



Group Structure, Nest Size and Reproductive Success in the Cooperatively Breeding Cichlid *Julidochromis ornatus*: A Correlation Study

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Abstract

The effect of group size on reproductive success has long been studied in cooperatively breeding species, as it might provide an adaptive explanation for group-living in social species. Numerous studies have shown positive effects of subordinates on reproductive success ('helper effect'), but these studies have also revealed the importance of controlling statistically, or experimentally, for the effect of other factors that might affect reproductive success. Here, we first examine the relationships between group size, body size of group members and nest size in the cooperatively breeding cichlid *Julidochromis ornatus*, in which unrelated helpers frequently participate in reproduction and their breeding nests inside rock crevices may be crucial for reproduction and survival of all group members. Then, we subsequently investigate the relationship between group size and reproductive success, while controlling for these factors. The results showed that group size was significantly related to body size of group members rather than nest size; and larger breeders had larger helpers. It was found that group size significantly increased group reproductive output. More importantly, reproductive success of male breeders did not depend on the presence of mature helpers, whereas female reproductive success increased when two males assisted her and tended to decrease when two females bred cooperatively. We conclude that breeding groups of *J. ornatus* have size hierarchical societies that relate to group size, and group composition of genetically unrelated and co-breeding members affects their reproductive success.

Introduction

One of the key questions concerning the evolution of cooperative breeding systems, wherein group members other than a breeding pair provide care to the offspring at a single nest (so called 'helpers'), is whether helpers increase reproductive success of breeders in the groups (Emlen 1991). In many birds and mammals showing cooperative breeding, group size has been shown to positively influence

group reproductive output and the survival of offspring (reviewed in Stacey & Koenig 1990; Emlen 1991; Cockburn 1998; Russell 2004). As in birds and mammals, studies of cooperatively breeding cichlid fishes have also focused on the effect of group size on reproductive success (*Neolamprologus pulcher*: Taborsky 1984; Balshine et al. 2001; Brouwer et al. 2005; Heg et al. 2005a; *Julidochromis ornatus*: Awata et al. 2005; Heg & Bachar 2006), but the positive experimental influence of helping on reproductive

success has been detected in only one species, *N. pulcher* (Brouwer et al. 2005).

Understanding helper effects on reproductive success has been a major focus of cooperative behaviour over the past 30 yr. However, a number of studies suggest that it is considerably difficult to distinguish direct effects of helpers on reproductive success from other confounding effects (e.g. Brown et al. 1982; Cockburn 1998; Dickinson & Hatchwell 2004). For example, if territory quality and/or breeder quality positively influence reproductive success, increased number of helpers would be expected as a result of delayed dispersal of juveniles. In this case, a simple positive correlation between group size and productivity will be found even if group size is not a causal factor (Brown et al. 1982). Several approaches have been implemented to circumvent this problem; e.g. multifactorial analyses, removal experiments of helpers and pair-wise comparisons of the same territory in sequential years with and without helpers (e.g. Legge 2000; Russell et al. 2002; Brouwer et al. 2005; Heg et al. 2005a; Canestrari et al. 2008; Cockburn et al. 2008). In any case, an accurate assessment of potential factors that influence reproductive success is prerequisite to test for helper effects on reproductive success.

Julidochromis ornatus is a cooperatively breeding cichlid fish endemic to Lake Tanganyika. This small cichlid (up to 80 mm standard length) lives in social groups along the rocky shores of the lake. Typically, groups consisted of a dominant pair of breeders and zero to six helpers that exhibit brood and territory defences (Awata & Kohda 2004; Awata et al. 2005; Heg & Bachar 2006). Sexually mature helpers of both sexes are usually genetically unrelated to dominant breeders and frequently participate in reproduction within breeding groups (Awata et al. 2005, 2006). Each breeding group utilizes one rock crevice for a breeding nest. Eggs are deposited at the inner part of the nest crevice and offspring are tolerated around the nest crevice for long periods. Previous studies of cooperative breeding in *J. ornatus* have shown no clear evidence of helper effects on group reproductive output, but there was a non-significant trend suggesting that groups with helpers had greater reproductive output than those without helpers (Awata et al. 2005; Heg & Bachar 2006).

The final goal of the present study was to investigate the influence of helpers on reproductive success within the groups in *J. ornatus*. However, before this step, we have to know what other factors are associated with group size that we should control for in our multifactorial analyses. Therefore, in this study,

first we describe natural variations in group size, body size of group members and nest size in two study populations. Larger (implicitly older because of indeterminate growth in fish) breeders are considered to be 'higher quality' parents, who may attain higher reproductive success (Balshine et al. 2001). *Julidochromis ornatus* breeding groups use a rock crevice not only as a breeding nest, but also shelter and sleeping sites for breeders, helpers and offspring, and thus nest size can be considered as an important component of 'territory quality'. The comparisons of these components between populations are worthwhile because if group size is found to be different between populations, this difference should be related to body size of group members and/or nest size. Second, we examine the body size relationships among group members to assess whether this fish has size-hierarchical societies as has been found for some group-living fishes (clown anemonefish *Amphiprion percula*: Buston 2003a, Buston & Cant 2006; coral-dwelling goby *Paragobiodon xanthosomus*: Wong et al. 2007), including some cooperatively breeding cichlids (Heg et al. 2005b; Heg & Bachar 2006). Assessments of the body size relationship among group members are crucial because the degree of reproduction by helpers depends on body size differences between breeders and helpers (Heg et al. 2008). Third, we examine the relationship between group size and body size of group members or nest size to determine which of these factors best explain the group size.

