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RESEARCH PAPERS

Cooperative Breeding and Group Structure in the Lake Tanganyika Cichlid *Neolamprologus savoryi*

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Abstract

As yet, cooperative breeding has been described only for some fish species. However, evidence is accumulating that it is widespread among Lake Tanganyika cichlids. We studied the cooperative breeding system of the substrate breeding cichlid *Neolamprologus savoryi*. Breeding groups typically consisted of a large breeding male with one to four breeding females and three to 33 helpers (mean group size: 14.3 members). Group size was significantly related to breeding male and female body sizes, and larger males had more breeding females and larger sized male helpers. The size of the largest female in the group was positively related to the number and sizes of secondary breeding females and female helpers. In case of multiple breeding females, these females usually divided the group's territory into sub-territories, each with its own helpers (subgroups). Interspersed between groups, independent fish were detected defending an individual shelter (4.4% of all fish). In 9% of the groups no breeding female was present. All group members participated in territory defence and maintenance, and showed submissive behaviours to larger group members. As expected, the level of between-subgroup conflicts was high compared with the level of within-subgroup conflicts. We compare these results with data available from other cooperatively breeding fishes.

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Introduction

Among the vertebrates, fish species show the highest variability in mating and parental care systems (Taborsky 1994). This variability may be accompanied by within-population variation in behavioural strategies (e.g. alternative reproductive tactics, Taborsky et al. 1987; Henson & Warner 1997; Taborsky 2001; Fishelson & Hilzerman 2002), sometimes mediated by phenotypic differences (e.g. parasitic spawning by dwarf or satellite males, Kolluru & Reznick 1996; Kohda et al. 1997; Schütz & Taborsky 2000; Gonçalves et al. 2003; Sato et al. 2004). Biparental cooperation in raising young is not uncommon, and occurs frequently in Lake Tanganyika cichlids, particularly in the Lamprologini (Kawanabe et al. 1997). Other forms of cooperative behaviour in mate acquisition or parental care are also regularly found in a variety of fish families (e.g. satellite males tolerated by dominant males, joint spawning, etc., see Taborsky 1994, 1999, 2001). Considering this variation and the prevalence of extensive biparental brood care in many fish taxa, it might seem surprising that only a few fish species have been described which show cooperative breeding as described for many birds and mammals, e.g. where offspring remain in the natal territory and assist their parents in raising young (Taborsky 1994, 2001; Wisenden 1999). The majority of cooperatively breeding fishes hitherto described are cichlids endemic to Lake Tanganyika belonging to the tribe Lamprologini (in total approx. 20 of 80 Lamprologine species, see D. Heg & Z. Bachar, unpubl. data).

All Lamprologine Lake Tanganyika cichlids share three main characteristics. First, eggs are laid in a well protected spot on the substrate, either inside snail shells, inside holes and crevices or on rocks. Second, biparental care is the rule, although in species where the male is substantially larger than the female (e.g. *Lamprologus callipterus*, *L. lemairii*), females do all direct brood care (fanning and cleaning eggs), whereas males defend the territory against intruders potentially harmful to the female or brood. Third, all species are highly territorial during breeding and some species hold long-term territories (Kuwamura 1997). Otherwise, spacing, habitat selection, feeding habits and body sizes are highly variable, ranging from the small, inside snail shells breeding cichlid *Neolamprologus multifasciatus* [maximum 3.5 cm standard length (SL), Kohler 1998], to the large piscivore cichlid *Lepidiolamprologus profundicola* breeding in the rocky littoral (max. 30 cm SL, Konings 1998).

Only limited behavioural and life-history data are available for most of the Lamprologine cichlids, including the species showing cooperative breeding. Most information on cooperative breeding has been accumulated for *Neolamprologus pulcher* (sub- or sister species of *N. brichardi* 'the Princess of Burundi', formerly known as *Lamprologus brichardi*, see Grantner & Taborsky 1998 for comments on the status of the species; Taborsky & Limberger 1981; Taborsky 1984, 1985; Balshine-Earn et al. 1998; Taborsky & Grantner 1998; Dierkes et al. 1999; Balshine et al. 2001; Heg et al. 2004a,b, in press; Skubic et al. 2004; Stiver et al. 2004; Bergmüller et al. 2005, in press; Bergmüller & Taborsky 2005) and *N. multifasciatus* (Rossiter 1993; Sato & Gashagaza 1997; Kohler 1998; Schradin & Lamprecht 2000, 2002). Recent studies show positive correlations between the group size and the body sizes of the group members in group-living fish (Kohler 1998; Buston 2003a,b; Mitchell 2003; Heg & Bachar, unpubl. data), mediated by dominant's expulsion of similar sized subordinates from the group (Balshine-Earn et al. 1998; Buston 2003a). Size differences in the group may be maintained by strategic growth decisions of subordinates (Buston 2003b; Heg et al. 2004b).

The purpose of the present paper is to describe the group composition, spacing and social behaviours of the cooperatively breeding cichlid *Neolamprologus* *savoryi*. No comprehensive data on the natural history and behaviour of this species are available, except for data on feeding behaviour (Kondo 1988; Kohda et al. 1997), and a qualitative description of the social system (Kondo 1988). We shall first describe the numbers, sizes and sexes of individuals living in groups, including the numbers of breeding individuals. Analyses of the group composition and the sizes of the individuals will be used to test whether *N. savoryi* shows similar correlations between group size and the body sizes of breeders and subordinates as other group-living fish do. These data will also be related to the number of breeding females in the group and patch usage. We use focal observation data to test whether subordinates in *N. savoryi* can be operationally classified as helpers, e.g. if and how much they invest in helping behaviour (territory defence and maintenance) and how these behaviours compare with those shown by the breeders in the group. Finally, we analyse the within-group social interactions, comparing them with social behaviours shown by other cooperatively breeding cichlids, and relate them to within-group spatial sub-structuring.

Methods

Study Site

Our main study site was at the southern tip of Lake Tanganyika, Kasakalawe Point and Nkumbula Island, near Mpulungu, Zambia (8°46.849′S, 31°04.882′E). Cichlids were studied by SCUBA diving from 2 Feb. to 21 Apr. 2003 (D.H. and Z.B., n = 28 breeding groups at Kasakalawe, including behavioural observations, and n = 2 breeding groups at Nkumbula) and 23 Oct. to 10 Nov. 2003 (M.T., n = 5 breeding groups at Kasakalawe, no focal behavioural records made). Fish catching and observations were conducted in two 'colonies' of *N. pulcher* and *N. savoryi* at Kasakalawe, both occurring at very high densities of several hundred breeding groups (D. Heg, Z. Bachar, L. Brouwer & M. Taborsky, unpubl. data). The Kasakalawe study site is a rather monotonous sandy area with rocks (typically Ø 10–40 cm in size) half submerged in the sand, at 9.0–11.5 m depth, with no boulders or steep cliffs. Hence, all substrate breeding cichlids and their breeding sites could be easily located, including individuals not associated with a breeding shelter. In contrast, our second study site at Nkumbula Island, approx. 2 km from Kasakalawe and close to the harbour of Mpulungu had layers of stones and patches of large boulders (> 1 m diameter), interspersed with patches of gravel and shell debris. Due to this habitat structure, individuals were difficult to observe and catch at this site. Therefore, only two groups were caught there, and no behavioural observations were conducted.

Mapping of Breeding Groups

The main study area at Kasakalawe (1708 m^2) was systematically surveyed and mapped for breeding groups using a 2 × 2 m grid made with ropes (see D. Heg, Z. Bachar, L. Brouwer & M. Taborsky, unpubl. data). Groups were defined according to the territory boundary defended by dominant breeder male. All focal group-territories (n = 33) were marked with uniquely numbered stones, and a detailed map was made of the shelters in the territory. Additionally, two groups were surveyed at Nkumbula Island, adding up to a total sample size of 35 groups sampled. We noted that group members sometimes defended distinct patches of stones within the breeding male's territory (Fig. 1a), and these 'subgroups' usually contained at least one breeder female. Subgroups were also sometimes apparent when group members defended one part of a large patch against group members from another part of the same patch (e.g. Fig. 1b). The 'subgroup territory boundaries' were often located on large stones or patches of empty snail shells. Note however that the breeder male visited and assisted all subgroups in territory defence.

