



Investment of group members is contingent on helper number and the presence of young in a cooperative breeder

Dario Josi^{*}, Michael Taborsky, Joachim G. Frommen

Division of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

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In cooperatively breeding societies dominant breeders are assisted by other individuals in raising their young. In many of these species helping behaviours and their benefits for breeders have been studied by investigating the helpers' contribution to direct offspring care, even though a significant proportion of help is not targeted specifically to offspring. Here, we investigated how breeders and helpers share the effort in shelter maintenance and how their investment is influenced by the presence of dependent young in the cooperatively breeding cichlid *Neolamprologus savoryi*. Shelters provide essential protection from predators, independently of a group's breeding status. Shelter maintenance is costly in terms of time investment and energy expenditure. In the field we manipulated the workload of groups that differed in the presence and number of helpers and the reproductive state of breeders by increasing the need for digging out the breeding shelter. Helper presence correlated with workload reduction of dominant females, even in the absence of dependent young. This emphasizes the importance of shelters for the whole group, independently of the current reproductive status of the breeding pair. The described benefits increased with the number and body size of the helpers. Additionally, breeding females and helpers visited the breeding chamber more often if young were present, and helper presence enhanced the reproductive success of breeders. These findings highlight the importance of studying the role of helpers and their benefits to breeders not only in the context of direct brood care, but also for other cooperative tasks, in order to understand the evolution of complex animal societies.

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Cooperatively breeding species, where individuals other than the dominant breeders help raise the offspring, are among the most complex social systems known (Brown, 1987; Clutton-Brock, 2016; Koenig & Dickinson, 2016; Rubenstein & Abbot, 2017; Taborsky, 1994). The evolution of the alloparental care involved in these systems is mediated by an interplay of costs and benefits for breeders and their helpers (Rubenstein & Abbot, 2017; Taborsky, Frommen, & Riehl, 2016). In many cooperatively breeding species, groups remain stable over a prolonged time and defend permanent territories year round, either because these are highly valuable breeding sites, containing, for example, necessary food resources or shelters, or because breeding occurs throughout the year (Baglione et al., 2005; Canestrari, Chiarati, Marcos, Ekman, & Baglione, 2008; Golabek, Ridley, & Radford, 2012; Taborsky, 2016).

Thus far, most studies aiming to elucidate the evolution of such cooperative breeding systems have focused on helping behaviours

that are directed towards dependent offspring, such as egg care (e.g. Josi, Taborsky, & Frommen, 2019a; Riehl, 2011) and food provisioning (e.g. insects: Choe & Crespi, 1997; spiders: Lubin & Bilde, 2007; birds: Koenig & Dickinson, 2016; fishes: Tanaka, Frommen, & Kohda, 2018; mammals: Jennions & Macdonald, 1994). However, especially in long-lasting groups, cooperative behaviours that are not directed towards the offspring can have similarly important fitness effects. These include maintaining a shared nest or burrow (Clutton-Brock, Russell, & Sharpe, 2004; Tanaka, Frommen, & Kohda, 2018) or defending the territory against conspecific and heterospecific competitors and predators (Golabek et al., 2012; Taborsky, 2016).

Subordinate helpers can benefit breeders in two ways, either by reducing the workload of breeders (load-lightening effects) or by increasing the overall investment and the resulting reproductive output (additive effects; Crick, 1992; Hatchwell, 1999; Johnstone, 2011; Tanaka, Frommen, Engqvist, & Kohda, 2018; Zöttl, Fischer, & Taborsky, 2013). Helpers in turn can gain either indirect fitness benefits by caring for related young, or direct fitness benefits such as enhanced protection in the group; (Taborsky, 1984; Tanaka, Frommen, Takahashi, & Kohda, 2016), participation in

^{*} Correspondence: D. Josi, Ethologische Station Hasli, Wohlenstrasse 50a, CH-3032, Hinterkappelen, Switzerland.