Finally, we investigate the effect of group size and other factors (body size of group members, nest size and population) on reproductive success of group members using multifactorial analyses. In *J. ornatus*, both male and female helpers are capable of reproducing and high frequency of within-group reproduction by male helpers was detected (approx. 40% of total offspring are fathered by male helpers, Awata et al. 2005, 2006). Therefore, we examine the effect of group composition (i.e. number of mature helpers) on reproductive success of male and female breeders as well as group size effects on group reproductive output. From the male's perspective, it is assumed that reproductive success of male breeders should be the greatest when he breeds cooperatively with several mature females because, for example, multiple females lay eggs (e.g. fish: Heg 2008; Heg & Hamilton 2008; Heg et al. 2008; birds: reviewed in Vehrencamp 2000). Alternatively, if reproductive competition between females is intense (e.g. fish: Heg & Hamilton 2008; birds: Mumme et al. 1983; Davies 1986; mammals: Clutton-Brock et al. 1998),

lower or the similar reproductive success of cooperative polygynous males would be expected compared with monogamous males. From the perspective of the females, reproductive success of female breeders is assumed to be the greatest when multiple males assisted in the brood care of a female (e.g. as in cooperatively polyandrous dunnocks *Prunella modularis*: Davies 1986; Davies & Houston 1986), for instance, through female control of paternity distribution amongst her males and the male's subsequent response in paternal brood care (Burke et al. 1989; Davies et al. 1996; Kohda et al. 2009).

Methods

Study Site, Field Observations and Sampling

Fieldwork was conducted at two sites, Kasenga Point (8°42.6'S, 31°08.3'E) and Wonzye Point (8°43.3'S, 31°08.0'E) at the southern tip of Lake Tanganyika, near Mpulungu, Zambia. We studied 62 *J. ornatus* groups from Sep. to Dec. 1998 and from Aug. to Nov. 1999 at Kasenga and 33 groups from Sep. to Nov. 2006 and from Sep. to Nov. 2007 at Wonzye. The study sites at Kasenga and Wonzye were on rocky shores at water depths of 3.6–10.6 m and 3.4–10.7 m, respectively. Scuba was used for underwater observations and fish capture.

Behavioural observations of group members on the assessment of the breeding systems were conducted once or more (mean observation number \pm SD = 3.6 ± 2.0 , $n = 62$ groups at Kasenga; 3.0 ± 1.3 , $n = 33$ at Wonzye). Further details of behavioural observations are given elsewhere (Awata et al. 2005). After the assessment, all breeding members were captured using gillnets and the hand nets with the aid of an anaesthetic (30% clove oil diluted in ethanol). On the day of fish capture, standard length (SL to the nearest 0.1 mm) and total length (TL to the nearest 0.1 mm) were measured using callipers, after the fish were killed by an overdose of the clove oil diluted in ethanol (in 1998 and 1999) or an overdose of the anaesthetic FA100 (in 2006 and 2007, Tanabe Seiyaku Inc., Osaka, Japan). Sex was determined by dissection. Note that most fish samples were killed for parentage analyses (Awata et al. 2005), analyses of testes size (Awata et al. 2006) and analyses of sperm characteristics (S. Awata et al. unpubl. data), but fish in 4 out of 33 groups studied at Wonzye were measured in TL and SL to the nearest 0.5 mm and sexed by the shape of genital papilla underwater, and then they were released. For uncollected individuals (38/441 at

Kasenga; 25/289 at Wonzye), estimated TL by eye was recorded to the nearest 5 mm underwater, and SL was estimated using the equation calculated from all collected individuals; Kasenga: $SL = 0.81 \times TL + 0.21$, $n = 403$, $r^2 > 0.99$; Wonzye: $SL = 0.82 \times TL + 0.03$, $n = 264$, $r^2 > 0.99$.

Measurements of nest crevices were taken underwater; crevice length, width, depth and height were measured every 10 cm, and the volume of nest space was calculated using these measured variables later. Because of the difficulty to measure the nest crevice owing to the complexity of overlapping rocks, we did not conduct the measurements for all nests (48 of 62 nests at Kasenga and 30 of 33 nests at Wonzye).

Definition of Group Size, Offspring and Rank

The definition of 'helpers' was different between two studies on *J. ornatus*. On the one hand, Awata et al. (2005) have classified the fish smaller than the breeding male and female, which join in territory defence and have well-developed gonads, as 'helpers'. Recent field observations of all group members, including fry, suggest that the individuals that showed attacks against other fish were all mature, and immature fish never did (S. Awata, unpubl. data). On the contrary, Heg & Bachar (2006) have labelled the fish larger than or equal to 20 mm SL, excluding breeding male and female, as 'subordinates = helpers'. These subordinates often exhibit digging behaviour and territory defence. Several bird studies show that subordinates do not always contribute to offspring care (e.g. Cockburn 1998). In these cases, the number of helpers that contribute offspring care rather than group size is a better predictor of reproductive success (e.g. Komdeur 1994; Innes & Johnston 1996; Woxvold & Magrath 2005). On the contrary, even if some subordinates do not exhibit offspring care, they may invest in sentinel or mobbing behaviours, which result in positive effects of group size on reproductive success (Arnold et al. 2005; Komdeur 2006). These studies indicate the importance of assessing which individuals are caretakers or care-receivers in cooperative breeding groups. Therefore, we defined two types of group size according to the above papers. (1) GS-1: total number of breeders plus mature helpers. The individuals except breeders and mature helpers in the group were defined as offspring in GS-1. (2) GS-2: total number of breeders plus mature and potential helpers (≥ 20 mm SL). The individuals smaller than 20 mm SL were labelled as offspring in GS-2.

Group members in GS-1 were ranked based on their SL relative to other individuals within the group; the largest being ranked 1, the second largest being ranked 2, and so on. Female breeders were usually larger than male breeders, but sometimes smaller than their mates (Awata & Kohda 2004). Hence, the rank1 individuals were not always females. Note that male helpers were more numerous than female helpers (see 'Results', and also Awata et al. 2005; Heg & Bachar 2006).