Occasionally, non-group members were located near the breeding groups, defending a shelter on their own, and these were also mapped. We also detected several small 'groups' of two to five fish without any breeders. We further refer to all fish not living in groups, or fish in groups without any breeder, as 'independents'.

Body Measurements

All members of the breeding groups were caught using tent nets with the help of the anaesthetic clove oil, also known as eugenol (1 part eugenol dissolved in 4 parts 70% ethanol, Kreiberg 2000). Eugenol was highly effective in immobilizing the fish, while recovery occurred within 5 min and no adverse effects on subsequent behaviour were detected. We measured body length (SL to the nearest 0.5 mm) of all fish. Group members larger than 15 mm, excluding the breeding male and female, were defined as 'helpers' and group size was defined as the total number of breeders plus helpers in the group. Fish were sexed by close inspection of the genital papilla, which was verified by dissection of the gonads with a part of the samples (courtesy T. Takeyama). Sexing was only possible for individuals larger than 19.5 mm SL, and 37 helpers between SL = 15.5 and 29.0 could not be reliably sexed. In total we caught 35 breeding males, 63 breeding females, 403 helpers and 16 offspring. Additionally and similarly, we caught and measured 23 independents using gill nets and transparent plastic tubes. Two independents could not be sexed.

As part of a removal experiment (see D. Heg, Z. Bachar, L. Brouwer & M. Taborsky, unpubl. data), all caught group members by D.H. and Z.B. were temporarily removed and kept in large pouch nets. Fish were fed flocked dry food (TetraMin) daily and released into their territories after the experiment. As part of a parallel project, all caught group members of M.T. were collected for gonadal sexing and gonads were weighed.

Focal Behavioural Observations

Focal observations were conducted on individually marked group members for 10 min each at Kasakalawe (n = 21 breeding females, 18 breeding males, 13 male helpers, two female helpers, selected to cover the range of body sizes from

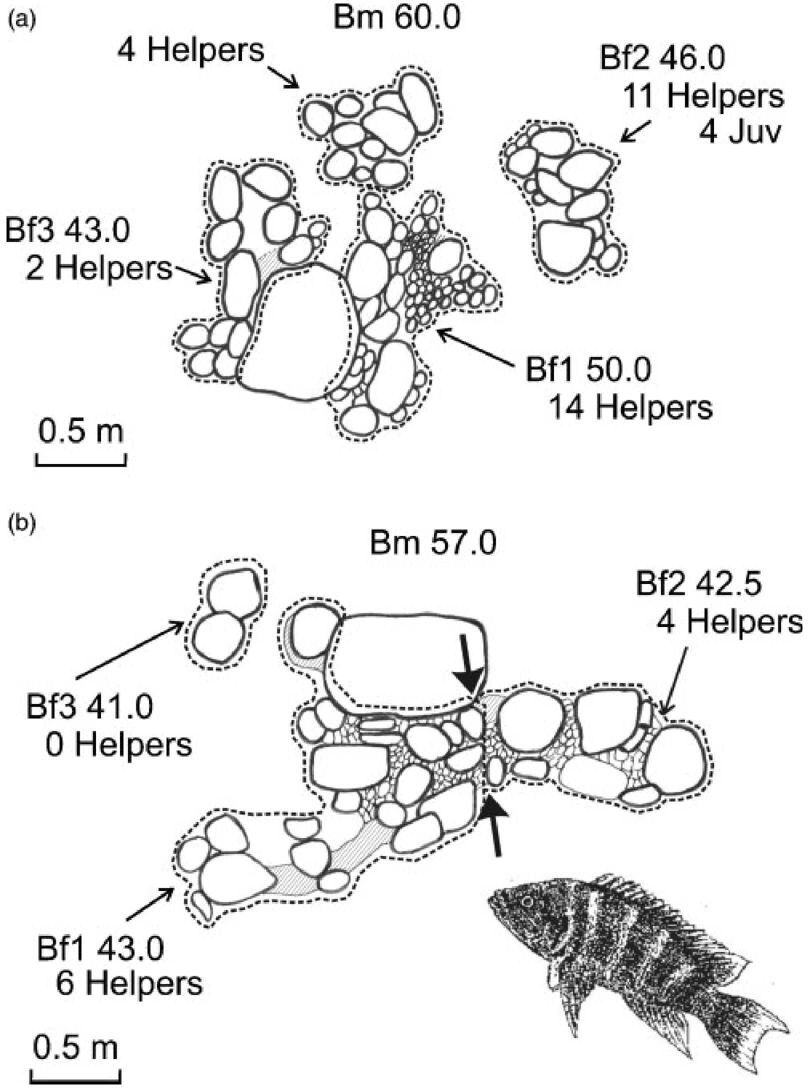

Fig. 1: Schematic representation of the patch usage by two *N. savoryi* groups, the standard lengths (mm) of the respective breeding males (Bm) are indicated on top. Per subgroup are indicated (connected with thin arrows): the standard lengths of the breeding females (Bf), and the numbers of helpers (Helpers) and juveniles (Juv). (a) Group territory divided in four patches with one subgroup each, with three breeding females (Bf1–3). (b) Group territory divided in two patches with three subgroups and three breeder females (Bf1–3). Note that here the subgroups of Bf1 and Bf2 share one patch, defended against each other over a small strip with stones and shells between the two bold arrows. Delineated are stones used as shelter, the subgroup boundaries on the basis of digging and defence activity (stippled lines), and the presence of empty snail-shells (hatched). Inset shows adult *N. savoryi* (after photo by R. Borstein)

medium helpers to breeders, i.e. 28–63 mm SL). Only one observation per individual was conducted. Smaller group members were not observed, but were more likely to hide between the stones and therefore more difficult to observe continuously. We recorded the distance focal individuals moved from their shelter (every minute, averaged), the frequency of digging and removing sand from the breeding shelter (by tail-beating and carrying sand in the mouth, respectively), the frequency of aggressive behaviours [including overt aggression: bites, chases, fast approaches, mouth-fights; and restrained aggression: opercula spreading (also called 'puffed throat'), head-down display, fin raising and S-shaped body bend directed at con- and heterospecific fishes], the frequency of submissive behaviours (tail-quivering and hook display) and social behaviour (soft-touching, also called 'bumping', of the body of group-members). These behaviours appeared very similar to behaviours as shown by *N. pulcher* and *N. brichardi* (described in Taborsky 1984, 1985; Taborsky et al. 1986; Bergmüller et al. 2005; Bergmüller & Taborsky 2005; see Baerends & Baerends-van Roon 1950 for pictures of cichlid displays). In case of interactions with conspecifics, we determined for the respective opponents: (1) the status (breeder, helper, independent); (2) for breeders and helpers the (sub-)group membership, with detailed notes when the opponent came from another (sub-)group; (3) for helpers the estimated size in three classes (small: 15.5–25.0 mm SL, medium: 25.5–35.0 mm SL, large: > 35.0 mm SL). Shelter defence behaviour was defined as all aggressive behaviours directed against non-group members.

Statistical analyses were performed using SPSS 11.0. Unfortunately, data for the distance moved from the shelter were missing for one breeding female, two breeding males, three helper males and two helper females. Variables were tested for a normal distribution by Kolmogorov–Smirnov tests, and if they were normally distributed, they were analysed with general linear models (GLM, analysis of variance allowing the incorporation of linear and fixed independent effects, where appropriate) or general linear mixed models (GLMM). GLMM is an analysis of variance using the restricted maximum likelihood method (REML) to decompose variances, e.g. allowing the incorporation of linear, fixed and random effects with nested effects and an unbalanced design (procedure MIXED in SPSS). If not, non-parametric tests were performed following the outline in Siegel & Castellan (1988).

