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Cooperative breeding in the Lake Tanganyika cichlid *Julidochromis ornatus*

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Abstract Cooperative breeding has been described for several cichlids from the genus *Julidochromis* (Perciformes: Cichlidae) under laboratory conditions, but field evidence is scarce. Here we describe the breeding system of the cichlid *Julidochromis ornatus* (Boulenger) in Lake Tanganyika (Zambia). Groups defended a breeding shelter under a large flat stone. Smaller group members stayed and fed under or close to the stone, actively guarded by the larger group members. Six out of 28 groups were newly established by breeders, joined by subordinates from a large pool of independent fish (comprising 50–70% of the total population), and four groups were seen to dissolve during a total of 77 observation days. Breeding groups consisted of a large breeding male and female with zero to five smaller subordinates (average 2). Larger breeders and subordinates were found in larger groups. All group members participated in territory defence and -maintenance, but the breeders were only present at the shelter 48% of the time, in contrast to the subordinates which guarded the breeding shelter 94% of the time. Smaller group members showed submissive behaviours to larger group

members. We conclude subordinates in *J. ornatus* are helpers, but we did not find evidence that helpers increased the group's current reproductive success. Personal observations combined with a literature review revealed at least 19 species of Lake Tanganyika cichlids show evidence of cooperative breeding, entirely confined to the substrate breeding tribe of the Lamprologini (24% of 80 species in total); 2 *Chalinochromis* spp., 5 *Julidochromis* spp., 12 *Neolamprologus* spp. More effort should be put into detecting cooperative breeding in American and Asian substrate breeding cichlid species.

Keywords Reproductive success · Reproductive behaviour · Social behaviour · Helping behaviour · Group size

Introduction

Cooperative breeding, wherein subordinates assist dominant breeders raising a brood, is a widespread phenomenon in birds, mammals and several invertebrates, notably the Hymenopterans (Stacey and Koenig 1990; Duffy 1996; Choe and Crespi 1997; Solomon and French 1997; Cockburn 1998). Albeit fish are the most speciose group found within the vertebrates, and show advanced levels of social behaviour, including cooperative territory defence and mate sharing, nonetheless

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cooperative breeding has rarely been described (Taborsky 1994). In a comprehensive literature review, Taborsky (1994) found only eight fish species having ‘helpers-at-the-nest’: *Betta brownorum* and *B. persephone*, and six species from the family Cichlidae, tribe Lamprologini, all endemic to Lake Tanganyika. Descriptive and experimental data on such breeding systems are known from only two species of Lake Tanganyika cichlids: *Neolamprologus pulcher* (sub- or sister species of *N. brichardi* the ‘Princess of Burundi’, formerly known as *Lamprologus brichardi*, see Grantner and Taborsky 1998, for comments on the species-status of these species; Taborsky and Limberger 1981; Taborsky 1984, 1985; Balshine-Earn et al. 1998; Dierkes et al. 1999; Balshine et al. 2001; Skubic et al. 2004; Stiver et al. 2004; Heg et al. 2004a, b; authorities are given in the Appendix, except when mentioned) and the dwarf snail-shell cichlid *N. multifasciatus* (Rossiter 1993; Sato and Gashagaza 1997; Kohler 1998; Schradin and Lamprecht 2000, 2002). Data on the other Lake Tanganyika cichlids showing similar behaviour is either absent or very limited (e.g. Awata et al. 2005; Heg et al. 2005).

The purpose of this paper is, first, to describe the cooperative breeding system of one of these less well studied cichlids, *Julidochromis ornatus* (Kalas 1976; Hattori 1993; Taborsky 1994; Kawanabe et al. 1997; Konings 1998; Awata and Kohda 2004; Awata et al. 2005). Second, we review the literature on the incidence of cooperative breeding in Lake Tanganyika cichlids, and identify species where cooperative breeding has been described, or where cooperative breeding is suspected to occur (e.g. from observations on fish held in aquaria), but more detailed observations are needed. Both enterprises depend critically on the definition of cooperative breeding employed, i.e. what facts are considered evidence for the occurrence of cooperative breeding in a certain species? Ligon and Burt (2005) define cooperative breeding as ‘...social units composed of two or more breeding [individuals], plus one or more (often presumed) non-breeding “helpers-at-the-nest”.’ (see also Brown 1987 who lists 13 types of cooperative breeding systems).

We will follow this definition but have three clarifying comments to make, which have imme-

diately bearing on our study. First, the definition leaves the possibility open that more than two individuals are reproducing. Ligon and Burt (2005) proceed by using the restricted definition of cooperative breeding, wherein helpers are non-breeders, i.e. showing true alloparental care. Employing this restricted definition to a population where some groups have reproducing helpers, whereas others have non-reproducing helpers (see for examples Magrath et al. 2005), we would end with the following situation: (a) we would need to take an arbitrary cut-off point, e.g. proportion of groups with non-breeding helpers, from a reasonable sample of groups and populations, to reach a verdict whether the species is a ‘true’ cooperative breeder or not; (b) detailed genetic paternity and maternity analyses are needed before we can judge whether a certain species is a ‘true’ cooperative breeder; (c) the definition whether a species is a cooperative breeder might depend on the study population, study groups and time-periods wherein genetic analyses have been conducted, since helper reproduction may vary through space and time (e.g. Magrath et al. 2005). We think this is undesirable and rather opt for a broad definition of cooperative breeding, wherein we leave the possibility open that (sometimes) more than two individuals within a group are contributing offspring. Actually, this broad definition has also been used in most other comparative studies of cooperative breeding in e.g. birds (e.g. Ligon and Burt 2005 use a large number of bird species in their analyses, but in the majority of species no data on reproduction by helpers is available), exactly for the above mentioned reasons (a, b, c).

Second, the definition implies that helpers assist the current brood. Several types of helping behaviours may be involved which either directly or indirectly influence the growth and/or survival of the brood (e.g. Arnold et al. 2005). In case of cichlids, these include digging at the breeding shelter, fanning and cleaning the brood, guarding the brood, chasing egg and offspring predators (Taborsky 1984).

Third, the definition does *not* refer to any of the ultimate (fitness) causes and consequences of group living and helping behaviour to the various group members. Helpers may sometimes benefit

or harm the fitness prospects of the breeders in the group, depending on ecological circumstances (e.g. Komdeur 1994). Helping behaviour may often accrue no noticeable direct benefits to the breeders ('helper effect', e.g. because breeders reduce their workload when assisted by helpers, Balshine et al. 2001), although future benefits, like increased survival and future productivity, may be notoriously difficult to detect (Dickinson and Hatchwell 2005). Potentially, group size, reproductive partitioning, parental and helping behaviours may all be the outcome of *both* inter- and intrasexual cooperation *and* conflict, modified by e.g. relatedness, the relative and absolute competitive abilities of the various group members and the ecological circumstances. Thus, the fitness consequences for each group member may vary accordingly, and may lead to no benefits of group living to certain individuals compared to non-group living individuals.