Body Size Relationships Between Breeders and Helpers

Body size of breeders is usually a good predictor of reproductive success because larger breeders may have larger groups and better territories (e.g. Balshine et al. 2001). Therefore, we assessed whether larger male breeders mated larger female breeders and had larger mature helpers, and whether *J. ornatus* have size-hierarchical societies. In addition, to test whether the body size ratios of group members of adjacent ranks were not randomly distributed (Buston & Cant 2006; Wong et al. 2007), the observed distribution of size ratios was compared with the expected distribution of ratios created using a Monte Carlo procedure (e.g. Buston & Cant 2006; Wong et al. 2007; Kohda et al. 2008) implemented in the software MICROSOFT EXCEL 2008 (Microsoft Corp., Redmont, WA, USA). As rank1 and rank2 were hetero-sexual pairs, the expected distribution of size ratios was generated in male-female combinations only. Rank3 was composed of both sexes, and then the expected size-ratio distribution was generated in rank2-rank3 combinations. The Monte Carlo procedure creating null model distributions were iterated 100 times, and the observed and the expected distributions were compared with two-sample Kolmogorov-Smirnov tests.

Group Size, Body Size of Group Members and Nest Size

In all cooperatively breeding fishes studied to date, larger breeders have larger groups (reviewed in Heg et al. 2005b). To investigate whether this relationship applies to group composition in *J. ornatus*, group size was related to SL of the largest individual of the group (i.e. rank1). Group size has also been found to relate to territory quality in *N. pulcher* (Balshine et al. 2001; Bergmüller et al. 2005). Each breeding group of *N. pulcher* uses one to three rocks as the breeding nests and other rocks in the territory as shelter sites (Balshine et al. 2001), and territory size

(=shelter number) is considered to be an indicator of territory quality. Contrary to *N. pulcher*, each *J. ornatus* group has only one rock crevice as a breeding nest which all group members (i.e. breeders, helpers and offspring) use as shelter and sleeping sites (except harems, Awata et al. 2005). Therefore, the volume of nest space may indicate territory quality and it is assumed that the volume of nest space should be related to group size. Since most of the groups had zero or one mature helper in GS-1, we excluded group size 4 and 5. Using binomial generalized linear models (GLMs) with logit link function, GS-1 was related to rank1 SL, nest volume (log transformed to produce a normal distribution) and population. GS-2 was also related to the same explanatory terms, but linear models were used.

Group Reproductive Output and Per Capita Reproductive Success

We defined the number of offspring guarded by group members as 'group reproductive output', which often included young unrelated to breeders or to mature helpers (Awata et al. 2005). When offspring were counted several times on different days, the maximum number of offspring observed was used for the analyses. First, we assessed whether group size increased group reproductive output. As group reproductive output is a count data, Poisson GLM can be normally used. Our dataset, however, violated the characteristic structural relationship between mean and variance. Therefore, in this study, negative binomial GLM (with log link function) was used instead of Poisson GLM to accommodate the overdispersed data (Crawley 2002). Body size of breeders and helpers should be related to group reproductive output because larger individuals have higher abilities to protect their brood against predators and larger females produce more eggs. However, body sizes of reproductive capable group members were highly correlated with each other (see 'Results'), thus only body sizes of female breeders (i.e. larger females lay larger clutches in cichlids, Heg 2008; and may provide more protection) were entered into the GLMs. Increased nest size might also increase group reproductive output because larger spaces allow more fish to stay in the nest. Therefore, in the GLM, group size, female breeder SL, log nest volume and population were fitted as explanatory terms.

Second, we assessed whether reproductive success of breeders was influenced by the number of the same sex and the opposite sex group members. In the separate negative binomial GLM, reproductive success

of male breeder or female breeder was related to group structure (without mature helpers, with a mature male helper, with a mature female helper), female breeder SL, log nest volume and population. As dominant paternity is approx. 60% of total offspring when dominant breeders breed cooperatively with male helpers (Awata et al. 2005, 2006), reproductive success of male breeders with male helpers was calculated as $0.6 \times$ total group reproductive output. Similarly, reproductive success of female breeders with female helpers was calculated as $0.4 \times$ total group reproductive output (Awata et al. 2005).

All data analyses were carried out using the statistical software R version 2.8.1 (R Development Core Team 2008). All probabilities reported are two-tailed and significance levels set to $\alpha = 0.05$. Although the significance of two-way interactions between population and other explanatory terms were tested in all models of this study, none was significant and thus all interactions were deleted from the model.

Results

Difference in Group Structure and Nest Size Between Two Populations

In most cases, *J. ornatus* groups consisted of a breeding pair with zero or one sexually mature helper(s), but GS-1 of the Wonzye population was slightly, but significantly, larger than that of the Kasenga population (Fig. 1a; Table 1). In both populations, mature male helpers were more numerous than mature female helpers (although not statistically significant at Kasenga: 18 vs. 10, binomial test, $p = 0.18$;