Results

Group Composition

A typical group consisted of a breeding male with one to four breeding females and a number of helpers of various sizes (Fig. 2, median group size = 12, $\bar{x} \pm \mathrm{SD} = 14.3 \pm 8.4$, range = 5–36, n = 35). In three groups no breeding females were found and were presumed missing, i.e. had died or dispersed. The number of breeding females per group was 0 (n = 3), 1 (n = 10), 2 (n = 14), 3 (n = 7) and 4 (n = 1, $\tilde{x} = 2$, $\bar{x} \pm \mathrm{SD} = 1.80 \pm 0.96$), respectively. Breeding

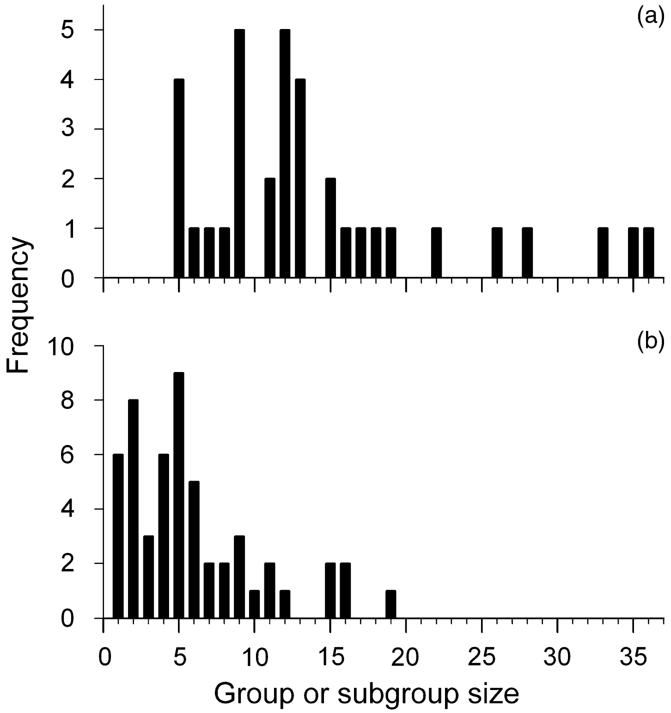

Fig. 2: (a) Group (n = 35) and (b) subgroup sizes (n = 53) of cooperative breeding groups in *N. savoryi*

females in multiple breeding female groups either defended distinct patches of stones and shelters (n = 29, see for example Fig. 1a: Bf1–Bf3 and Fig. 1b: Bf3), or part of the same patch (n = 22, see for example Fig. 1b: Bf1 and Bf2). Up to seven distinct patches of stones were defended ($\tilde{x}$ = 1, $\bar{x}$ ± SD = 1.8 ± 1.2) and there was a positive correlation between the total number of breeder females in the group (0–4) and the number of distinct patches of stones defended (1–7, Spearman rank correlation: r = 0.35, n = 35, p = 0.039). We detected 19 groups divided in subgroups (n = 53 subgroups), i.e. where group members defended distinct patches of stones or where a large patch was divided into two or more sub-territories, with aggressive interactions occurring against group members of different subgroups (see also behaviour data presented below). Nine groups had two subgroups, seven had three subgroups, two had two subgroups and one group was divided into six subgroups ($\bar{x}$ ± SD = 2.8 ± 1.0, $\tilde{x}$ = 3, n = 19). On average 0.79 breeding females per subgroup were present (±0.53 SD, $\tilde{x}$ = 1; no female: 14, one female: 36, two females: three subgroups). The average subgroup size was 5.9 individuals (±4.4 SD, $\tilde{x}$ = 5, range = 1–19, n = 53, Fig. 2).

Helpers of both sexes were present in most groups, except groups with only a small number of helpers. We detected significantly more male than female helpers (210 vs. 156, Binomial test: p = 0.006). This seemed mainly due to female helpers quicker attaining a breeding position than male helpers, as the sex ratio of the breeders in these groups was significantly female-skewed (35 male vs. 63 female breeders, Binomial test: $p = 0.006$), and the sex ratio of breeders and helpers combined did not deviate significantly from 1:1 (245 males vs. 219 females, Binomial test: $p = 0.25$). *Neolamprologus savoryi* is size-dimorphic (see below) and therefore, more female helpers might be present in the smaller sized cohorts and more males in the larger sized cohorts. This was corroborated by our data: in the small helpers (SL = 15.5–20.0 mm) and medium helpers (SL = 20.5–35.0 mm) the sex ratio was equal (small: 24 males vs. 25 females, Binomial tests: $p = 1.0$; medium: 100 males vs. 89 females, $p = 0.47$), whereas in the large helpers it was male-skewed (86 males vs. 42 females, $p < 0.001$).

Of all the fish larger than 15 mm, 4.4% were not living in groups (23 independents vs. 501 breeders plus helpers). Seventeen male and four female independents were found, the sex ratio was significantly male-biased (Binomial test: $p = 0.007$; two independents were not sexed). Also, independents had a higher male-skewed sex ratio than both the breeders [likelihood ratio (LR) test for frequency table: $\chi^2_1 = 14.9$, $p < 0.001$] and the helpers (LR: $\chi^2_1 = 5.0$, $p = 0.025$). Independents were defending a shelter singly, but sometimes associated with each other (number of independents per patch: one n = 5, two n = 5, three n = 1 and five n = 1), and were in close proximity to *N. savoryi* breeding groups (distance to the nearest group was 0.3–2 m).

Body Size of Group Members and Independents

Breeder males were substantially larger than the breeder females (Table 1, paired t-test for groups with both breeders present: $t = 14.6$, $df = 31$, $p < 0.001$), and paired size-assortative (Fig. 3, Pearson correlation coefficient: $r = 0.48$, $p = 0.005$, $n = 32$). Male breeders were always larger than the largest helper group member, which were usually helper males (Table 1; paired t-test for groups with breeder male: $t = 9.7$, $df = 34$, $p < 0.001$). In three groups the largest helper male was close in size to the breeder male (SL difference 0.5, 0.5 and 1.5 mm, with

Table 1: Body sizes of group and non-group members in *N. savoryi* (standard length SL)

Status	n	Mean SL ± SE (mm)	Range
All group members	517	34.6 ± 0.5	6.5–65.0
Breeder males	35	55.9 ± 0.9	46.0–65.0
Breeder females	63	43.7 ± 0.4	38.0–53.0
All helpers	403	32.2 ± 0.4	15.5–57.0
Male helpers	210	35.0 ± 0.6	19.5–57.0
Female helpers	156	31.3 ± 0.5	18.0–50.5
Largest helper per group	35	45.3 ± 1.1	32.5–57.0
Offspring	16	11.8 ± 0.8	6.5–15.0
Independents	23	35.3 ± 2.0	20.5–53.5
Males	17	35.6 ± 2.6	20.5–53.5
Females	4	34.8 ± 2.2	30.0–40.0

Fig. 3: Breeder males and females are paired size-assortatively in *N. savoryi* (n = 32 groups). Symbol sizes represent the different group sizes (breeders plus helpers: 5–9, 10–14, 15–19, 20–24, 25–30, > 30 members, respectively)

three, two and two breeding females, respectively). In contrast, female breeders were similar in size to the largest helper in the group (paired t-test, selecting the largest breeding female in groups with multiple breeding females: $t = -1.5$, $df = 31$, $p = 0.23$). The sizes of group members varied a lot, presumably due to the presence of different age cohorts of helpers (Table 1, Fig. 4).

Also the independents living between the groups were of highly variable sizes (Table 1, Fig. 4), comparable with the body sizes of all group members including offspring (t-test: $t = -0.34$, $df = 538$, $p = 0.73$; Levene's test for equality of variances: $F = 1.21$, $p = 0.27$) and all helpers (t-test: $t = -1.76$, $df = 424$, $p = 0.08$ with Levene's test: $F = 0.31$, $p = 0.58$). However, independents were significantly smaller and more variable in size compared with both breeding males (t-test with unequal variances: $t = 9.76$, $df = 30.0$, $p < 0.001$ with Levene's test: $F = 6.8$, $p = 0.012$) and breeding females (t-test with unequal variances: $t = 4.26$, $df = 23.6$, $p < 0.001$ with Levene's test: $F = 39.7$, $p < 0.001$). Female independents were similar in size SL to male independents (Table 1, t-test with unequal variances: $t = -0.27$, $df = 12.39$, $p = 0.80$), although males tended to be more variable in body size (Levene's test: $F = 3.48$, $df = 19$, $p = 0.077$).