Employing these criteria and using our knowledge of other cooperatively breeding cichlids (see references above), a cichlid species shows evidence for cooperative breeding when (1) subordinates assist breeders in raising a brood, i.e. show behaviours likely to increase the fitness of the brood when at the same time these behaviours are unlikely to increase fitness directly e.g. the survival of the subordinates (but the net effect might not increase the fitness of the brood, if breeders e.g. reduce their workload accordingly); (2) subordinates show submissive behaviours to the breeders, if not and the subordinates apparently engage in reproduction, the breeding system may be better described as a communal breeding system (a special case of cooperative breeding); (3) if (2) applies and same-sex reproducing individuals show no parental care, the breeding system may be better described as e.g. a dominant-satellite system, or sneaker male-territorial male system, as found in many species of fishes (Taborsky 1994).

In this paper, we present data on habitat and breeding site selection, group composition, body length and sex of group members, and parental-, spacing- and social behaviours in *J. ornatus*. Recently, Awata et al. (2005) have shown that both male and female subordinates in *J. ornatus* are usually unrelated to the breeders, both may

participate in varying degrees in reproduction, and groups with subordinates tend to produce more offspring than single breeding pairs. We complement their findings by showing, first, that *J. ornatus* groups show the typical group compositions found in other cooperatively breeding cichlids, with a large dominant breeding pair and up to several smaller sized subordinates (see also Heg et al. 2005). Second, subordinates show the same helping and social behaviours as subordinates in other cooperatively breeding cichlids do, including chasing of egg and offspring predators and submissive behaviours towards the breeders. Third, we show that subordinates may join breeding pairs to help, which may account for the low relatedness found between subordinates and breeders (Awata et al. 2005).

Finally, based on the definition of cooperative breeding above and the types of helping behaviours and group compositions shown by all well studied cooperatively breeding cichlids (see references above, Heg et al. 2005 and this paper), we evaluate which Lamprologine cichlid species show evidence of cooperative breeding. For this purpose, we conducted a literature survey including less accessible papers, we gathered personal observations and correspondence from both the field and captive populations on the majority of the 80 Lamprologine species. We conclude with a preliminary mapping of the emergence of cooperative breeding in these cichlids (Sturmbauer et al. 1994), to argue for a multiple origin of cooperation in this lineage and to target future directions of research.

Methods

Study site and subjects

Our main study site lies at the south tip of Lake Tanganyika, at Kasakalawe near Mpulungu, Zambia (8°46.849' S, 31°04.882' E). Cichlids were studied by SCUBA diving from 2 February to 21 April 2003. The main study site was a sandy area, with rocks half submerged in the sand, at 9.0–11.5 m depth. The present observations were conducted at a site dominated by two 'colonies' of *N. pulcher* and *N. savoryi* both occurring at very

high densities. The habitat at our main study site has no layers of stones or boulders inaccessible to divers. All substrate breeding cichlids and their breeding shelters were easy to find and observe. *J. ornatus* is a particular conspicuous species, with its black-and-whitish longitudinal stripes, which facilitated locating even the very small individuals or individuals not associated with a breeding shelter. In contrast, our second study site at Nkumbula Island, ca. 2 km from Kasakalawe, near Mpulungu had a lot of sub-structuring: patches of large boulders (>1 m diameter) were interspersed with patches of gravel and shell debris and patches of layered stones; quite similar to other studied populations of *J. ornatus* (Hattori 1993). Locating all breeding groups at this study site appeared difficult, since fish could hide between the boulders, and therefore no attempt was made to find all groups and estimate breeding densities at Nkumbula in the present study.

Detection and mapping of breeding groups

The main study area at Kasakalawe (1708 m²) was systematically surveyed for breeding groups using a 2 × 2 m grid made with ropes (32 × 42 m, plus two adjoining areas of 10 × 10 m and 12 × 22 m, respectively). All potential breeding shelters (i.e. large stones with shelter underneath) were mapped, marked and controlled for breeding activity (i.e. presence of subordinates and offspring or apparent digging activity). We are convinced we detected all breeding groups in the main study area ($n = 23$ groups). Breeding shelters were invariably located under large, usually flat, stones and we measured the length and height of this stone in a sub-sample of the breeding groups using a ruler. Additional groups just outside the main study area were also marked and individuals measured and observed to increase sample sizes ($n = 5$ groups). At the second study site, Nkumbula Island, only four breeding groups were located at 2.3–2.5 m depth, and at three shelters stone measurements were taken.

Interspersed between the groups, numerous non-breeding individuals were seen. Non-breeders included fish of all sizes, presumably including both sexually mature and immature individuals. Hence, to avoid confusion with the small presumably

non-breeding group members, we further refer to all non-group members as ‘independents’ (instead of non-breeders).

Body measurements and sexing

Within 1 week of the discovery of a breeding group, members of the breeding group (except the offspring, see below) were caught using tent nets with the help of the anaesthetic clove oil (also known as Eugenol, Kreiberg 2000) dissolved in ethanol. Tent nets were conical nets, at the base 1 m in diameter fitted with lead weights, at the top fitted with a small buoy. One part clove oil was dissolved in four parts 70% ethanol, and transported underwater in 25 ml syringes. The tent net was placed over the breeding shelter as soon as all group members were present, and the dissolved clove oil was injected under the stone slab (10–25 ml depending on the size of the slab). Clove oil was highly effective in immobilising the fish, recovery occurred within 5 min and no adverse effects on subsequent behaviour were detected. We measured body length (standard length SL to the nearest 0.5 mm) of all caught fish, sexed fish by close inspection of the genital papilla (only possible for individuals >20 mm SL, and some individuals escaped before sexing). Subsequently, all fish were individually marked by fin clipping the dorsal—(5 positions) and/or anal fins (3 positions) in unique combinations for each size class, allowing future individual identification. All clipped fins had regrown at the end of the study period, and no adverse effects were detected from clipping, like desertion from the group/area or fungal infections. Group members larger than or equal to 20 mm SL, excluding the breeding male and female, were defined as ‘subordinates’. Subordinates showed digging, brood guarding, territory defence, and submissive behaviour towards the breeders at the breeding shelters, and were not chased from the breeding site by the breeders.