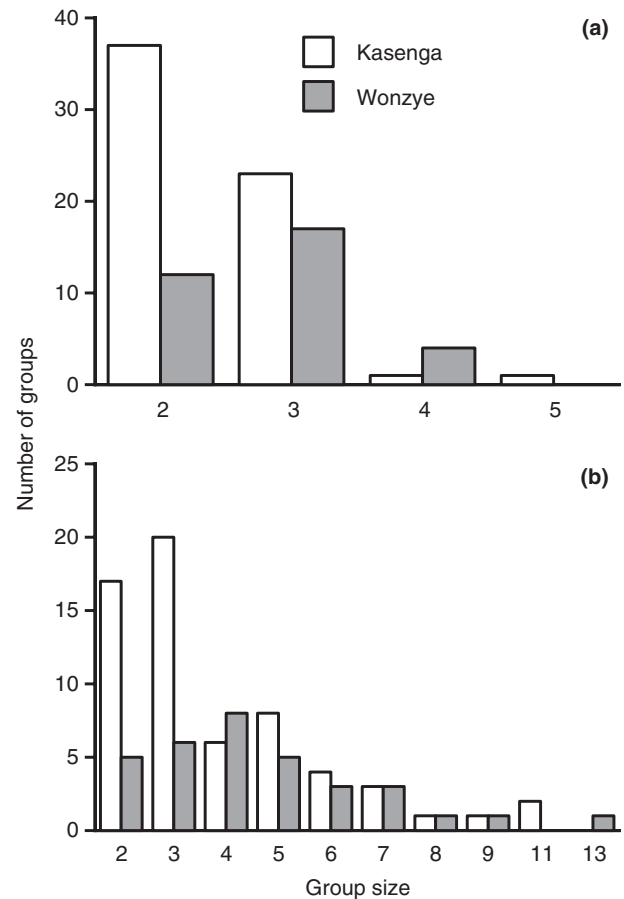


Fig. 1: Frequency distribution of group size. (a) GS-1: number of breeders plus sexually mature helpers. (b) GS-2: number of breeders plus mature and potential helpers (≥ 20 mm SL).

Wonzye: 23 vs. 2, $p < 0.0001$). When potential helpers were included into the group size estimate, average group size (GS-2) at the Kasenga population

Table 1: Differences in group size, number of offspring, body size of each rank and nest size between Kasenga and Wonzye populations

	Kasenga population			Wonzye population			Statistics ^a		
	Mean \pm SD	Range	n	Mean \pm SD	Range	n	t	z	p
Group size									
GS-1	2.5 \pm 0.6	2–5	62	2.8 \pm 0.7	2–4	33	–	–2.34	0.02
GS-2	3.9 \pm 2.1	2–11	62	4.7 \pm 2.4	2–13	33	–	–1.95	0.05
Offspring number									
GS-1	4.7 \pm 5.0	0–25	62	6.0 \pm 6.8	0–39	33	–	–1.43	0.15
GS-2	3.2 \pm 4.1	0–17	62	4.1 \pm 5.6	0–29	33	–	–0.73	0.47
Body size (mm)									
Rank1	57.0 \pm 8.2	35.8–76.6	62	66.5 \pm 11.9	45.7–85.4	33	–4.11	–	0.0002
Rank2	47.1 \pm 8.2	31.7–71.5	62	54.4 \pm 11.0	34.1–72.0	33	–3.35	–	0.002
Rank3	39.2 \pm 4.4	32.1–45.0	25	44.4 \pm 7.9	31.1–58.8	21	–2.68	–	0.01
Rank4	39.6	37.5–41.7	2	38.9 \pm 5.3	32.7–45.6	4	–	–	–
Rank5	38.1	–	1	–	–	–	–	–	–
Nest size (volume, cm ³)	2198 \pm 2180	86–12341	48	1472 \pm 1454	168–5885	30	–	–1.77	0.08

^aUnpaired t-test or Mann–Whitney U-test was performed; –, no data.

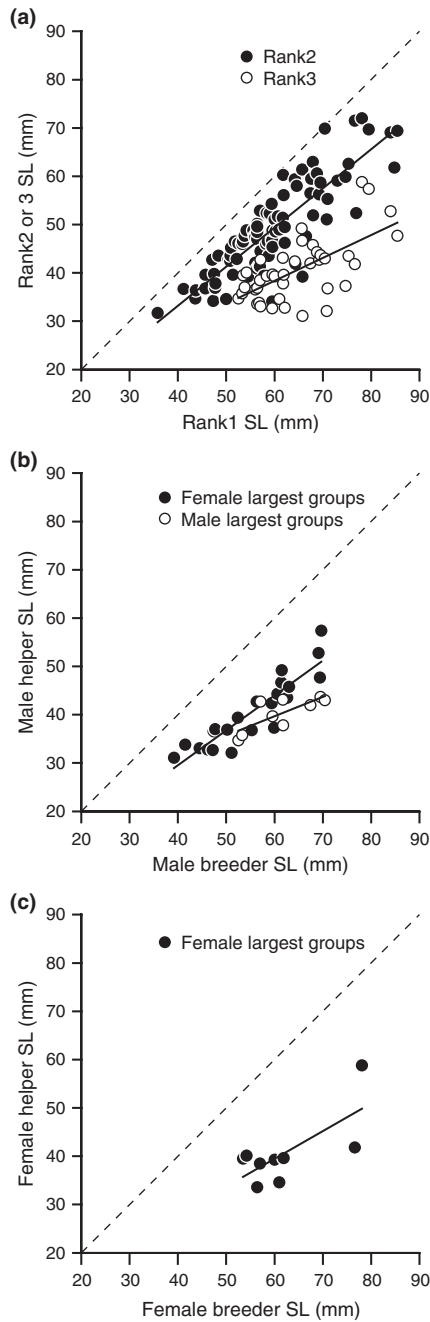


Fig. 2: Body size relationships within breeders and between breeders and helpers. (a) Relationship between rank1 SL and rank2 SL or rank3 SL. Since the relationship between SL of different ranks was not different between the populations (results not shown), the data from both populations were combined. Regression lines are from simple regression models (rank2: $y = 0.81x + 0.81$, $r^2 = 0.73$, $p < 0.0001$, $n = 89$; rank3: $y = 0.47x + 10.06$, $r^2 = 0.41$, $p < 0.0001$, $n = 40$). (b) Relationships between male breeder SL and male helper SL (female largest groups, $y = 0.72x + 0.65$, $r^2 = 0.82$, $p < 0.0001$, $n = 22$; male largest groups, $y = 0.40x + 15.83$, $r^2 = 0.59$, $p = 0.02$, $n = 9$). (c) Relationship between female breeder SL and female helper SL (female largest groups, $y = 0.57x + 5.07$, $r^2 = 0.51$, $p = 0.03$, $n = 9$).