Body Size of Group Members in Relation to Group Size

Large breeder males occupied territories with more group members compared with small breeder males (Table 2, Fig. 3), and also the size of the largest breeder

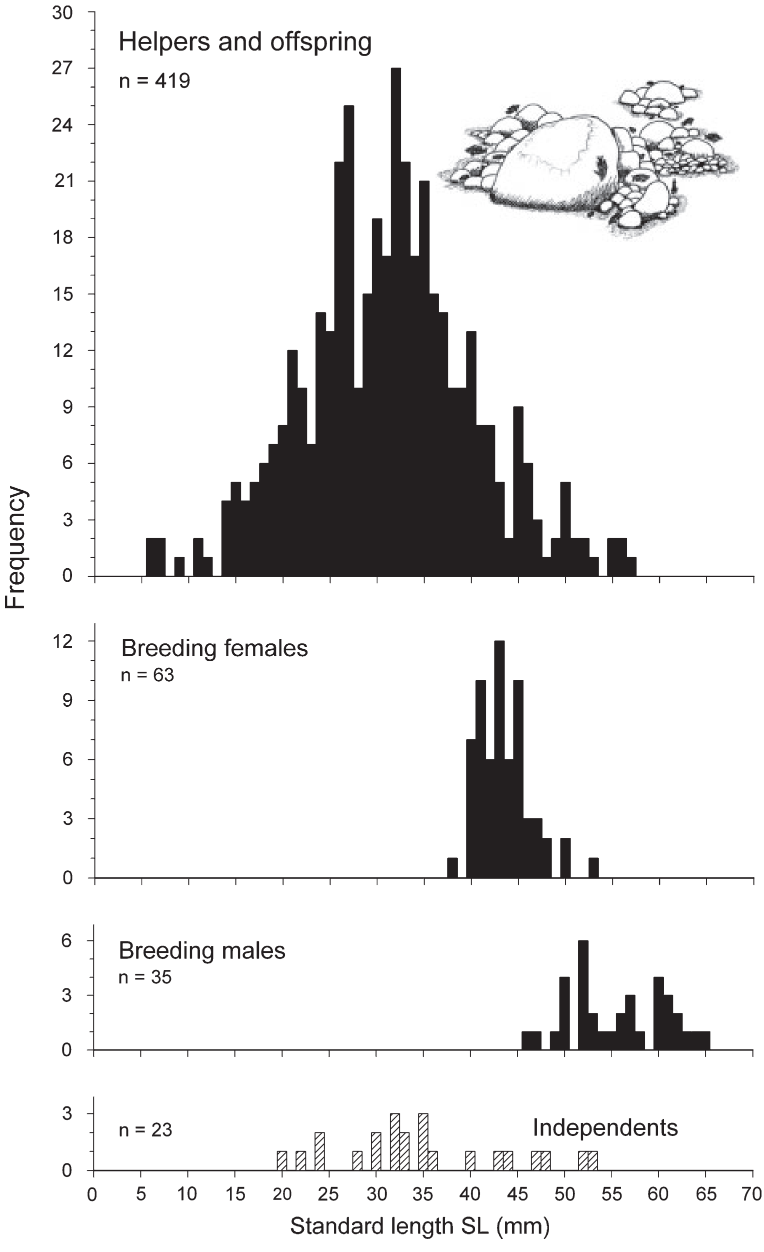

Fig. 4: Body size [standard length (SL)] of group members (black bars) and independent *N. savoryi* (hatched bars): 0.5 mm. Values rounded downwards into mm classes. Inset shows typical territory and group of *N. savoryi* at Kasakalawe

Table 2: Pearson's correlations between the body size [standard length (SL), mm] of the breeder male or breeder female with the body size of the largest helper, number of large helpers (> 35 mm SL) and group or subgroup size *N. savoryi*

	Pearson correlation		
	n	r	p
Breeder male size vs.			
Group size	35	0.56	< 0.001
Number of large helpers	35	0.53	0.001
Body size largest helper	35	0.43	< 0.02
Breeder female size vs.[a]			
Group size	32	0.43	< 0.02
Number of large helpers	32	0.44	< 0.02
Body size largest helper	32	0.11	0.55
Subgroup size	39	0.42	< 0.01
Number of large helpers in the subgroup	39	0.34	< 0.05
Body size largest helper in the subgroup[b]	37	0.11	0.51

[a] In case of multiple breeding females: with the largest female in the group or subgroup.
[b] Two breeding females did not have helpers in their subgroup.

female correlated with group size (Table 2, Fig. 3). Positive correlations were found between breeder male or female sizes and the number of large helpers (> 35 mm SL) in the group and between breeder size and the size of the largest helper in the group for breeder males only (Table 2). However, as many females were living in subgroups (39 of 53 subgroups had a breeder female), it makes more sense to compare the sizes of the breeding females with the size of their own subgroup and the sizes of helpers living in their subgroup. Breeding female size was correlated with the subgroup size and the number of large helpers in the subgroup, but again not with the size of the largest helper in the subgroup (Table 2).

From the above analyses, it appears that the sizes of the group members critically relates to the size of the group and the size of the breeding male and female(s). To analyse this structuring in more detail, the group members were ranked according to body size, per group and sex. Only helpers larger than 19.5 mm SL were used for these analyses, as the majority of these were sexed. First, the size of the breeding females was analysed by ranking the largest breeding female 1, the second largest breeding female 2, etc. (Fig. 5). A multiple regression analysis showed that female rank and the number of breeding females in the group related to breeding female's SL (Table 3). Very large breeding females had more secondary breeding females, which were relatively large as well (e.g. the second largest female in the group with four females was larger than the average largest female in groups with only one or two females, see Fig. 5).

Second, the size of the females were compared with the size of their female group members per subgroup, by ranking the largest female rank 1, the next largest female of the subgroup rank 2, etc. Figure 6a shows that larger groups had relatively large females with relatively large additional females. This effect can be succinctly visualized by plotting the predicted values from a GLMM (Table 4) of

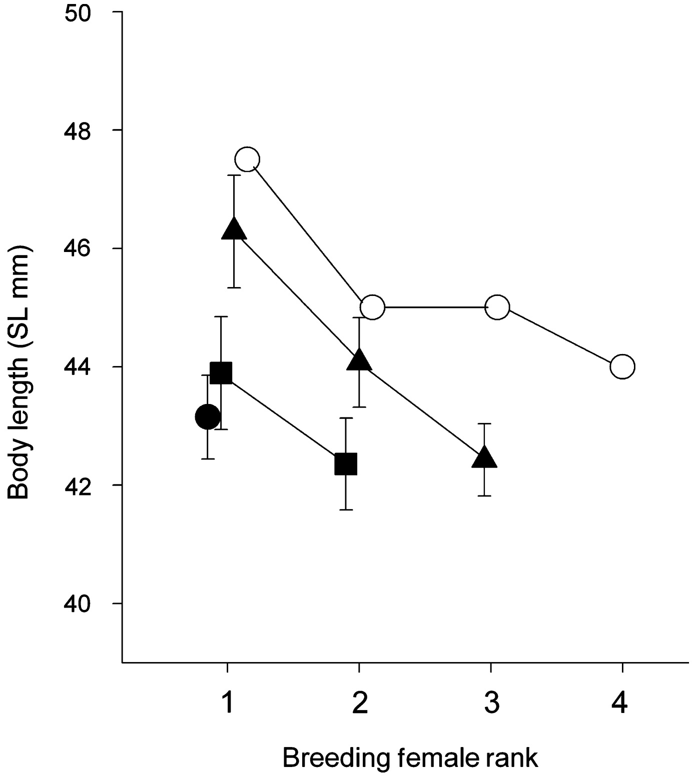

Fig. 5: Body size [mean standard length (SL) ± SE] of breeding females in *N. savoryi* groups with one (black dot, n = 10), two (black squares, n = 14), three (black triangles, n = 7) and four breeding females in total (white dots, n = 1), ranked according to size

Table 3: Results of a multiple regression analysis on the body sizes of breeder females (n = 63, mm SL) in relation to the number of breeding females in the group and breeder female rank. The interaction was not significant and deleted from the model. Error mean square = 6.8 with df = 60

Independent variable	F	df	p	Coefficient ± SE
Constant	1744.2	1	< 0.001	42.71 ± 1.02
Number of breeding females	11.0	1	0.002	1.59 ± 0.48
Female rank	10.5	1	0.002	−1.65 ± 0.51

female SL with ln-transformed female rank, number of females in the subgroup and their interaction as effects (Fig. 6c). Additionally, the GLMM showed that females in the colony at Nkumbula were relatively larger than the females in both colonies at Kasakalawe (Table 4).