All group members smaller or equal to 20 mm SL were defined as offspring, i.e. these individuals were usually hiding under the breeding shelter and rarely engaged in social interactions (D. Heg & Z. Bachar, personal observations). Offspring were counted by turning up the breeding shelter

stone every week, where they were found swimming upside down on the stone surface (see also Kuwamura 1986; Konings 1998; Brichard 1999). Their sizes were estimated with a ruler and cohorts of approximately equal SL were assigned to the same brood. At the end of the study period all remaining offspring were caught using a tent net and clove oil as described above, and measured to the nearest 0.5 mm SL using a ruler. In total, 203 group members were caught and measured.

Additionally, we caught, measured, marked and released 131 independents (75 at Kasakalawe and 56 at Nkumbula). Independents were chased into gill nets or transparent plastic tubes (one end open, one end sealed, 20 cm × 40 cm length) and moved to a hand-net for measuring etc., before they could entangle or harm themselves in the gill net or the plastic tube.

Reproductive success

In 20 groups at Kasakalawe, we determined the total reproductive output over at least a period of 9 days (mean ± SE = 29 ± 3 days, range = 9–47 days). We summed all offspring produced over all broods in that period, including pairs producing no offspring, to calculate the productivity per week.

Productivity should increase with the level of protection a group might provide to the eggs and young. We expected the level of protection to increase with (a) group size (i.e. more members available to chase away egg predators and piscivores), (b) standard length of the male and the female breeder, and/or (3) standard length of the largest subordinate in the group (i.e. larger group members might be able to chase away larger sized piscivores).

Focal behavioural observations

Focal observations were conducted on individually marked group members for 10 min ($n = 37$ individuals: 10 breeding females, 9 breeding males, 13 male subordinates, 4 female subordinates, plus one subordinate we were not able to sex) in the Kasakalawe population only, selected at random from all the groups within the main study area. The observations were conducted during the daytime (between 08:53 and 16:47). To

avoid pseudo-replication, all individuals were only observed once. We recorded the maximum distance moved from the shelter (using our grid lines as reference) and the proportion of the total observation time they spent within 50 cm from the shelter for the analyses of spacing behaviour. Additionally, we recorded the frequency of digging and carrying sand from the breeding shelter, the frequency of aggressive behaviours (including overt attacks: bites, chases, mouth-fights; plus display aggression: frontal approaches, spreading of the opercula, head-down display and s-shaped bend directed at con- and heterospecific fishes), the frequency of submissive behaviours (tail-quivering and zig-zag swimming) and ‘appeasement’ or socializing behaviour (soft-touch also called ‘bumping’ of the body of group-members). These behaviours are very similar in appearance to related social Lamprologine species (Taborsky et al. 1986; Heg et al. 2005), see for a detailed description of these behaviours Taborsky (1984, 1985). Frequencies were also calculated per time near the breeding shelter, but they will not be presented because they gave essentially the same results.

Cooperative breeding in other Lake Tanganyika cichlids

We conducted a literature survey of Lake Tanganyika cichlids, and included some recent unpublished observations and personal communications, to update our understanding of the extent of cooperative breeding in these cichlids (see Appendix for the list of scientific species names).

Data analyses

All statistical analyses were performed using SPSS 11.0 with significance levels set at $\alpha = 0.05$. We failed to catch all group members in four groups at Kasakalawe, as these groups had already (partly) dissolved before we could catch them all. We also failed to catch all the members of two groups at Nkumbula Island, as catching was more difficult due to the large number of hiding possibilities between stone slabs. These account for missing values in some of the

analyses. Since the group sizes, the body sizes and the sex ratio of the group members did not differ between the two populations (all P values > 0.1), these data were lumped in all analyses. The observational data (time at shelter, distance from shelter, frequencies of different behaviours) were lumped for the two sexes, because none of them differed between males and females, neither within the breeders, nor within the subordinates (all P values > 0.4).

Results

Breeding densities and breeding shelter selection

The breeding density at Kasakalawe was 0.135 groups per 10 m². Groups in both populations selected large flat stones as breeding shelters (Kasakalawe/Nkumbula, mean length \pm SD: 82.2/100.0 \pm 16.5/5.0 cm, range: 53/95–123/105 cm; and height: 17.3/27.3 \pm 5.8/2.5 cm, range: 11/25–30/30 cm; $n = 26$ Kasakalawe, plus 3 Nkumbula groups).

Group formation and dissolution

During the 79 days study period at the Kasakalawe site, 6 of 28 groups were newly established at previously unoccupied large stone slabs, including one single breeding pair without subordinates; and five breeding pairs, joined by one subordinate each within one week after establishment (the SL of these subordinates was 24, 32, 33, 44 and 52 mm respectively; the 33 mm fish was marked 41 days earlier as an independent fish 6.2 m away from the new breeding site). At the same time, 4 of the 28 groups dissolved.

The first group dissolved one day after discovery just at the start of our study period and before the fish could be caught. In the second group the breeding male was no longer present at the beginning of the study period when we caught the group members (although present at the preliminary observations), and the breeding female plus one subordinate (SL = 47.5 mm) left the shelter area 16 days afterwards. Both breeders had left the third group before catching,

leaving three subordinates at the shelter (SL = 36, mm 38 mm and 53.5 mm) until the end of the study period. Finally, the fourth group was the only group which established and dissolved during the study period (breeding pair plus subordinate of SL = 44 mm, see above), after 17 days of shelter occupation (two independents were found near this shelter afterwards). We used the Life Table procedure in SPSS, which accounts for censored data, to calculate the duration of shelter occupancy based on the daily occupation rate ($n = 28$ groups): 68.3% were still occupied after 48 days, our longest time-interval between discovery and last observation, indicating that the expected median time of occupancy for any shelter is well above 48 days.

Group composition and body measurements

A typical group consisted of a breeding pair with one or two subordinates (Fig. 1a, mean group size \pm SD: 4.0 \pm 1.2, range = 2–7, $n = 29$. Breeder males and females did not differ in their average body size (Table 1), and did not mate size-assortatively (Pearson $r = 0.06$, $n = 27$, $P = 0.77$). Both breeder males and females were always larger than the largest subordinate group member (Fig. 1b, 26 out of 26 cases, excluding one breeding pair with no subordinates; Paired t -tests, $df = 25$, $t = 12.5$ and 10.8 respectively, both $P < 0.001$). Other group members were of very variable sizes (Fig. 2a). Subordinate males and females did not differ significantly in size (Table 1).