Table 2: Summary of Pearson's correlation coefficients between standard length (SL, mm) of group members ranked as 1, 2 and 3

	Kasenga population		Wonzye population	
	r	n	r	n
Rank1 vs. rank2	0.86***	60	0.81***	29
Rank2 vs. rank3	0.64***	23	0.89***	17
Rank1 vs. rank3	0.43*	23	0.69**	17

Group size 4 ($n_{Kasenga} = 2$, $n_{Wonzye} = 4$) and group size 5 ($n_{Kasenga} = 1$) were excluded from the analyses. n, number of individuals. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

was 4 and that of the Wonzye population was 5 (Fig. 1b; Table 1). GS-2 of the Wonzye population was also greater than that of the Kasenga population. GS-1 positively correlated with GS-2 (Spearman's rank correlation, Kasenga: $r_s = 0.71$, $p < 0.0001$, $n = 62$; Wonzye: $r_s = 0.56$, $p = 0.002$, $n = 33$). In addition to population difference in group size, body size of each rank was significantly different between two populations: rank1, rank2 and rank3 individuals of the Wonzye population were larger than the fish of the same rank in the Kasenga population (Table 1). Although nests used by *J. ornatus* groups tended to be larger for the Kasenga population compared with the Wonzye population, the difference was not statistically significant.

Body Size of Breeders and Helpers

Female breeders were usually larger than male breeders within groups; 49 and 29 females were larger and 13 and 4 males were larger (rank1) than their breeding mates (rank2) at Kasenga and Wonzye, respectively. Larger female breeders mated larger male breeders, and larger breeders had larger sexually mature helpers (Fig. 2a; Table 2). Significant and positive correlations in body size were also detected between breeders and helpers of the same sexes (Fig. 2b, c). In both populations, correlation coefficients on SL of adjacent ranks were higher than those of not adjacent ranks (Table 2). Consistent body size ratios were found between two adjacent ranks (Fig. 2a), but body size ratios between rank1 and rank2 were significantly lower than those between rank2 and rank3 (two-way ANOVA, rank combination: $F_{1,131} = 26.1$, $p < 0.0001$, population and rank combination \times population: both $p > 0.65$; Fig. 3). As predicted, the observed distribution of size ratios was significantly different from the expected distribution of ratios from randomly created pairs of

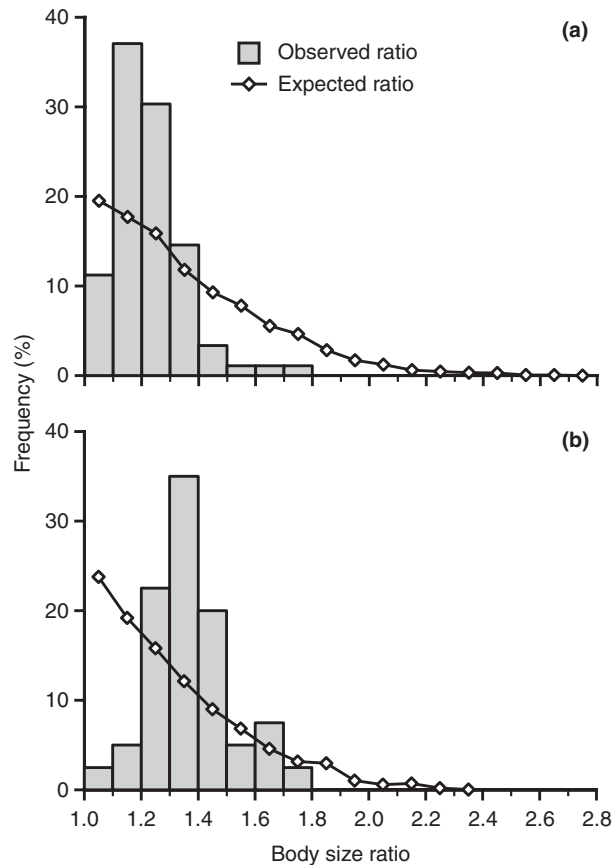


Fig. 3: Frequency distributions of body size (standard length, SL) ratios within each group of adjacent rank. The observed frequency distribution of ratios and the expected frequency distributions generated by a Monte Carlo procedure are indicated as bars and lines, respectively. (a) Size ratios between rank1 and rank2. Mean observed and expected rank1/rank2 \pm SD = 1.23 ± 0.13 , $n = 89$ and 1.35 ± 0.28 , $n = 8900$, respectively. (b) Size ratios between rank2 and rank3. Mean observed and expected rank2/rank3 \pm SD = 1.36 ± 0.14 , $n = 40$ and 1.30 ± 0.25 , $n = 4000$, respectively.

fish (two-sample Kolmogorov–Smirnov test, rank1/rank2: $D = 0.29$, $p < 0.0001$; rank2/rank3: $D = 0.38$, $p < 0.0001$; Fig. 3).