Third, the size of the males were compared with the size of their male group members. Similarly as in the previous analyses, the largest males were ranked 1,

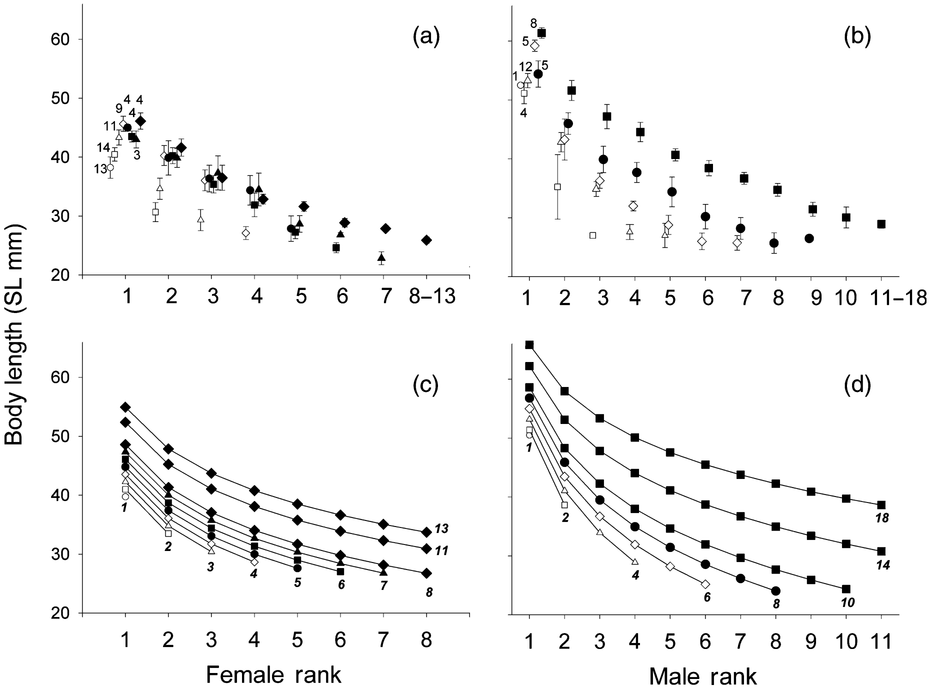

Fig. 6: Body sizes SL of female subgroup members, and male group members in relation to the number of same-sex members in the (sub)group, ranked according to size. Mean SL (± SE) per rank of (a) females per female subgroup sizes and (b) males per male group sizes. The predicted mean SL from a GLMM fit (see Table 4) for (c) females and (d) males in relation to rank, (sub)group size and their interaction. Sample sizes (number of (sub)groups) are indicated in the graph (a, c) and the group sizes are depicted in graphs (b, d, from which the symbol types can be read for the other two panels). Note that for clarity in (a) the subgroup sizes and the ranks 8–13 are lumped, in (b) adjacent group sizes are lumped from group size 2 onwards (and group sizes 10–13 lumped, ranks 11–18 lumped); and in (c, d) only a subsample of (sub)group sizes are indicated up to rank of 8 (females) and 11 (males) only

the second largest male rank 2, etc. Similar to the previous analysis, larger groups had relatively large males with relatively large additional males (Fig. 6b). As before, this effect can be visualized by plotting the predicted values from a GLMM (Table 4) of male SL with ln-transformed male rank, number of males in the group and their interaction as effects (Fig. 6d). Finally, the GLMM showed that males were of similar size at all three colonies, i.e. comparing the one colony at Nkumbula with both colonies at Kasakalawe (Table 4).

Behaviour: Spacing, Feeding, Territory Maintenance and Defence

None of the focal fish were seen to leave the group's territory during behavioural recording, except a breeding male visiting a neighbouring group for 26 s. Nevertheless, often the large group members approached other groups during feeding when moving away from the periphery of their shelter area (the

Table 4: Results of two GLMMs relating body size to the number of same-sex group members and rank, for male and female group members, respectively. The analyses control for colony (fixed) and family identity within colony (random) effects. For males, the ln-transformed male rank within the group, the number of male group members and their interaction were fitted as covariates ($n = 242$ individuals from 35 groups). For females, the ln-transformed female rank within the subgroup, the number of female subgroup members and their interaction were fitted as covariates ($n = 215$ individuals from 61 subgroups in 34 groups)

Independent variable	F	df	Error df	p	Coefficient ± SE
Male group members					
Fixed effects					
Constant	1096.4	1	56.2	< 0.001	50.47 ± 2.63
Colony[a]					
Colony 2	0.1	2	30.8	0.87	−0.58 ± 2.67
Colony 3					−1.07 ± 2.49
Number of males	30.3	1	54.5	< 0.001	0.90 ± 0.16
Ln(male rank)	521.8	1	217.7	< 0.001	−19.29 ± 0.84
Interaction[b]	35.9	1	217.7	< 0.001	0.44 ± 0.07
Random effect: Family	Wald z = 3.1, p = 0.002				
Female group members					
Fixed effects					
Constant	1000.0	1	37.8	< 0.001	44.63 ± 2.79
Colony[a]					
Colony 2	2.9	2	19.6	0.08	−6.11 ± 2.99[c]
Colony 3					−6.68 ± 2.79[c]
Number of females	45.0	1	133.8	< 0.001	1.27 ± 0.19
Ln(female rank)	136.8	1	154.8	< 0.001	−10.99 ± 0.94
Interaction[d]	0.2	1	154.7	0.64	0.06 ± 0.13
Random effect: Family	Wald z = 2.3, p = 0.02				

[a] Colony 1 = Nkumbula, and is set as the reference category with coefficient 0; Colony 2 and 3 are at Kasakalawe.

[b] Interaction between the number of males and ln(male rank).

[c] Colony 2 and 3 females were on average smaller than Colony 1 females ($t = -2.04$, $p = 0.054$ and $t = -2.39$, $p = 0.026$, respectively), but did not differ from each other ($t = -0.37$, $p = 0.71$).

[d] Interaction between the number of females and ln(female rank).

part of the territory where digging occurred) in the high density area of the colony. Usually, the group members stayed close to any of the shelters available in the group's territory, also during feeding (0–30 cm). Forays further than 30 cm from protective shelter for any group member including the males were very rare. The mean distance moved from protective shelter was 6.0 cm (± 4.2 cm SD, range 1–19, $n = 46$) and did not depend on body size SL (GLM: $F_{1,46} = 0.08$, $p = 0.78$), sex ($F_{1,46} = 0.06$, $p = 0.81$) or status (breeder or helper, $F_{1,46} = 0.03$, $p = 0.86$). Feeding rates of helpers and breeders were low and did not differ significantly (mean number of bites/10 min ± SE: 17.7 ± 6.5, $n = 15$ and 18.6 ± 3.7, $n = 39$, respectively, Mann–Whitney U-test: $U = 269$, $p = 0.65$). Helpers and breeders showed similar amounts of digging behaviour, albeit at very low frequencies and high day-to-day variability ($\bar{x}$/10 min ± SE: 0.60 ± 0.47, n = 15 and 0.28 ± 0.11, n = 39, respectively, Mann–Whitney U-test: U = 286, p = 0.85). No differences in feeding rate or digging frequencies were detected between males and females (Mann–Whitney U-tests: breeders, p = 0.79 and 0.46; helpers, p = 0.80 and 0.38, respectively).