Large breeder males occupied territories with more group members compared to small breeder males (Pearson $r = 0.45$, $n = 27$, $P = 0.02$; this relationship was not found in breeder females: $r = 0.16$, $n = 27$, $P = 0.42$). Moreover, it appeared that large breeders had relatively large subordinates as well, resulting in a complex relationship between group size, breeder body size and subordinate body size. This can be visualised and analysed by lumping the breeder males and females, since they did not differ significantly in size, into rank 1, and ranking the subordinates according to size (descending) into rank 2, 3, 4 etc. and plot the average sizes for each group size separately (Fig. 1b; rank is equivalent to dominance rank, see section on Social Behaviour). The accompanying

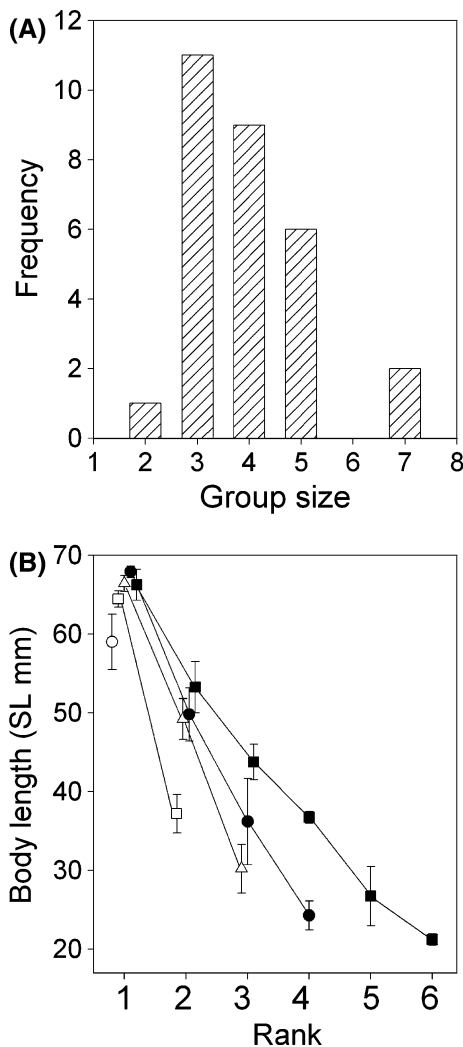


Fig. 1 (A) Frequency distribution of the group sizes in the breeding groups of *J. ornatus* (all fish ≥ 20 mm counted, $n = 29$ groups). (B) Standard length of breeders and subordinates was related to the rank and the interaction between group size and the rank ($n = 27$ groups and 80 individuals), showing that sizes of all group members increase with group size, resulting in large breeders being assisted by large subordinates and small breeders by small subordinates. Group size symbols are: white circles: 2, white squares: 3, white triangles: 4, black circles: 5 and black squares: 7 fish. Depicted are means \pm SE for the two breeders averaged (rank = 1) and the subordinates (rank = 2–6)

GLM revealed a significant effect of rank and the interaction between group size and rank on the SL ($n = 80$ and all $df = 1$, parameter estimates \pm SE of group size: -0.21 ± 1.35 , $p = 0.88$; of rank: -24.84 ± 2.85 , $P < 0.001$; of group size*rank: 1.86 ± 0.53 , $P = 0.001$; with intercept: 82.70 ± 6.22).

As described above, subordinates were joining new breeding pairs from the pool of independents. Independents were available throughout the two populations, in a broad range of sizes (Table 1, compare Fig. 2b with Fig. 2a). The independents at Kasakalawe were significantly smaller (mean \pm SD: 49.5 ± 11.5 mm SL, range = 31–70 mm, $n = 75$) than the independents at Nkumbula (58.9 ± 10.4 mm SL, range = 38–77 mm, $n = 56$, ANOVA $F_{1,129} = 23.3$, $P < 0.001$). Note that no independents smaller than 31 mm SL were discovered at Kasakalawe, except the joining subordinate of 24 mm SL described above, despite intensive searching and the conspicuousness of these fish. Instead, all fish smaller than 31 mm occurred at the breeding shelters, i.e. were protected by larger group members. Similarly, no independents smaller than 38 mm SL were found at Nkumbula, but it must be noted this area was more difficult to survey due to the many hiding possibilities between the stones, meaning some small independents might went unnoticed.

It is very likely that joining subordinates are not a random sample of independents from the whole population for two reasons. First, re-sightings of individually marked independents at Kasakalawe indicated that they used a limited home range. The average distance between the site of marking and the site of re-sighting was 3.2 m (2.7 m SD, range = 0.0–9.8 m, $n = 15$ independents, multiple data-points per individual were averaged before analyses), and in this respect there were no modifying effects of sex (t -test, $df = 12$, $P = 0.19$) nor SL (Regression, $df = 1$, $P = 0.34$). Second, there were significantly more male than female subordinates (36 versus 17, Binomial Test, $P = 0.013$, seven group members could not be sexed), despite the breeders having an equal sex ratio and showing no sexual dimorphism (Table 1). The subordinate sex ratio was also significantly different from the sex ratio of the independents. For this analysis we compared the sexes of all fishes larger than 30 mm, since independents were only found from 30 mm SL onwards (see Fig. 2, subordinates: 27 males vs. 11 females, independents: 59 males vs. 65 females, $\chi^2_1 = 6.6$ $P = 0.01$, excluding seven unsexed independents). The fact that independent males were significantly smaller than independent females (Table 1) suggests that particularly

Table 1 Body sizes of group and non-group members (independents) in *J. ornatatus* (standard length SL: mean, SE and range) and results of three separate ANOVA tests for sex differences (each with $df = 1$)

Status	<i>n</i>	Mean SL	SE	Range	Sex difference	
					<i>F</i>	<i>P</i>
All breeders	56	65.8	0.6	54–75		
Breeder males	27	65.6	0.8	57.5–72	0.17	0.68
Breeder females	29	66.1	0.9	54–75		
All subordinates	60	38.2	1.5	20–60.5		
Subordinate males	36	39.3	1.8	21.5–59.5	0.10	0.92
Subordinate females	17	39.0	3.2	20.5–60.5		
All independents	131	53.5	1.0	31–77		
Independent males	59	48.8	1.4	31–70	17.4	<0.001
Independent females	65	57.2	1.4	31.5–77		

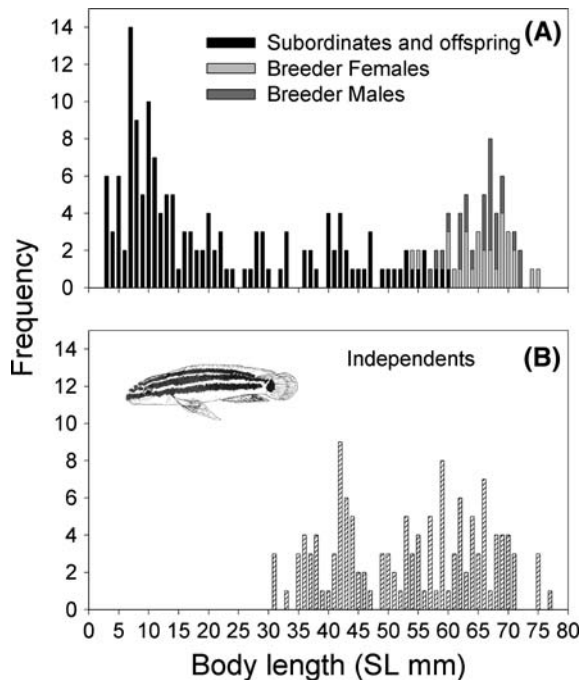


Fig. 2 Standard length of (A) group members and (B) independent *J. ornatatus* (0.5 mm values rounded downwards into mm classes). Inset shows adult individual (drawing after photo by Ad Konings)

relatively large independent males recruit as subordinates.