E-mail address: dario.josi@iee.unibe.ch (D. Josi).

reproduction (Awata, Kohda, Shibata, Hori, & Heg, 2010; Heg, Jutzeler, Mitchell, & Hamilton, 2009) or an increased chance to inherit the territory and breeding position in the future (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Field & Leadbeater, 2016; Kingma, 2017).

Nevertheless, the cooperative investment of subordinate group members also imposes costs, for instance in terms of energy investment, missed opportunities and elevated risk. Accordingly, helpers may vary extensively both within and between species in their investment, which may depend on attributes such as age, size and body condition (Arnold, Owens, & Goldizen, 2005; Barclay & Reeve, 2012; Bruintjes & Taborsky, 2011). Disentangling the costs and benefits for breeders and helpers is essential to understand the evolution of complex social structures involving philopatry, the delay of reproduction and the investment in a variety of cooperative tasks, including alloparental care (Taborsky & Wong, 2017). While the benefits of helping behaviours that are directed towards breeders' offspring (e.g. food provisioning and egg care) have frequently been studied, our knowledge of why and how subordinates benefit from contributions to territory defence and maintenance is limited. These behaviours may not only promote the reproductive effort of the breeders, but also benefit all group members.

Cooperative breeding has been described in approximately 25 fish species, belonging to the substrate-brooding cichlid tribe Lamprologini in Lake Tanganyika (Heg & Bachar, 2006; Taborsky, 1994, 2016). In contrast to many other cooperatively breeding animals, helpers of fishes usually do not provide food to the young (for an exception see Tanaka, Frommen, & Kohda, 2018), but instead assist the breeders in direct egg care (Josi et al., 2019a; Taborsky, 1984), territory defence against conspecific and heterospecific competitors and predators (Bruintjes & Taborsky, 2011; Groenewoud et al., 2016; Jungwirth, Josi, Walker, & Taborsky, 2015; Taborsky & Limberger, 1981; Tanaka, Frommen, Engqvist, & Kohda, 2018), and digging out and maintaining shelters (Taborsky, 1984; Tanaka, Frommen, & Kohda, 2018). The costs and benefits for helpers have been studied in only a few fish species, including *Neolamprologus pulcher* (Heg, Bachar, et al., 2004; Heg & Taborsky, 2010; Jungwirth & Taborsky, 2015; see Taborsky, 2016 for a review), *Julidochromis ornatus* (Awata et al., 2010; Awata, Munehara, & Kohda, 2005) and *Neolamprologus obscurus* (Tanaka, Frommen, Engqvist, et al., 2018). In these fishes, digging out shelters is one of the most important helping tasks, which is costly in both energy and time expenditure (Taborsky & Grantner, 1998). Shelters serve as breeding substrate and protection from predators for both the digging individual and other group members, including the breeder's offspring (Balshine et al., 2001; Groenewoud et al., 2016; Taborsky, 1984; Tanaka, Frommen, & Kohda, 2018). As territories are defended throughout the year and access to hideouts is essential, shelter maintenance is also an important task when there are no young present.

The highly social cichlid *Neolamprologus savoryi* is a cooperative harem breeder endemic to Lake Tanganyika. Breeding females defend their own subterritories within a male's harem, and they are often assisted by helpers of various sizes and both sexes. Harems are socially and genetically structured, with higher relatedness within subgroups compared to members of different subgroups within the same harem (Josi et al., 2019). As in other cooperatively breeding cichlids, relatedness between breeders and helpers declines strongly with increasing helper size (Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005). Group members usually stay close to protective shelters, which they typically dig out themselves (Garvy et al., 2015; Heg, Bachar, & Taborsky, 2005). Small and medium-sized helpers also use the breeding chamber for shelter, whereas larger helpers often maintain an individual shelter within the

female's territory but visit the breeding chamber regularly. Like most Tanganyika cichlids, these fish show no distinct breeding seasons, but breeders produce clutches throughout the year. Therefore, groups with and without current offspring may occur next to each other. Helpers engage in alloparental egg care (Josi et al., 2019a), and in maintenance and defence of the territories (Garvy et al., 2015; Heg et al., 2005). To what extent helpers engage in these helping tasks, how they adjust their help to the need of dependent offspring and the degree to which female breeders benefit from the investment of helpers remain elusive.