As *N. savoryi* stayed close to their home territory, hardly any aggressive interactions with neighbouring *N. savoryi* groups were observed (mean frequency of acted or received interactions/10 min: 0.09 ± 0.35 SD, $\tilde{x}$ = 0, n = 54; see also the Appendix). The shelter area was defended by all group members against all other fish intruding, mainly other cichlid species, including predators, shelter competitors and egg-stealers (Appendix). There was no effect of body size on the frequency of shelter defence behaviour (SL vs. shelter defence, helpers: Spearman rank correlations: r = 0.04, p = 0.89, n = 15; breeders: r = −0.07, p = 0.68, n = 39). Helpers defended shelters against intruders more often than breeders did ($\bar{x}$ ± SE and $\tilde{x}$/10 min: 8.1 ± 1.9 and 6, n = 15; 5.0 ± 1.0 and 2, n = 39, respectively, Mann–Whitney U-test: U = 191.5, p = 0.05; no significant differences between the sexes, U-tests: breeders, p = 0.93 and helpers, p = 0.35). However, male helpers did defend more often against piscivores potentially dangerous to themselves and breeders (21 of 114 events), compared with female helpers (0 of 11 events, LR test for frequency table: $\chi^2_1 = 4.3$, p = 0.039; data in the Appendix). This was not the case for the breeders, where males (28 of 108 events) and females (27 of 89 events) defended the territory against large piscivores at similar frequencies (LR test for frequency table: $\chi^2_1 = 0.5$, p = 0.49; data in the Appendix).

Behaviour: Interactions within the Group

As expected, (1) aggression of group members was mainly directed towards smaller group members (Table 5). Note that female breeders received aggression from the largest male helpers in the group, which usually were larger than the female breeders. Most aggressive behaviours were aggressive displays (helpers: all nine, breeding females: 10 of 12, breeding males: 19 of 20), which were usually immediately reconciled by the smaller group members by submissive behaviour or bumping, after which the larger group members often reacted by bumping. (2) Submissive behaviours were directed towards larger group members and were never observed in breeding males. They were also often followed by mutual bumping. (3) Bumping was mainly directed against larger group members, but also occurred towards smaller group members (e.g. from breeding male to breeding female). The interaction between status and status of the opponent on the frequency of behaviour was significant for all three types of behaviours (Table 6: interaction 'status*status opponent' from loglinear models), and the rate of submission significantly decreased from helper to breeder female and to breeder male (and the converse: submission received significantly increased, Table 6, Jonckheere–Terpstra tests). The rate of bumping received significantly increased

Table 5: Frequencies of social interactions within breeding groups of *N. savoryi*, split in directed or received behaviours, and according to the status of the focal actor and the status of the opponent, and type of behaviour

Focal status Behaviour	Mean frequency/ 10 min (range)	% Within subgroup	Status opponent					
			SH	MH	LH	BF	BM[a]	Total
Helper (MH or LH) (n = 15)								
Aggression	0.20 (0–3)	0.0	0	0	1	2	0	3
Aggression received	0.40 (0–4)	33.3	0	1	1	2	2	6
Submission	0.40 (0–2)	100.0	0	0	0	1	5	6
Submission received	0.33 (0–2)	80.0	0	3	2	0	0	5
Social[b]	0.87 (0–3)	100.0	0	5	0	1	7	13
Social received[b]	0.73 (0–3)	90.9	0	9	2	0	0	11
Breeder female (BF) (n = 21)								
Aggression	0.33 (0–2)	57.1	0	5	2	0	0	7
Aggression received	0.24 (0–2)	60.0	1	0	4	0	0	5
Submission	0.43 (0–4)	100.0	0	0	3	0	6	9
Submission received	1.24 (0–7)	88.5	4	19	3	0	0	26
Social[b]	1.71 (0–8)	94.4	0	6	3	0	27	36
Social received[b]	0.81 (0–3)	94.1	0	11	1	0	5	17
Breeder male (BM) (n = 18)								
Aggression	0.44 (0–3)	–	0	2	6	0	–	8
Aggression received	0.67 (0–9)	–	0	5	7	0	–	12
Submission	0.0 (0–0)	–	0	0	0	0	–	0
Submission received	2.39 (0–10)	–	0	19	12	12	–	43
Social[b]	1.17 (0–6)	–	0	6	4	11	–	21
Social received[b]	4.83 (0–20)	–	5	19	32	31	–	87

SH = small helper (15.5–25.0 mm SL), MH = medium helper (25.5–35.0 mm SL), LH = large helper (> 35.0 mm SL). –, Not applicable (only one breeding male per group interacting with all subgroups).

[a] All interactions with the breeding male occurred when it visited a subgroup, and were scored as subgroup interactions.

[b] Bumping the body of a group member.

from helper to breeder female and to breeder male, and as for submission, this reflects the larger number of smaller group members combined with the fact that the bumping and submission were primarily directed towards the larger group members (Tables 5 and 6, and also apparent from the significant interactions from the loglinear models: 'directed or received behaviours*status' and 'directed or received behaviours*status opponent').

Finally, submissive and bumping behaviours of helpers and breeding females usually occurred within the subgroup (Tables 5 and 6, significant effect of 'subgroup'). In contrast, aggression frequently occurred against members of adjacent subgroups, particularly between the helpers and neighbouring helpers or breeding females (Tables 5 and 6, significant interactions 'subgroup*status' and 'subgroup*status opponent'). Unexpectedly, no aggressions was recorded between

Table 6: Left: Non-parametric Jonckheere–Terpstra tests for ordered data, testing the hypotheses that the median frequencies of within-group interactions decrease or increase from breeding male (n = 18) to breeding female (n = 21) and to helper (n = 15), separately for directed and received interactions. Right: Hierarchical loglinear models of the frequency of interactions in relation to focal 'status' (helper, breeding female, breeding male, df = 2), 'status opponent' (small-, medium-, large helper, breeding female or breeding male, df = 4), 'subgroup' (i.e. within or between subgroup members, df = 1) and 'directed or received' behaviour (df = 1). Shown are the significant effects from a backward deletion of the non-significant terms from the fully saturated model containing all main effects and interactions per type of behaviour, based on the likelihood ratio χ^2 change (G). For the data see Table 5

	Jonckheere–Terpstra tests[a]				Hierarchical loglinear models		
	Directed		Received				
Significant effects and interactions	z	p	z	p	df	G	p
Aggression	−0.97	0.33	−0.23	0.82			
Status*status opponent					8	24.7	< 0.002
Status*subgroup					2	23.2	< 0.001
Status opponent*subgroup					4	12.7	0.013
Submission	2.09	0.04	−3.03	0.002			
Status*status opponent					8	30.9	< 0.001
Status*directed/received					2	14.9	< 0.001
Status opponent*directed/received					4	46	< 0.001
Subgroup					1	90.7	< 0.001
Social	0.23	0.82	−4.00	< 0.001			
Status*status opponent					8	139	< 0.001
Status opponent*directed/received					4	58	< 0.001
Status*subgroup					2	7.2	0.027

[a] See Siegel & Castellan (1988, p. 216) for a description of this test.

breeding females of different subgroups during the focal observations, although they were seen on other occasions.

Discussion

Are Subordinates in *N. savoryi* True Helpers?

Male and female helpers in *N. savoryi* performed helping behaviours also shown by other cooperatively breeding cichlids, i.e. territory defence (incl. aggression against piscivores) and maintenance (digging and removing sand to create shelters). Indeed, helpers performed higher frequencies of territory defence behaviour than the breeders, but otherwise showed comparable levels of digging behaviour. Unfortunately, direct brood care behaviour (i.e. cleaning eggs and fanning) could not be observed in the field, but is likely to be shown by helpers, as helpers visited the breeding shelters of the females. The occurrence of direct brood care behaviour should be confirmed under laboratory conditions, where breeding shelters and the brood can be observed without disturbance. We found that submissive behaviours were directed against all larger members of the group. Based on these observations, we conclude subordinates in *N. savoryi* can be operationally classified as ‘helpers’, and we conclude this species is a cooperative breeder. Whether helpers truly provide help, i.e. increase the fitness of recipients, remains to be tested, as this cannot be unequivocally concluded from their helping behaviour. For instance, in the seychelles warbler, a small tropical songbird living in extended families, helpers increase the fitness of the breeders in high quality territories, but actually decrease the fitness of the breeders when multiple helpers are assisting breeders living in low quality territories (Komdeur 1994).