Time at the breeding shelter and distance travelled

Subordinates spent significantly more time at the breeding shelter (Table 2, Fig. 3) and ventured less far from the shelter than the breeders (Table 2, Fig. 3). Small subordinates stayed close to the shelter, while large subordinates were more similar to the breeders in the distance travelled

from the shelter and the amount of time they spent near the shelter (Fig. 3).

There was no correlation between the size of the smallest group member (range = 10.0–47.5 mm) and the proportion of time the breeders were within 50 cm from the shelter (Spearman $r_s = 0.06$, $P = 0.80$, $n = 19$) or the maximum distance breeders moved from the shelter ($r_s = -0.02$, $P = 0.93$, $n = 19$).

Shelter maintenance and social behaviour

Both subordinates and breeders showed digging behaviour, albeit at very low frequencies (Table 2). Digging behaviour was not related to status (Table 2) nor to body size SL (Spearman Correlations, digging per 10 min: $r_s = 0.21$, $n = 37$, $P = 0.21$). Similarly, no differences were detected in the frequencies of shelter defence behaviour between subordinates and breeders against conspecifics (Table 2). Conspecifics were never seen to venture close to or inside the breeding shelter, and therefore did not encounter the subordinates which tended to stay always close to or inside the shelter (see above). Aggression against heterospecific intruders was more common, but also these intruders were rarely seen to approach or enter the breeding shelter, in which case they were invariably attacked. Again, in this respect there were no differences between subordinates and breeders (Table 2). Defence behaviour was also not related to body size SL (Spearman Correlations, conspecifics per 10 min: $r_s = 0.16$, $n = 37$, $P = 0.33$, heterospecifics per 10 min: $r_s = 0.20$, $n = 37$, $P = 0.23$). Fish species attacked included potential breeding shelter competitors (i.e. using

Table 2 Mean percentage of time within 50 cm, and maximum distance moved from the breeder shelter; and mean frequencies (\pm SE) of behaviours per 10 min observation time; comparing breeders ($n = 19$) with subordinates ($n = 18$; Mann–Whitney U -tests)

Parameter	Status		Mann-Whitney U-test	
	Breeder	Subordinate	U	p
<i>Breeding shelter</i>				
Time (%)	48 \pm 8	94 \pm 3	35	<0.001
Maximum distance (m)	3.20 \pm 0.29	0.53 \pm 0.13	11.5	<0.001
Digging and carrying away sand	0.39 \pm 0.27	0.06 \pm 0.06	153	0.31
<i>Territory defence against</i>				
Conspecifics	0.05 \pm 0.05	0.00 \pm 0.00	162	0.80
Heterospecific	2.2 \pm 0.9	1.2 \pm 0.9	134.5	0.27
<i>Types of species attacked</i>				
<i>J. ornatus</i>	1	0		
Shelter competitor ^a	19	10		
Piscivores ^b	4	4		
Egg predator ^c	1	1		
Scale eater ^d	13	7		
Other species	5	2		

Also depicted are the total number of attacks against six types of intruders

^a*Neolamprologus pulcher* and *Telmatochromis temporalis*

^b*Lamprologus callipterus* and *L. tetracanthus*: mainly young; *Lamprologus lemairii* and *Lepidiolamprologus*: young, subordinates and breeders

^c*Telmatochromis vittatus*

^d*Perrisodus microlepis*

similar breeding habitat), egg predators and piscivores (of both young and adults, Table 2).

We observed a limited number of social behaviours between group members. Small group members performed two types of submissive behaviours (zigzag swimming and tail quivering) towards larger group members. As well group members engaged in soft touches on the body which occurred more often when a breeder returned to the breeding shelter, e.g. between the returning breeder and the present breeder or between the returning breeder and the subordinate(s). Breeders were also observed on five occasions (in four different groups) to chase back to the breeding shelter a larger subordinate who had wandered far away (>50 cm). Breeders also bit these large subordinates (45.5, 49, 50, 54 and 59.5 mm SL) who responded with submissive behaviours (see above).

Reproductive success

The average number of emerging young, ‘broods’, was 2.82 offspring (0.35 SE, $n = 34$), but the

modal brood size was one young only (median = 2, Fig. 4). Productivity was highly skewed to the left, with an average of 0.98 offspring produced per week (0.24 SE, $n = 20$ groups, median = 0.55, range = 0.00–3.11 offspring/week). A multiple regression with stepwise deletion of non-significant terms revealed only an almost significant effect of male SL on productivity ($R^2 = 0.19$, estimates \pm SE: intercept = -6.56 ± 3.73 , male SL = 0.12 ± 0.057 , $P = 0.058$), whereas group size, SL of the female and SL of the largest subordinate did not affect productivity ($P = 0.74, 0.84$ and 0.25 respectively).

Cooperative breeding in Lake Tanganyika cichlids

We identified 19 cichlid species showing evidence of cooperative breeding, entirely confined to the Lamprologini tribe (24% of 80 species in total): 2 *Chalinochromis*, 5 *Julidochromis*, and 12 *Neolamprologus* species (see Appendix). Two species show evidence for cooperative breeding behaviour in aquarium observations (*N. buescheri* and