Relationships Among Group Size, Body Size of Group Members and Nest Size

Larger breeders had larger groups (GS-1, binomial GLM, $\chi_1^2 = 16.47$, $p < 0.0001$, $n = 73$, group size 4 and 5 were excluded; Fig. 4) in both populations (no effect of the population: $\chi_1^2 = 0.16$, $p = 0.69$). Group size also increased with nest size (GS-1, binomial GLM, $\chi_1^2 = 9.34$, $p = 0.002$, $n = 73$, coefficient \pm SE = 0.98 ± 0.39 , group size 4 and 5 were excluded) and was affected by differences between the two populations ($\chi_1^2 = 4.10$, $p = 0.04$). When

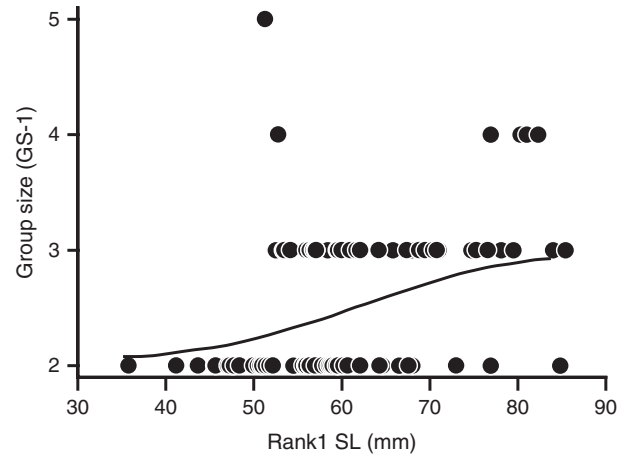


Fig. 4: Relationship between rank1 SL and group size (GS-1). Group size 4 and 5 were excluded for the analysis (see text for statistics), but their plots are shown in the figure. A regression line is from GLM [GS-1 = $2 + 1/(1 + e^{6.78 - 0.11 \times \text{Rank} 1 \text{ SL}})$]. Two outliers of group size 4 and 5 are from the Kasenga population.

both rank1 SL and nest volume were included in GLM on GS-1, only the relation between rank1 SL and GS-1 remained significant and positive (rank1 SL: $\chi_1^2 = 8.24$, $p = 0.004$; nest size: $\chi_1^2 = 1.05$, $p = 0.30$; population: $\chi_1^2 = 0.11$, $p = 0.74$, $n = 74$). This indicates that body size of breeders plays important roles in producing variation in group size. When potential helpers were counted as group size, similar relationships among group size (GS-2), body size of group members and nest size were detected (linear model: rank1 SL: $F_{1,74} = 14.10$, $p = 0.0003$, coefficient \pm SE = 0.06 ± 0.03 ; nest size: $F_{1,74} = 0.59$, $p = 0.45$; population: $F_{1,74} = 0.24$, $p = 0.63$).

Reproductive Success in Relation to Group Size

Groups with a helper had larger number of offspring reared in the nests than monogamous pairs ($\chi_1^2 = 4.75$, $p = 0.03$; Fig. 5a; Table 3 model 1), whereas no difference in group reproductive output was detected between groups with two helpers and groups with a helper ($\chi_1^2 = 0.63$, $p = 0.43$) or monogamous pairs ($\chi_1^2 = 1.25$, $p = 0.26$). In addition, when potential helpers were included, group reproductive output was positively correlated with group size (Table 3 model 2). Female body size, nest size and population did not affect group reproductive output. Reproductive success of male breeders was not dependent on the presence of mature helpers (Fig. 5b; Table 3 model 3). In contrast and as expected, reproductive success of female breeders

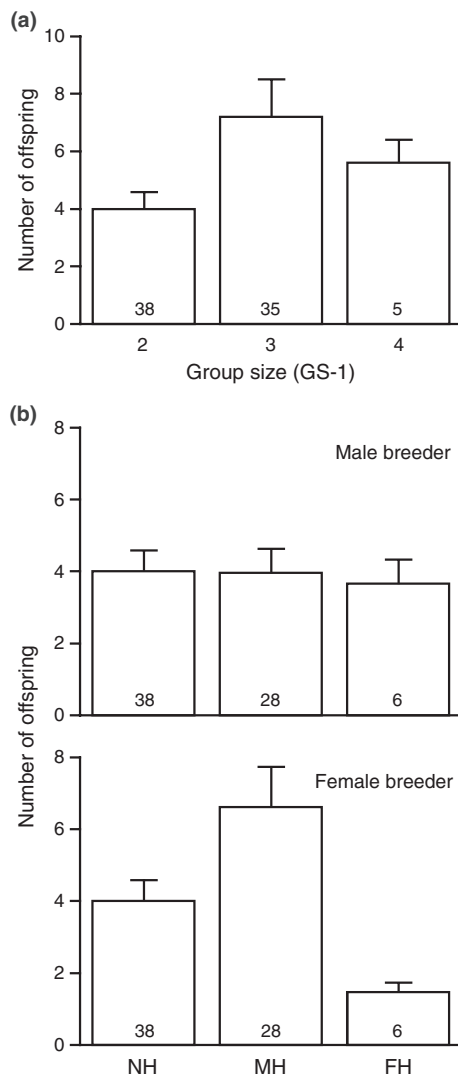


Fig. 5: Helper effects on reproductive success. (a) Group reproductive output in relation to group size (GS-1). (b) Reproductive success of male breeders and female breeders. NH, no helper, MH, one male helper, FH, one female helper. Bars present mean \pm SE. Numerals in bars show sample sizes (number of groups).

increased when two mature males assisted her with paternal care at the nests ($\chi_1^2 = 6.07$, $p = 0.01$, Fig. 5b; Table 3 model 4). Female breeders tended to attain lower reproductive success when multiple mature females were present at the nest ($\chi_1^2 = 4.02$, $p = 0.05$). Unexpectedly, breeder reproductive success tended to be negatively correlated with nest size.