Here, we investigated the function of a costly cooperative behaviour in the field using an experimental approach. We manipulated the workload of group members by experimentally inducing digging behaviour. We hypothesized that (1) digging serves the offspring of dominant breeders and predicted that the helpers' investment should be increased in the presence of dependent young. We also hypothesized that (2) the breeders benefit from helpers by either additive or load-lightening effects, and (3) the costly task of digging is shared unequally among group members. Finally, we predicted that the relative workload of group members would be contingent on body size.

METHODS

Study Site and Colony Structure

Data were collected at the southern tip of Lake Tanganyika, close to the village of Kasakalawe, Republic of Zambia, between September and November 2016 and 2017. The study site is a sandy area with rocks 10–40 cm in diameter at a depth of 9.5–11.5 m. Here, *N. savoryi* defends shelters under rocks (Heg et al., 2005). The main focal colony was separated from neighbouring colonies by at least 50 m.

All data were collected by SCUBA diving. Across the main focal colony, we established a grid measuring 10 × 10 m, subdivided into 1 m² cells to easily assess and map the position of all territories. The complete grid was video recorded to create a topographic map of the stone composition using Adobe illustrator CS2. The map was printed on waterproof paper. We identified all individuals based on their size and spatial distribution. Comparable to other cooperatively breeding fishes (Awata et al., 2010; Taborsky & Limberger, 1981; Tanaka, Kohda, & Frommen, 2018), individuals larger than 1.5 cm start showing helping behaviour such as territory maintenance and defence outside the shelter (Heg, Bachar, Brouwer, & Taborsky, 2004). Individuals smaller than 1.5 cm rarely leave the shelter, but might take on egg-cleaning duties, comparable to other cooperatively breeding cichlids (Taborsky, 1984). However, at this size they depend strongly on the protection and effort of larger individuals. Therefore, fish smaller than 1.5 cm were considered as dependent young, while larger individuals were considered as helpers. The home range of every individual larger than 1.5 cm was monitored for 20 min and its borders were drawn on the map (see Fig. 1 for an example). Individuals were distinguished from each other by their body size, home range and unique patterns on the head and/or body sides. Based on these observations and the interactions of individuals we marked all male and female territories with numbered stones. Group compositions were assessed based on social interactions such as submission and tolerance in the breeding chamber. In total, we found 22 male territories containing 59 breeder females and their groups in the main focal colony.

Experimental Manipulation

We recorded the behaviour of all females that could clearly be assigned to a breeding shelter ($N_{\text{total}} = 33$). To increase sample