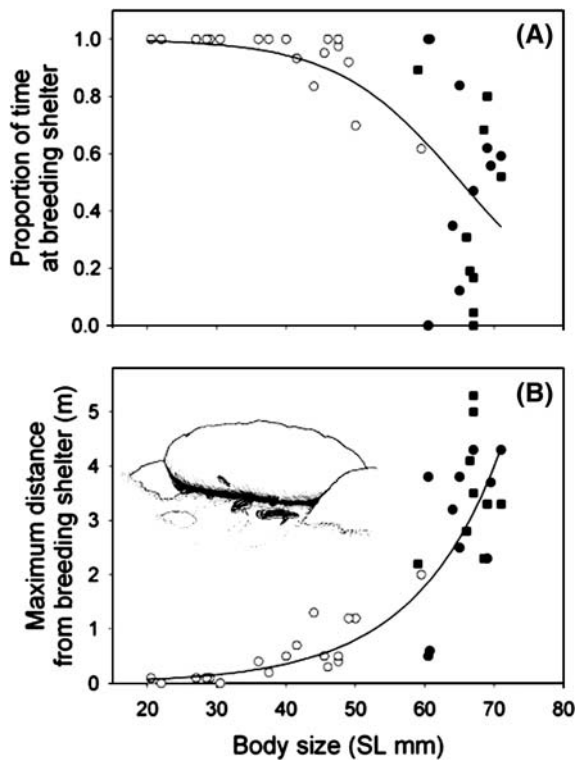


Fig. 3 (A) Proportion of time spent within 50 cm of the breeding shelter, and (B) maximum distance travelled from the breeding shelter for subordinates (white dots), breeder females (black dots) and breeder males (black squares) depended on standard length. Also depicted are (A) the logistic regression equation with coefficients \pm SE: $\text{proportion} = 1/(1 + \exp^{(-7.308 \pm 2.320 + 0.112 \pm 0.036 \times \text{SL})})$, $R^2 = 0.51$; and (B) regression equation: $\ln[\text{distance} + 0.1] = -3.62 \pm 0.27 + 0.071 \pm 0.005 \times \text{SL}$, $R^2 = 0.86$. Inset shows typical breeding shelter with adult, subordinate and offspring

N. crassus: Büscher & Heg, personal observations), including subordinates visiting breeding shelters and showing submissive behaviours to dominants (e.g. tail-quivering), which would raise the number of cooperatively breeding species to 21. Additional field observations on these two species and *N. nigriventris* are needed. The latter species shows prolonged parental care and offspring retention in the home territory, and might prove to be a cooperative breeder in at least some populations after more detailed field studies (Büscher, personal observations). Additional to these, more information is needed on the breeding biology of *Lamprologus finalimus*, *L. stappersi*,

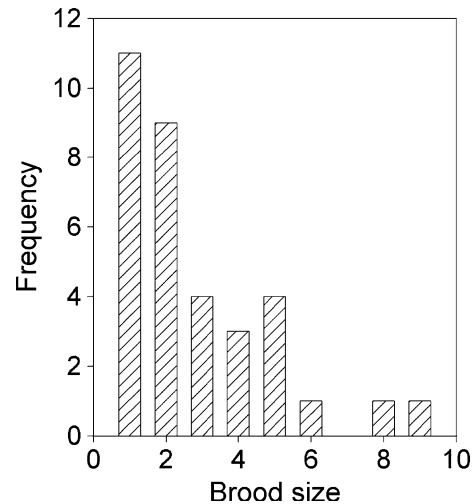


Fig. 4 Brood sizes (number of offspring emerging, $n = 34$ broods of 20 groups) in *J. ornatus*

N. longicaudatus, and *Telmatochromis brachygnathus*.

Preliminary tracing of the incidence of cooperative breeding onto the molecular phylogeny suggests at least three separate origins of cooperative breeding in Lamprologines, once in *Chalinochromis*, once in the *N. brichardi*-complex and once in *Julidochromis* spp. (Fig. 5). A fourth lineage might consist of the two closely related cooperatively breeding dwarf cichlids, *N. multifasciatus* and *N. similis*, but their placement in the molecular phylogeny is still unresolved and we have tentatively placed these species close to the other snail-breeding Lamprologines (see 1 in Fig. 5), as suggested by the morphologically based phylogeny (Stiassny 1997). Finally, the *N. brichardi*-complex contains cooperatively breeding species ('*helianthus*' and '*olivaceous*'-clades in Salzburger et al. 2002) interspersed with non-cooperatively breeding cichlids (see Salzburger et al. 2002), suggesting either multiple origins, or secondary loss of cooperative breeding. Therefore, it is at present not possible to estimate the maximum number of separate origins of cooperative breeding in these cichlids. We await the completion of the Lamprologine phylogeny (S. Koblmüller and C. Sturmbauer, in preparation) to solve these points.

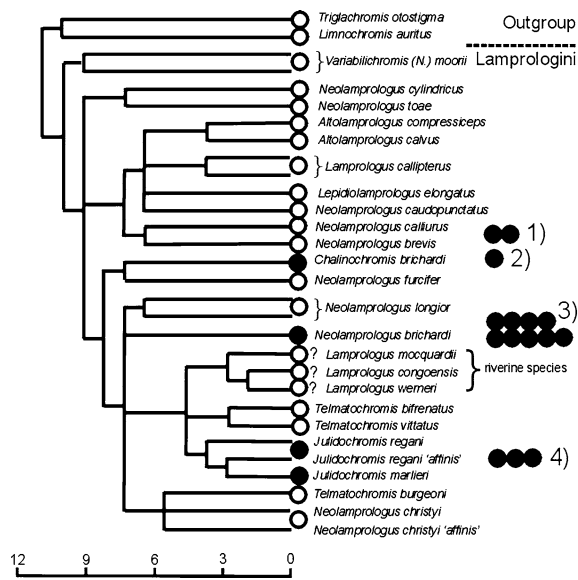


Fig. 5 Preliminary phylogenetic mapping of the incidence of cooperative breeding in the Lamprologini cichlid tribe (phylogeny modified after Sturmbauer et al. 1994: Figure 4 strict consensus tree). Black circles: cooperative breeding (see Appendix), white circles: non-cooperative breeding. The 15 cooperative species missing from the phylogeny are placed on the right to their nearest relatives (see text): (1) snail-shell breeding dwarf cichlids *Neolamprologus multifasciatus* and *N. similis*; (2) *Chalinochromis popelini*; (3) *N. brichardi*-complex (see Salzburger et al. 2002), (4) *Julidochromis* spp.

Discussion

Cooperative breeding in *Julidochromis ornatus*

Since subordinate *J. ornatus* showed all the behaviours that breeders showed to ensure reproductive success, i.e. digging, territory defence (against piscivores and egg predators), and spent a considerably amount of time guarding the breeding shelter, we conclude our operational classification of these fish as ‘helpers’ is justified (see also Awata et al. 2005). We did not find evidence that helpers increased the reproductive success of the breeders. Two papers have found correlative evidence that *J. ornatus* helpers may increase the reproductive success of breeders. First, Awata et al. (2005) reported more offspring in groups with helpers compared to groups without helpers, although the difference was just not significant. Second, a recent study showed a

positive correlation between helper size and group reproductive success, controlling for confounding factors, suggesting that at least breeders with large helpers may benefit from the helper’s presence (Awata et al. 2006). Helper removal experiments are currently analysed to solve these points (Heg and Bachar, in preparation). The social behaviours shown were similar to *N. pulcher* (Taborsky 1984, 1985) and *N. savoryi* (Heg et al. 2005), except that *J. ornatus* breeders showed apparent ‘policing behaviour’: chasing large helpers back to the shelter when helpers wandered too far of from the shelter. We do not know why breeders show this behaviour, but it might relate to the breeders ‘needing’ the helpers to protect the offspring against predators when the breeders are on foraging trips. Ranging behaviour and helping behaviours in *J. ornatus* were very similar to *J. marlieri* (Yamagishi and Kohda 1996): in this species helpers stayed 98% of their time at the shelter, whereas breeders were only present 40% of the time.