Discussion

We found that group size was significantly related to the body size of breeders in *J. ornatus*. Larger breeders had larger helpers, and larger groups had greater

group reproductive output. In addition, *J. ornatus* showed size-hierarchical societies, in which the size ratios between adjacent ranks were distinctly different from a random expectation and quite constant. We analysed two types of group size (GS-1: breeders plus only sexually mature helpers and GS-2: breeders plus subordinates larger than 2 cm) considering two published papers (Awata et al. 2005; Heg & Bachar 2006), and results were quite similar in either case, which was predictable because of the positive correlation between GS-1 and GS-2. Field observations of all *J. ornatus* group members including fry suggest that the individuals that exhibited attacking behaviours against other fish species were all mature, and immature individuals never showed such behaviours (S. Awata, unpubl. data). This result is different from that in *N. pulcher* and *N. savoryi*, where both mature and immature fish attacked against other fish species (Taborsky & Limberger 1981; Taborsky 1984, 1985; Heg et al. 2005b). However, the fact that both GS-1 and GS-2 significantly and positively associated with group reproductive output suggests that even if small potential helpers never assist in territory defence, they might increase the survival of smaller offspring; e.g. by assisting in direct brood care such as cleaning and fanning eggs (like small helpers in *N. pulcher*, Heg 2008; Heg et al. 2008) or by guarding the smaller offspring (who will flee to protection if a guardian flees, S. Awata & D. Heg pers. obs.). Alternatively, small potential helpers might affect neither positively nor negatively the survival of smaller offspring.

Group Structure

Size hierarchies are described in several group-living fishes, where the constant body size ratios between individuals are regulated (Buston 2003a; Heg et al. 2005b; Buston & Cant 2006; Heg & Bachar 2006; Wong et al. 2007). As has been found in a previous study by Heg & Bachar (2006), this study also showed that larger breeders had larger helpers. Especially, correlation coefficients on SL of adjacent ranks were higher than those of not adjacent ranks, indicating strict size ratios are regulated between adjacent ranks. Additionally, the observed distribution of size ratios is specific and not random (approx. 1.23 in rank1–rank2 combinations and approx. 1.36 in rank2–rank3 combinations). There may be three reasons to explain why such strict size ratios are found between breeders and helpers in this fish. First, breeders may evict helpers (especially same sex helpers) when size differences between breeders and

Table 3: Results of multifactorial negative binomial GLMs of factors affecting group reproductive output or reproductive success of male or female breeder

Model	Model term	df	χ^2	p	Coefficient (SE)
1. Effect of group size (GS-1) on group reproductive output (n = 78 groups)	GS-1 (2, 3, 4)	2	5.58	0.06	
	2				0
	3				0.52 (0.22)
	4				0.20 (0.46)
	Female breeder SL	1	2.62	0.11	
	Nest size	1	1.10	0.29	
2. Effect of group size (GS-2) on group reproductive output (n = 78 groups)	GS-2 (2–11)	1	4.97	0.03	0.11 (0.06)
	Female breeder SL	1	1.67	0.20	
	Nest size	1	2.08	0.15	
	Population	1	0.65	0.42	
3. Effect of mature helper number on reproductive success of male breeder (n = 72 groups) ^a	Group structure	2	0.11	0.94	
	Female breeder SL	1	2.26	0.13	
	Nest size	1	3.24	0.07	–0.20 (0.11)
	Population	1	3.47	0.06	–0.47 (0.26) ^b
4. Effect of mature helper number on reproductive success of female breeder (n = 72 groups) ^a	Group structure	2	14.29	0.0008	
	Without helpers				0
	With a male helper				0.56 (0.23)
	With a female helper				–0.96 (0.47)
	Female breeder SL	1	2.22	0.14	
	Nest size	1	3.42	0.06	–0.21 (0.12)
Population	1	3.49	0.06	–0.48 (0.26) ^b	

^aGroups having two females and having three males in Wonzye population were excluded from the analyses.

^bCoefficient (SE) for Wonzye population, Kasenga = 0 as the reference population.

helpers become smaller (Balshine-Earn et al. 1998; Buston 2003b). Second, breeders only accept recruits that are constantly smaller than the breeders as helpers (Balshine-Earn et al. 1998; Buston 2003b; Heg et al. 2005b). In field removal experiments of helpers, new helpers joined in the groups in some nests after removal of original helpers, and all new helpers were as large as or smaller than the original helpers (S. Awata, unpubl. data). Third, helpers may adjust their growth rates to prevent eviction from the group by breeders (Heg et al. 2004; Wong et al. 2008). In addition, low growth rate of male helpers seems likely be due to high investment in testes (Awata et al. 2008). In this study, constant size ratios were also found within pairs of breeders. Such size ratios seem to be related to sexual conflict over parental care and additional mating (Awata & Kohda 2004). Even within breeders, both higher rank and lower rank breeders might regulate their growth to resolve the sexual conflict over parental care.

As described in the previous study on cooperative breeding cichlids (reviewed in Heg et al. 2005b), group sizes in *J. ornatus* positively correlated with the body size of breeders. Moreover, a multifactorial logistic regression analysis suggests that the body size

of the breeders, rather than the nest size, was the main factor explaining variation in group size. Group size was larger in the Wonzye population than in the Kasenga population (Table 1). The difference in body size of rank1 individuals may explain the difference in group size: maximum 85 and 75 mm SL in the Wonzye and Kasenga population, respectively (Table 1). Considering the mature size (>30 mm SL) and size ratios between rank1 and rank2 and between rank2 and rank3, we can predict maximal group sizes as follows: 5 in Wonzye population (30, 40, 55, 70, 85 mm SL) and 4 in Kasenga population (32, 44, 60, 75 mm SL). Therefore, qualitatively the predicted maximal group size fits the observation that the group size is larger in the Wonzye population than in the Kasenga population. However, quantitatively, the observed group size was slightly smaller than the predicted maximal group size (the data of group size 4 and 5 at Kasenga was excluded from the analysis because each was found in only one case, and these two data were both outliers in Fig. 4). This supports the findings by Buston & Cant (2006) on the clownfish *A. percula*, who also showed that the observed group size does not exceed the maximum predicted group size, based on body

size ratios of adjacent ranks and the body size of the largest individual in the group.

