as compared with other vertebrates, because external fertilization creates opportunities for parasitic spawning. But gender-specific costs of one sort or another are expected whenever reproduction occurs in a social context (Cockburn 2004); same sex subordinates may be reproductive competitors of a dominant individual and may also be facilitators of one another's reproductive efforts. Our observations demonstrate the importance of considering gender composition in behavioural studies of group-living species.

Literature Cited

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M. & Werner, N. 2001: Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). Behav. Ecol. Sociobiol. **50**, 134—140.

Bates, D. 2007: lme4: Linear Mixed-Effects Models Using S4 Classes. R Package Version 0.99875–7.

Bruintjes, R. & Taborsky, M. 2008: Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. Anim. Behav. **75**, 1843—1850.

Clutton-Brock, T. H., Russel, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z. & McIlrath, G. M. 2002: Evolution and development of sex differences in cooperative behavior in meerkats. Science **297**, 253—256.

Cockburn, A. 1998: Evolution of helping behavior in cooperatively breeding birds. Annu. Rev. Ecol. Syst. **29**, 141—177.

Cockburn, A. 2004: Mating systems and sexual conflict. In: Ecology and Evolution of Cooperative Breeding in Birds (Koenig, W. D. & Dickinson, J. L., eds). Cambridge Univ. Press, Cambridge, pp. 81—101.

Cockburn, A. 2007: Solitary obsession or ménage à trois, but cooperative breeding is never a two-party game. Behav. Proc. **76**, 106—108.

Desjardins, J. K., Fitzpatrick, J. L., Stiver, K. A. & Balshine, S. 2008: Differential responses to territory intrusions in cooperatively breeding fish. Anim. Behav. **75**, 595—604.

Dierkes, P., Taborsky, M. & Kohler, U. 1999: Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. Behav. Ecol. **10**, 510—515.

Dierkes, P., Heg, D., Taborsky, M., Skubic, E. & Achmann, R. 2005: Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. Ecol. Lett. **8**, 968—975.

Dierkes, P., Taborsky, M. & Achmann, R. 2008: Multiple paternity in the cooperatively breeding fish *Neolamprologus pulcher*. Behav. Ecol. Sociobiol. **62**, 1581—1589.

Dubois, F., Giraldeau, L.-A., Hamilton, I. M., Grant, J. W. A. & Lefebvre, L. 2004: Distraction sneakers decrease the expected level of aggression within groups: a game-theoretic model. Am. Nat. **164**, E32—E45.

Duftner, N., Sefc, K. M., Koblmüller, S., Salzburger, W., Taborsky, M. & Sturmbauer, C. 2007: Parallel evolution of facial stripe patterns in the *Neolamprologus brichardi/pulcher* species complex endemic to Lake Tanganyika. Mol. Phylogenet. Evol. **45**, 706—715.

Emlen, S. T. 1997: Predicting family dynamics in social vertebrates. In: Behavioural Ecology: An Evolutionary Approach (Krebs, J. R. & Davies, N. B., eds). Blackwell Scientific, Oxford, pp. 228—253.

Emlen, S. T., Emlen, J. M. & Levin, S. A. 1986: Sex-ratio selection in species with helpers-at-the-nest. Am. Nat. **127**, 1—8.

Faraway, J. 2006: Extending the Linear Model with R. Chapman and Hall, London.

Fitzpatrick, J. L., Desjardins, J. K., Stiver, K. A., Montgomerie, R. & Balshine, S. 2006: Male reproductive suppression in the cooperatively breeding fish *Neolamprologus pulcher*. Behav. Ecol. **17**, 25—33.

Fitzpatrick, J. L., Desjardins, J. K., Milligan, N., Stiver, K. A., Montgomerie, R. & Balshine, S. 2008: Female-mediated causes and consequences of status change in a social fish. Proc. R. Soc. Lond. B **275**, 929—936.

Grantner, A. & Taborsky, M. 1998: The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). J. Comp. Physiol. B. **168**, 427—433.

Griffin, A. S., Pembertson, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kansky, R., O'Riain, J. & Clutton-Brock, T. H. 2003: A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). Behav. Ecol. **14**, 472—480.

Hamilton, I. M. & Heg, D. 2007: Clutch-size adjustments and skew models: effects on reproductive partitioning and group stability. Behav. Ecol. **18**, 467—476.

Hamilton, I. M., Heg, D. & Bender, N. 2005: Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid. Behaviour **142**, 1591—1613.

Heg, D. 2008: Reproductive suppression in female cooperatively breeding cichlids. Biol. Lett. **4**, 606—609.

Heg, D. & Hamilton, I. M. 2008: Tug-of-war over reproduction in a cooperatively breeding cichlid. Behav. Ecol. Sociobiol. **62**, 1249—1257.

Heg, D., Bergmüller, R., Bonfils, D., Otti, O., Bachar, Z., Burri, R., Heckel, G. & Taborsky, M. 2006: Cichlids do not adjust reproductive skew to the availability of independent breeding options. Behav. Ecol. **17**, 419—429.