Cooperative breeding groups in *J. ornatus* show several similarities and dissimilarities with other cooperatively breeding Lake Tanganyika cichlids, the major points are discussed in Heg et al. (2005). We will only highlight some striking results. First, *J. ornatus* breeding sites were at best intermittently occupied, whereby helpers joined new breeders, probably from the nearby pool of independents. This may explain the low relatedness between helpers and breeders reported for this species (Awata et al. 2005). No such group formation has been observed in *N. pulcher* (Taborsky and Limberger 1981; Balshine-Earn et al. 1998, 2001), although helper migration between groups does sometimes occur (Stiver et al. 2004; Dierkes et al. 2005). Genetic relatedness analyses suggest that both in *N. pulcher* (Dierkes et al. 2005) and *N. multifasciatus* (Kohler 1998) offspring remain at home for a prolonged time. Disappearing breeders may be replaced by the largest helpers in the group (Dierkes et al. 2005), or maybe by nearby large helpers and breeders leaving their territory. This seems not to be the case in *J. ornatus*, although it remains possible that limited dispersal of independents from their natal breeding site causes genetic population substructuring, such that helpers joining breeders are

actually assisting close relatives (Awata et al. 2005 show that 14% of the helpers are related to either the male or female breeder).

Second, male body length correlated with group size and the size of the largest helper in the group, as it does in *N. pulcher* (Balshine et al. 2001), *N. multifasciatus* (Kohler 1998) and *N. savoryi* (Heg et al. 2005). On average, body length increased with group size and rank, which might be typical for most group living fish (e.g. also found in anemone fish Buston 2003; Mitchell 2003). This means that in all four cooperatively breeding cichlid species studied so far, large breeders defend territories with a large number of helpers, which tend to be large themselves as well. Such size-hierarchies may be maintained by status-dependent and strategic adjustments in growth (Heg et al. 2004b).

Cooperative breeding in Lake Tanganyika cichlids

We identified 19–21 species showing evidence of cooperative breeding in substrate breeding Lake Tanganyika cichlids (Lamprologini), whereas cooperative breeding was completely absent in all other substrate- and all mouth-breeding lineages in Lake Tanganyika (e.g. Haplochromini, Ectodini, Tropheini). We would like to stress that this listing should not be taken as the final verdict on the incidence of cooperative breeding in these cichlids, but should rather be taken as a starting point for more in-depth studies in the less well-known cichlids. However, we do have two notes of comfort. First, all three species we have studied both intensively in the laboratory and in the field show essentially similar types of group living and helping behaviour in both situations. This suggests that laboratory studies may be as worthwhile as field studies to establish whether subordinates are accepted in the breeder's territory and if yes, whether they are allowed to assist the breeders in raising offspring. Second, all cooperatively breeding Lamprologines show remarkable similarities in the types of helping and social behaviours performed, which should make detection of these target behaviours in the laboratory and field easy.

Stable, long-term territories, often accompanied by extended parental care, may be respon-

sible for the high incidence of cooperative breeding in the Lamprologines, since these characters are often associated with substrate breeding in cichlids (e.g. Kawanabe et al. 1997) and have been hypothesised to be prerequisites, 'pre-stages', for the evolution towards cooperative breeding (e.g. Choe and Crespi 1997; Emlen 1997). We propose all these 'pre-stages' can be found in Lamprologine cichlids, which are currently not showing cooperative breeding. First, several species show extended parental care, but parents and offspring abandon the territory after offspring independence (e.g. *Lepidiolamprologus* spp., Kawanabe et al. 1997). Second, some species show extended parental care and have long-term territories, but the offspring leave or are chased from the territory after independence (e.g. *Variabilichromis moorii*, Kawanabe et al. 1997). Third, in *Neolamprologus meeli* (Poll) some adult offspring are philopatric (i.e. live inside/partly inside the territory of their parents) and interact with the parents, but do not assist the breeders in raising offspring (Sunobe and Munehara 2003).

Alternatively, our data and Awata et al. (2005) results on *J. ornatus* suggests there may be an alternative route towards cooperative breeding, wherein large subordinates are not retained offspring, but are unrelated individuals joining a breeding pair. Clearly, more field data on the other (supposedly) cooperatively breeding cichlids are needed (e.g. genetic relatedness between helpers and breeders, mode of group formation) to assess the likelihood and incidence of these two routes towards cooperative breeding (by reconstructing the timing of character evolution on a phylogenetic tree of the Lamprologines; see for example Goodwin et al. 1998).

Many of the American and Asian cichlid species and at least some of the riverine African cichlids share the above mentioned characters of Lamprologines (substrate breeding, territorial, extended parental care, see Goodwin et al. 1998; Barlow 2000). Therefore, one could expect that some of these species or at least populations might have developed cooperative breeding systems as well. However, no such evidence exists today, although other types of breeding systems have been described (e.g. Martin and Taborsky 1997). Of course, this might be due to a lack of field data on the

breeding systems of many cichlids, in which case we suggest more effort should be directed in studying the breeding systems of the less well known cichlids. Alternatively, some ecological factor(s) specific to Lake Tanganyika may be responsible for this high incidence of cooperative breeding in Lamprologines. In any case, we regard the cooperatively breeding cichlids as a prime model system to test theories about how cooperation may have evolved and may be currently maintained.