Helper Effects on Reproductive Success and Stable Group Size

Positive influences of group size on reproductive success are widely known in cooperatively breeding birds (e.g. Stacey & Koenig 1990; Emlen 1991; Cockburn 1998; Canestrari et al. 2008), mammals (e.g. Russell 2004) and one cooperatively breeding fish species (Taborsky 1984; Balshine et al. 2001; Brouwer et al. 2005; Heg et al. 2005a). In the present study, we found a significant positive association between group size and group reproductive output and this relationship appeared consistent between the two studied populations. Although previous attempts have failed to detect positive effects of group size on productivity in *J. ornatus* (Awata et al. 2005; Heg & Bachar 2006), our study using multifactorial analyses and larger samples sizes was able to detect the helper effect. However, *J. ornatus* helpers usually share their paternity or maternity with their dominant breeders (Awata et al. 2005, 2006), and thus group reproductive output does not always indicate reproductive success of individual group members.

Reproductive success of male breeders with mature female helpers is assumed to be greater compared with monogamous males because of e.g. multiple females laying eggs (e.g. Vehrencamp 2000; Heg 2008; Heg & Hamilton 2008; Heg et al. 2008) or females in larger groups laying larger eggs with higher survivorship (e.g. Russell & Lummaa 2009). In our second analyses, however, reproductive success of male breeders did not depend on the presence of male and female helpers. This result suggests that dominant breeders are unlikely to gain direct fitness benefits beyond those from survival benefits, even if a male or a female helper assists in brood care. In addition, male helpers may invoke some costs to male breeders such as a high investment in testes (Awata et al. 2006, 2008) and reproductive sharing (Awata et al. 2005; Heg et al. 2006, 2008). Dominant female reproductive success was the highest when two males assisted her in brood care. This result appears to well explain the fact that, under laboratory conditions, cooperatively polyandrous females of the closely related species *J. transcriptus* may control paternity distribution of her two males and obtain more brood care as a result, compared with monogamous females (Kohda et al. 2009). In contrast to the polyandrous situation, we found a tendency that two females sharing the same nest

experienced decreased reproductive success of female breeders. This might be due to intense reproductive competition among females. For example, acorn woodpecker females destroy their sister's eggs prior to laying their own (Mumme et al. 1983). In cooperatively breeding cichlids *N. pulcher*, reproductive success of female helpers is quite low because of cannibalization of helper females' eggs and reproductive suppression of helpers by dominant females (Heg 2008; Heg & Hamilton 2008), but at the same time the presence of a female helper reduced dominant female's growth (Heg & Hamilton 2008) and this is likely to affect her long-term reproductive success, as clutch size increases linearly with female body size in cichlids (e.g. Heg 2008). At present, we have not yet tested whether reproduction in *J. ornatus* is low or highly skewed towards the dominant females, because female helpers are rare, although Awata et al. (2005) provides evidence of female helpers' reproductive participation (dominant maternity is approx. 40%). Parentage analyses using many groups with female helpers should solve these points.

This study and previous studies have shown that the average group size in *J. ornatus* (4 in GS-2, Heg & Bachar 2006; 3 in GS-1, 4–5 in GS-2, this study) is much smaller than the group sizes in the closely related cichlid species *N. pulcher* (15; Balshine et al. 2001; Heg et al. 2005b) and *N. savoryi* (14; Heg et al. 2005b). This difference might be related to the differences in the degree of helpers' reproduction within groups. *Julidochromis ornatus* helpers of both sexes frequently participate in reproduction (Awata et al. 2005). In contrast, helpers of *N. pulcher* consisted of large number of immature and some mature fish of both sexes. Large mature helpers join in reproduction, but the degree of reproductive participation by helpers is low because of reproductive suppression (Dierkes et al. 1999, 2008; Fitzpatrick et al. 2006; Heg et al. 2006; Heg 2008). In birds, cooperatively polyandrous species generally form smaller groups compared with extended family species where grown offspring help their parents to care for younger siblings in their natal territory (Brown 1987; Hartley & Davies 1994). Groups in cooperative polyandrous dunnocks seem to be limited to small group sizes because of the reduction of male parental care because of paternity loss and the increase in sexual harassment (Hartley & Davies 1994). In this study, the largest breeders had three male helpers in four groups at Wonzye, but per male reproductive success would decrease with increasing mature males if group reproductive output is not

different between the groups with a male helper and with two or more helpers (see Fig. 5a). Considering the evidence together, group sizes in cooperatively breeding fishes appear to depend on the body size of the largest individual in the group and the balance between cooperation and reproductive competition within and between sexes.

In summary, our study shows that *J. ornatus* has size hierarchical societies, where the constant body size ratios among group members are regulated, and large female breeders having one large male helpers that are unrelated to breeding pairs and participate in reproduction within groups gain higher reproductive success. Female helpers tend to decrease per female reproductive success probably because of reproductive conflict between females. While male helpers may invoke some costs to male breeders such as inducing higher investment in male breeder testes (Awata et al. 2006), the benefits of cooperative breeding to male breeders are still unclear. Field experiments of helper removals (e.g. Brouwer et al. 2005) and long-term field studies to trace marked fish are needed to evaluate whether helpers reduce the workload of the male breeders (Emlen 1991; Balshine et al. 2001), and in turn whether the helpers enhance the survival of the (male) breeders (known as the group augmentation hypothesis, Kokko et al. 2001).

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