Due to the sexual dimorphism in *N. savoryi*, we expected differences between males and females in the types and sizes of intruding fish attacked. Indeed, this was apparent, despite our limited data-set: female helpers were never seen to attack large piscivores potentially dangerous to themselves, whereas male helpers did. In contrast, female and male breeders were equally likely to attack large piscivores. Unfortunately, our data-set on the exact sizes of intruders attacked was limited and therefore not analysed, and we did not conduct focal observations of the small helpers (15.5–25 mm SL, which were relatively rare in our study population) to resolve these points in more detail. Overall, male and female helpers showed similar levels of helping behaviours, but unfortunately only two female helpers were observed, and therefore this finding has to be corroborated by more focal observations.

Group Structuring

Groups either defended one patch of stones, or up to seven distinct patches of stones. We found that distinct patches of stones were defended against intruders but also against group members from other patches, i.e. creating distinct subgroups. Also, large patches of stones were sometimes divided into two or more subgroups. Virtually all affiliative interactions and submissive behaviours occurred between members of the same subgroup, except for the breeder male which interacted with members of all subgroups within his territory. In contrast, many aggressive displays were directed against group members of neighbouring subgroups. The majority of subgroups contained one breeder female (68%), and only 7.6% of the subgroups contained two breeder females. Therefore, it seems likely that these subgroups are mainly created around breeder females which defend part of the male’s territory against other breeder females and produce or attract their own helpers to assist them. We found a positive correlation between the number of breeder females in the group and the number of distinct stone patches defended by the group, which is consistent with this hypothesis.

The existence and stability of distinct subgroups in *N. savoryi* might also be partly due to the very limited ranging behaviour of these fish, compared with, e.g.

N. pulcher (Heg et al. 2004a). *Neolamprologus savoryi* were rarely seen to venture more than 30 cm away from protective shelter, and most feeding behaviour occurred within 20 cm from the substrate, which is largely a benthivorous type of feeding behaviour. Large helpers and breeders in *N. brichardi* (Gashagaza 1988, formerly *Lamprologus brichardi*) and *N. pulcher* (D. Heg & M. Taborsky, pers. obs.) feed preferentially in the zooplankton layer 50–100 cm above the substrate. We found feeding rates typical for benthivorous Lake Tanganyika cichlids (compared with 1–20 bites/10 min reported by Kuwamura 1997), whereas feeding rates of more zooplanktivorous cichlids are much higher (> 100 bites/10 min, Kuwamura 1997; Balshine-Earn et al. 1998; Balshine et al. 2001).

Comparison with Other Cooperatively Breeding Cichlids

We shall compare our other findings on *N. savoryi* with other cooperatively breeding cichlids (Table 7), in particular with its close relative *N. pulcher* (Table 8), with which it often occurs in mixed-species colonies (D. Heg, Z. Bachar, L. Brouwer & M. Taborsky, unpubl. data). The total group size does not differ significantly between these two species, e.g. breeder males in either species have a similar number of group members (Table 8). In contrast, *N. savoryi* subgroups are

Table 7: Typical group compositions and body sizes of Lake Tanganyika cooperatively breeding cichlids (all Lamprologini). In brackets: range for group size and maxima for the number of breeder males and females. Also depicted is the correlation coefficient between male body size and group size for each species separately: $^{**}p < 0.01$, $^{***}p < 0.001$

	Neolamprologus spp.			*Julidochromis* spp.	
Variable	*pulcher*	*savoryi*	*multifasciatus*	*ornatus*	*marlieri*
Group size	15 (4–61)	14 (5–36)	6 (2–14)	4 (2–7)	2–3
Number of breeding males	1	1	1–2 (3)	1	1 (2)
Number of breeding females	1–2 (−4)	1–3 (−4)	1–3 (−5)	1	1
Body size breeding male[a]	6.0 ± 0.3	5.6 ± 0.9	2.5	6.6 ± 0.4	5.6 ± 0.4[b]
Body size breeding female[a]	5.2 ± 0.3	4.4 ± 0.4	1.9	6.6 ± 0.5	7.7 ± 0.5[b]
Body size helpers[a]	3.6 ± 1.3	3.2 ± 0.4	?	4.6 ± 0.8	4.2 ± 0.2[b]
Correlation male SL vs. group size	+0.28***	+0.56***	+0.46***	+0.54**	+0.62[c]
References[d]	1	2	3	4	5

[a] In cm standard length SL.
[b] Total length instead of standard length measured.
[c] Calculated from Table 1 in Yamagishi & Kohda (1996). Based on eight groups by treating one polyandrous group as two separate groups (p = 0.10).
[d] References: 1 = Balshine et al. (2001), Dierkes et al. (in press); 2 = This study; 3 =Kohler (1998); 4 = Heg & Bachar (unpubl. data); 5 = Yamagishi & Kohda (1996).

Table 8: Group and subgroup sizes of *Neolamprologus savoryi* and *N. pulcher* compared

Species	n	Mean group size ± SE	Range	Mann–Whitney U-tests[a] 1 vs. 2	1 vs. 3	2 vs. 3	Ref[b]
Subgroup size							
N. pulcher 1	30	9.8 ± 0.9	4–21	−3.76***			a
N. pulcher 2	239	7.1 ± 0.6	3–16		−2.80**	−3.53***	b
N. savoryi 3	53	5.9 ± 0.6	1–19				c
Group size[c]							
N. pulcher 1	20	14.7 ± 2.9	4–61		−0.47		a
N. savoryi 3	35	14.3 ± 1.4	5–36				c

[a] The z-values are depicted with: **$p < 0.01$, ***$p < 0.001$.

[b] References: a = Dierkes et al. (in press), b = Balshine et al. (2001), c = This study.

[c] Also denoted as ‘harems’ in the listed references, i.e. family groups sharing the same breeding male were summed to give the total group size. The number of breeding females per breeding male for groups with at least one breeding female is given for *N. pulcher* in Dierkes et al. (unpubl. data): one n = 14, two n = 3, three n = 2, four n = 1, significantly less than the number of breeding females per group in *N. savoryi* (this study, for valid comparison only subgroups with at least one breeding female were included, Mann–Whitney U-test: U = 216, p = 0.034).

significantly smaller than *N. pulcher* subgroups, measured in the same population on two different occasions (Table 8). This is due to *N. savoryi* groups containing significantly more breeding females compared with *N. pulcher* (Table 8), each defending their own subgroup territory. We found that all subgroup members showed aggressive interactions against members of other subgroups. This also occurs within ‘harems’ of *N. pulcher* (Limberger 1982, 1983), although it may be less frequent, due to the subgroups being more out-spaced in *N. pulcher* compared with *N. savoryi* (Limberger 1983; D. Heg & M. Taborsky, pers. obs.). Multiple breeding females are also common in the cooperative dwarf shell breeding cichlid *N. multifasciatus* (Table 7). Based on these results, we predict that (1) the within-group genetic relatedness is higher within the subgroups than between the subgroups in *N. savoryi*; (2) the within-group genetic relatedness is on average lower for *N. savoryi* than for *N. pulcher* (see Dierkes et al., in press). Genetic relatedness analyses of groups and subgroups in *N. savoryi* are underway to test these hypotheses.

We found that *N. savoryi* has a high degree of sexual dimorphism: breeding females are 78.2% the size (SL) of breeding males comparable with *N. multifasciatus* (76%, Table 7), whereas the corresponding figure is only 86.7% in *N. pulcher* (Table 7). This might have important consequences for the sex-dependent life-history strategies, e.g. the age at (potential) reproduction and helper strategies (Skubic et al. 2004), when comparing male and female helpers between, e.g. *N. savoryi* and *N. pulcher*. The majority of *N. savoryi* individuals were living in breeding groups, as in *N. pulcher* (approx. 95% in the Kasakalawe population, D. Heg, pers. obs.) and *N. multifasciatus* (Kohler 1998). In contrast, many individuals seem to live outside of breeding groups (independents) in the cooperatively breeding *Julidochromis* species (Yamagishi 1988; Yamagishi & Kohda 1996; Brichard 1997, 1999; Konings 1998), and a quantitative estimate is available for *J. ornatus* (42%, Heg & Bachar, unpubl. data).