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Appendix

Evidence for cooperative breeding in Lake Tanganyika cichlids

Species	CB	GL	M	S	References and comments ^a
<i>Chalinochromis</i>					
<i>Ch. brichardi</i> (Poll 1974)	Yes	Yes	Yes	R	M. Kohda (personal communication); Brichard (1999): offspring stay,
<i>Ch. popelini</i> (Brichard 1989)	Yes	Yes	Yes	R	Brichard (1999): offspring stay
<i>Julidochromis</i>					
<i>J. dickfeldi</i> (Staeck 1975)	Yes	Yes	No?	R	Brichard (1999): offspring stay
<i>J. marlieri</i> (Poll 1956)	Yes	Yes	Yes	R	Kalas (1976), Yamagishi (1988), Yamagishi and Kohda (1996), Sunobe (2000)
<i>J. ornatus</i> (Boulenger 1898)	Yes	Yes	Yes	R	This study, Kalas (1976), Hattori (1993), Awata et al. (2005)
<i>J. regani</i> (Poll 1942)	Yes	Yes	Yes?	R	Kalas (1976) , Kuwamura (1997)
<i>J. transcriptus</i> (Matthes 1958)	Yes	Yes	Yes?	R	Kuwamura (1997)
<i>Neolamprologus</i> ^{b†}					
<i>N. brevis</i> (Boulenger 1899)	No	Yes	Yes	O	Sato and Gashagaza (1997); M. Aibara (2003 personal communication) individually marked fish suggest high turn-over rate of territorial males and satellite males, no stable groups (Wonzye Point, Zambia)
<i>N. brichardi</i> ^c (Poll 1974)	Yes	Yes	Yes	R	See references in Introduction
<i>N. buescheri</i> (Staeck 1983)	Yes?	Yes	Yes	R	Bü scher (1992d and personal communication). H.H. Bü scher and D. Heg, aquarium observations: adult offspring stay in and close to breeding shelter and show submissive behaviours to adult breeders
<i>N. calliurus</i> (Boulenger 1906)	No	No	Yes	O	Sato and Gashagaza (1997); M. Aibara (2003 personal communication): variant of <i>brevis</i> at sand-rock margins, shows ordinary polygyny (Wonzye Point, Zambia)
<i>N. crassus</i> (Brichard 1989)	Yes?	Yes	Yes	R	H.H. Bü scher (personal communication). H.H. Bü scher and D. Heg, aquarium observations: adult offspring stay in and close to breeding shelter and show submissive behaviours to adult breeders
<i>N. falcicula</i> (Brichard 1989)	Yes	Yes	Yes	R	M. Taborsky (personal communication): mixed colonies with <i>N. pulcher</i> (Tanzania); Brichard (1999): lives in pairs or very small groups, usually close to <i>N. brichardi</i> (Burundi)

Species	CB	GL	M	S	References and comments ^a
<u><i>N. gracilis</i></u> (Brichard 1989)	Yes	Yes	Yes	R	Woodland (2002), H.H. Büscher (personal communication)
<u><i>N. helianthus</i></u> (Büscher 1997)	Yes	Yes	Yes	R	H.H. Büscher (personal communication)
<u><i>N. marunguensis</i></u> (Büscher 1989)	Yes	Yes	Yes	R	H.H. Büscher (personal communication)
<i>N. multifasciatus</i> (Boulenger (1906)	Yes	Yes	Yes	F	Rossiter (1993), Kohler (1998), Schradin and Lamprecht (2000, 2002)
<i>N. niger</i> (Poll 1956)	Yes	Yes	Yes	R	Konings (1998): young of previous broods are tolerated in shelter (aquarium observations only); Brichard (1999): co-dominant with <i>N. savoryi</i> in main habitat
<i>N. nigriventris</i> (Büscher 1992b)	No?	Yes	Yes	R	Büscher (1992b and personal communication): more field studies needed, offspring stay
<i>N. obscurus</i> (Poll 1978)	No?	Yes	No	R	Brichard (1999): offspring stay, but juveniles are expelled from natal territory and defend communal shelter
<u><i>N. olivaceous</i></u> (Brichard 1989)	Yes	Yes	Yes	R	H.H. Büscher (personal communication)
<u><i>N. pulcher</i></u> ^c (Trewavas & Poll 1952)	Yes	Yes	Yes	R	See references in Introduction
<u><i>N. savoryi</i></u> (Poll 1949)	Yes	Yes	Yes	R	Kondo (1986), Heg et al. (2005)
<i>N. similis</i> (Büscher 1992a)	Yes	Yes	Yes	F	Barlow (2000): dwarf snail-cichlid, cooperative breeder like <i>N. multifasciatus</i> ; H.H. Büscher (1992a and personal communication)
<i>N. splendens</i> (Brichard 1989)	Yes	Yes	Yes	R	H.H. Büscher (personal communication)
<i>Telmatochromis</i> [*]					
<i>T. dhonti</i>	No?	Yes	Yes	F	Sato and Gashagaza (1997): polygyny, probably no cooperative breeding
<i>T. temporalis</i>	No	Yes	Yes	F	Katoh et al. (2005): occasional polyandry with satellite males
<i>T. vittatus</i>	No	Yes	Yes	F	Ota and Kohda (2006): various breeding systems, including satellite and sneaker males, no evidence for long-term stable group formation, offspring retention or helpers

Only Lamprologine species were identified as potential cooperative breeders. Cooperative breeding was suspected in all species listed based on the main sources, which also excluded the species where extensive work has shown no evidence of cooperative breeding. Underlined are the species from the 'brichardi'-complex ('helianthus & olivaceous-clades' from Salzburger et al. 2002). Definition of terms: CB 'Cooperative breeding': positive evidence that subordinates assist breeders raising a brood (e.g. territory defence, shelter maintenance and/or direct brood care), may include subordinates engaging in reproduction (e.g. Kohler 1998; Dierkes et al. 1999; Awata et al. 2005). GL 'Group living': lives in closely packed groups or colonies, indicative of cooperative breeding, but where group living might also be due to the presence of satellite males, polygyny, polyandry and/or polygynandry. M 'Multi-male or multi-female groups': lives in polygynous, polyandrous and/or polygynandrous groups, i.e. more than two breeders are (probably) engaged in reproduction. S 'Spawning inside snail': 'O' = obligate, 'F' = facultative, 'R' = rare or absent

^aMain sources: Büscher (1989–1998), Staeck and Linke (1981), Taborsky and Limberger (1981), Taborsky (1994), Brichard (1997, 1999), Kawanabe et al. (1997), Kuwamura (1997), Sato and Gashagaza (1997), Konings (1998). Comments: 'offspring stay' = offspring of successive broods stay in the natal territory

^bInsufficient information is available on (in brackets name giver(s)): *N. finalimus* (Nichols & La Monte 1931), *N. stappersi* (Pellegrin 1927), *N. longicaudatus* (Nakaya & Gashagaza 1995), and *T. brachygnathus* (Hanssens & Snoeks 2003)

^cProbably sub-species or sister-species, see Grantner and Taborsky (1998)

^{*}Note that the genus *Neolamprologus* and *Lamprologus* are under continuing revision and some species have been formerly grouped under the latter name. *Lamprologus meleagris* vs. *L. stappersi* are treated as separate species by www.fishbase.org, but are more likely synonyms. The same applies to *Telmatochromis burgeoni* vs. *T. temporalis*

[†]Grouped under non-cooperative breeders, but more information needed on (in brackets name giver(s)): *N. longior* (Staeck 1980) and *N. wauthioni* (Poll 1949).

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