Heg, D., Jutzeler, E., Bonfils, D. & Mitchell, J. S. 2008: Group composition affects male reproductive partitioning in a cooperatively breeding cichlid. Mol. Ecol. **17**, 4359—4370.

Hughes, C. 1998: Integrating molecular techniques with field methods in studies of social behaviour: a revolution results. Ecology **79**, 383—399.

Koenig, W. D. & Dickinson, J. 2004: Ecology and Evolution of Cooperative Breeding in Birds. Cambridge Univ. Press, Cambridge.

Komdeur, J. 2004: Sex-ratio manipulation. In: Ecology and Evolution of Cooperative Breeding in Birds (Koenig, W. D. & Dickinson, J. L., eds). Cambridge Univ. Press, Cambridge, pp. 102—117.

Krause, J. & Ruxton, G. D. 2002: Living in Groups. Oxford Univ. Press, Oxford.

Magrath, R. D., Heinsohn, R. G. & Johnstone, R. A. 2004: Reproductive skew. In: Ecology and Evolution of Cooperative Breeding in Birds (Koenig, W. D. & Dickinson, J. L., eds). Cambridge Univ. Press, Cambridge, pp. 157—176.

Mitchell, J. S., Jutzeler, E., Heg, D. & Taborsky, M. 2009: Dominant members of cooperatively-breeding groups adjust their behaviour in response to the sexes of their subordinates. Behaviour **146**, 1665—1686.

Noë, R. 2007: Despotic partner choice puts helpers under pressure? Behav. Proc. **76**, 120—125.

Noë, R. & Hammerstein, P. 1994: Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav. Ecol. Sociobiol. **35**, 1—11.

R Development Core Team 2007: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Reeve, H. K. & Keller, L. 2001: Tests of reproductive skew models in social insects. Annu. Rev. Entomol. **46**, 347—385.

Richardson, D. S., Burke, T. & Komdeur, J. 2002: Direct benefits and the evolution of female-biased cooperative breeding in Seychelles Warblers. Evolution **56**, 2313—2321.

von Siemens, M. 1990: Broodcare or egg cannibalism by parents and helpers in *Neolamprologus brichardi* (Poll 1986) (Pisces: Cichlidae): a study on behavioural mechanisms. Ethology **84**, 60—80.

Skubic, E., Taborsky, M., McNamara, J. M. & Houston, A. I. 2004: When to parasitize? A dynamic optimization model of reproductive strategies in a cooperative breeder. J. Theor. Biol. **227**, 487—501.

Solomon, N. G. & French, J. A. 1997: Cooperative Breeding in Mammals. Cambridge Univ. Press, Cambridge.

Stacey, P. B. & Koenig, W. D. 1990: Cooperative Breeding in Birds: Long Term Studies of Ecology and Behavior. Cambridge Univ. Press, Cambridge.

Stiver, K. A., Dierkes, P., Taborsky, M. & Balshine, S. 2004: Dispersal patterns and status change in a co-operatively breeding cichlid *Neolamprologus pulcher*: evidence from microsatellite analyses and behavioural observations. J. Fish Biol. **65**, 91—105.

Stiver, K. A., Dierkes, P., Taborsky, M., Gibbs, H. L. & Balshine, S. 2005: Relatedness and helping in fish: examining the theoretical predictions. Proc. R. Soc. Lond. B **272**, 1593—1599.

Stiver, K. A., Fitzpatrick, J., Desjardins, J. K. & Balshine, S. 2006: Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. Anim. Behav. **71**, 449—456.

Stiver, K. A., Fitzpatrick, J. L., Desjardins, J. K. & Balshine, S. 2009: Mixed parentage in *Neolamprologus pulcher* groups. J. Fish Biol. **74**, 1129—1135.

Taborsky, M. 1984: Broodcare helpers in the cichlid *Lamprologus brichardi*: their costs and benefits. Anim. Behav. **32**, 1236—1252.

Taborsky, M. 1985: Breeder-helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. Behaviour **95**, 45—75.

Taborsky, M. 1994: Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. Adv. Study Behav. **23**, 1—100.

Taborsky, M. 2001: The evolution of parasitic and cooperative reproductive behaviors in fishes. J. Heredity **92**, 100—110.

Taborsky, M. & Limberger, D. 1981: Helpers in fish. Behav. Ecol. Sociobiol. **8**, 143—145.

Vehrencamp, S. L. 1983: A model for the evolution of despotic versus egalitarian societies. Anim. Behav. **31**, 667—682.

Werner, N. Y., Balshine, S., Leach, B. & Lotem, A. 2003: Helping opportunities and space segregation in cooperatively breeding cichlids. Behav. Ecol. **14**, 749—756.

Woxvold, I. A., Mulder, R. A. & Magrath, M. J. L. 2006: Contributions to care vary with age, sex, breeding status and group size in the cooperatively breeding apostlebird. Anim. Behav. **72**, 63—73.