We showed that the number of breeding females in the group was positively correlated with their body sizes. No such data are available for other cooperatively breeding fish. It remains to be determined whether multiple breeding females occur in *N. savoryi* due to primary females accepting genetically related females (e.g. daughters) as co-breeders (all females deriving net benefits from kin selection), or due to some primary females experiencing no or low net costs of accepting secondary breeding females inside, for instance, large territories (i.e. the costs to prevent a secondary female from breeding are higher than the costs of acceptance). Large territories may have more space for multiple breeding females, or vice versa, groups with many large females are able to acquire and defend a larger territory, which in turn offers possibilities for each female to breed (assuming no net negative effects of the breeder females on each other's fitness below a certain within-group density of cichlids). Consistent with this prediction is our finding of a positive correlation between the number of distinct patches of stones and the total number of breeder females within the group. Alternatively, even at relatively high within-group densities, the net effect of multiple breeding females on each other's fitness might still be positive, e.g. due to group augmentation effects (Kokko et al. 2001) on survival and reproduction (Balshine et al. 2001; Heg et al. 2004a).

Group Size and Size-Hierarchies

Group sizes in *N. savoryi* were highly variable, and correlated positively with the body sizes of breeders and helpers, resulting in distinct size-hierarchies. These size-hierarchies were also detected amongst breeding females, resulting in, e.g. secondary breeding females being larger than many primary breeder females from other groups. The correlation between group size and the body sizes of members appears to be a common phenomenon in highly social, group-living fish (Table 7, see also Buston 2003b; Mitchell 2003). The reasons for this correlation might be explained by (a combination of) five general processes, as found in the congener *N. pulcher* wherever not specifically indicated: (1) group size relates positively to reproductive success (Balshine et al. 2001; Brouwer et al., 2005). (2) Large females are able to produce larger clutches (D. Heg, pers. obs.), particularly if assisted by helpers (Taborsky 1984). (3) Group size relates positively to survival (Heg et al. 2004a) and group stability (Heg et al. in press). (4) (New) breeders only accept large subordinates if they are substantially smaller than they are (Balshine-Earn et al. 1998; and in the clownfish *Amphiprion percula* Buston 2003a). (5) Subordinates strategically 'adjust' their growth to prevent eviction from the group by the dominants (*Amphiprion percula*: Buston 2003b; Heg et al. 2004b).

Combining points (1)–(3) and considering that fish have indeterminate growth, this will lead to larger groups having on average older and larger group members, and this will be maintained due to the presence of relatively large breeder females with a large number of assisting helpers. The helpers in large groups will be relatively large themselves, i.e. the group may gain substantial protection from predators due to joint territory defence of all large group members (breeders and large helpers combined, Taborsky et al. 1986). Combining points (4) and (5), cichlid helpers might be 'allowed' or 'choose' to grow to larger sizes when living in groups with large breeders of the same sex (assuming no or less conflict occurs between helpers and the breeders of the opposite sex). Finally, both group size and the sizes of group members may be a by-effect or consequence of the age of a group (i.e. time since establishment). Any process leading to age-differences between groups, including points (1)–(3) above, and also for instance stochastic effects, might determine both group size and the sizes of the group members. These six non-mutually exclusive processes will eventually lead to the positive correlation between group size and the body sizes of the individual members, as observed in many group-living fish. More experimental work is needed to clarify these processes, and in particular to understand the crucial factor in group-living animals in general: who influences group membership and who influences the degree of participation in reproduction (helpers, breeders or both, see Skubic et al. 2004). In *N. pulcher* helpers are sometimes aggressively evicted from groups (Taborsky 1985; Balshine-Earn et al. 1998), but it is less clear how often helpers also actively chose to immigrate into other groups (Bergmüller et al. in press), although immigration has been noticed in the field (Balshine et al. 2001; Stiver et al. 2004; Dierkes et al., in press).

As argued above, positive correlations between the total group size, the number of breeding females and the total reproductive output might lead to a faster accumulation of group members and future breeding females in larger groups compared with smaller groups. We envisage that under this scenario the positive group size effects on reproduction and survival will create a positive feedback loop, leading naturally to an increase in group size, the emergence of multiple breeding females and the emergence of a positive correlation between group size and the body sizes of its group members. There is evidence suggesting that positive effects of group size on fitness might lead to similar processes in cooperatively breeding vertebrates in general (e.g. Rasa 1989; Creel & MacDonald 1995; Doolan & MacDonald 1997; Schaffner & French 1997; Langen & Vehrencamp 1998; Clutton-Brock et al. 1999). Group size will increase until a certain upper-threshold group size is reached, whereupon the costs due to within-group competition will exceed the benefits of having additional subordinates (e.g. in kookaburras unusually large groups had reduced reproductive success, Legge 2000). At this stage, either some subordinates (are forced to) disperse, or the group has to acquire additional resources to reduce within-group competition, which might lead to the group and the territory eventually splitting into two groups and territories ('budding', Woolfenden & Fitzpatrick 1984; Stacey & Koenig 1990). In any case, Bergmüller et al. (2005) has shown experimentally that *N. pulcher* helpers rather disperse and breed independently, than stay and help, given ideal dispersal opportunities (i.e. laboratory situation with no predators, and with no heterospecific and limited conspecific competition for breeding shelters). Recently, Hamilton & Taborsky (2005) have shown that density-dependent effects on the likelihood of helpers acquiring the breeding position in the group through queuing can critically influence the likelihood of helpers staying in the territory and the amount of help they provide.

Conclusions

Despite a scarcity of data, some clear patterns in group-living fish are emerging, particularly the correlation between group size and body size. More experimental work is needed to clarify how much, when and why group members benefit from group living, and how these factors contribute to the apparent correlation between group size and body size. Whether similar factors are responsible for the maintenance of group living and whether similar factors produce this correlation in the various species of cooperatively breeding fish, remains to be established. Comparing experimental results among the cichlids with their varying degrees of cooperation and complexity of group-living might be particularly worthwhile.

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Appendix

Total frequencies of the different species of fish attacked by *N. savoryi* breeders and helpers, when defending the territory

	Group member				
	Breeders		Helpers		
Species attacked	Male	Female	Male	Female	Total
Total observation time (min)	180	210	130	20	540
Cichlids					
Altolamprologus spp.[a]	0	0	5	0	5
Julidochromis ornatus[b]	4	4	3	5	16
Lamprologus callipterus[a]	26	28	39	0	93
Lamprologus lemairii[a]	3	3	0	0	6
Lepidiolamprologus attenuatus[a]	1	0	0	0	1
Lepidiolamprologus elongatus[a]	12	10	19	0	41
Lobochilotes labiatus[a]	2	3	1	3	9
Neolamprologus caudopunctatus	2	0	1	0	3
Neolamprologus modestus	4	2	1	0	7
Neolamprologus pulcher[b]	28	5	31	0	64
Neolamprologus savoryi[b]	1	1	3	0	5
Neolamprologus tetracanthus[a]	4	3	5	0	12
Perissodus microlepus[c]	1	3	4	0	8
Telmatochromis temporalis[b]	1	0	0	2	3
Telmatochromis vittatus[d]	0	7	0	0	7
Xenotilapia flavipinnis	0	0	0	1	1
Xenotilapia sima	7	1	0	0	8

	Group member				
	Breeders		Helpers		
Species attacked	Male	Female	Male	Female	Total
Other fish					
Synodontis spp. (catfish)	0	5	0	0	5
Mastacembelidae eels[a]	12	14	2	0	28
Total	108	89	114	11	322

[a] Predators of fry: *Lamprologus callipterus*, *L. tetracanthus*, *Lobochilotes labiatus* and *Synodontis* spp. Predators of fry and small helpers: *Altolamprologus* spp. Predators of fry, helpers and breeders: *Lamprologus lemairii*, *Lepidiolamprologus* spp. and mastacembelid eels.

[b] Shelter competitors; in *N. savoryi* only non-group members were counted.

[c] Scales eater.

[d] Egg predator.