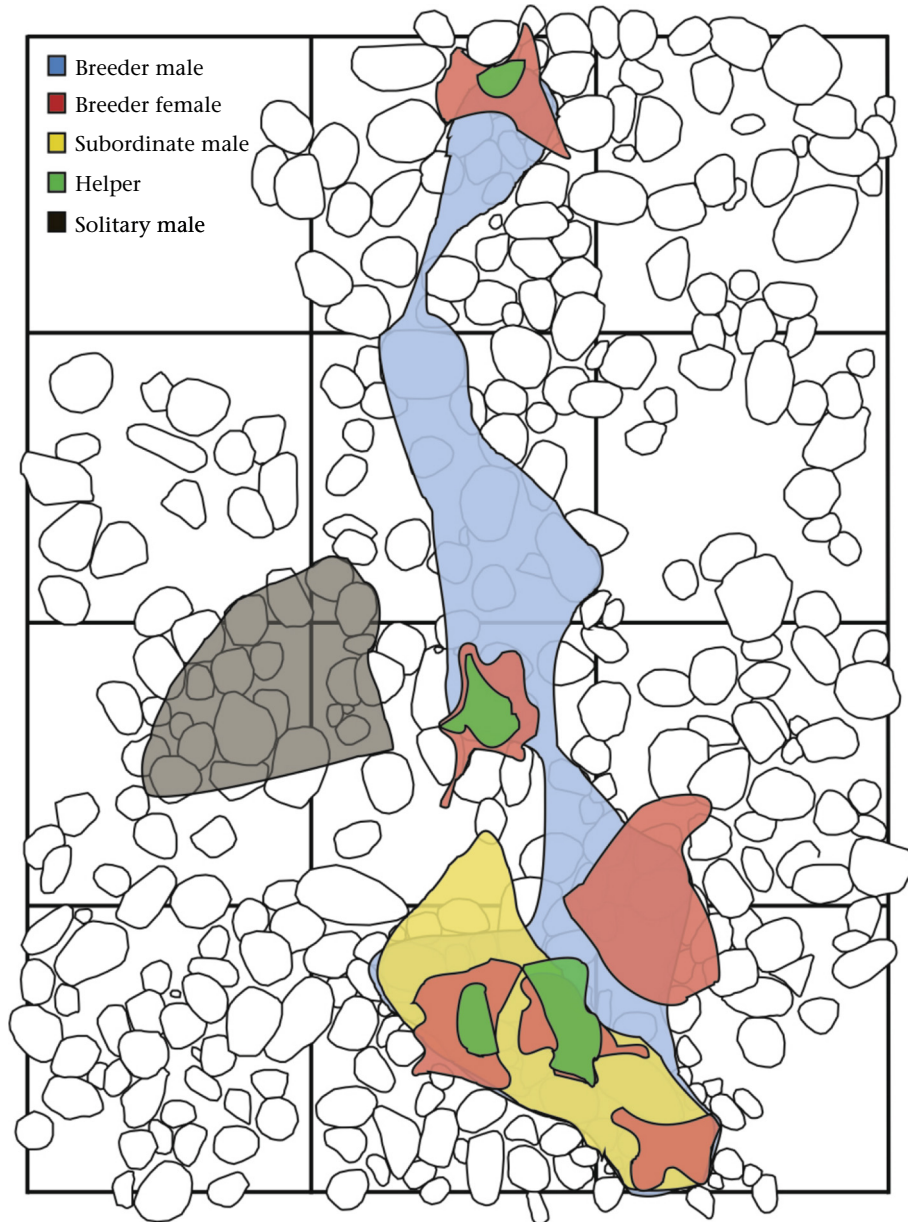


Figure 1. Home range distribution of a typical group of *N. savoryi* in the study colony. Depicted are the contours of stones and the home ranges of the breeder male (blue), his females (red) and helpers (green). Some breeder males tolerate large subordinate males (yellow) in their territories, which are also allowed to visit the other breeder females. Solitary males (grey) defend their own, nonoverlapping territory. The grid represents 1×1 m squares.

sizes, we additionally observed 18 females (from 11 additional male territories) in a neighbouring colony with comparable group structure (D. Josi, personal observation), giving a total of 51 observed females. Group compositions were assessed the same way in both colonies, except that we did not create a detailed map for the neighbouring colony. From these 51 females, 34 (67%) accepted at least one helper-sized individual in the territory, and 16 of these groups (47%) had dependent young. Seven of the 17 females without helpers (41%) had dependent young as well. To confirm the sex and to measure body size, all individuals were caught using fence nets. For individuals included in the experiment, this happened at least 12 days before its start (median = 23 days), or when the experiments were finished. Standard length (SL) was measured in situ from the tip of the snout to the posterior end of the vertebral column, accurate to a millimetre, using a measuring

board. Afterwards, all individuals were released back to their shelter, where they recovered within a few minutes.

At the beginning of each experiment, the observer remained motionless in front of the respective female territory for at least 5 min to acclimatize the fish to his presence (Groenewoud et al., 2016). Fish usually left their shelter and moved freely within the first 2 min. Prior to the sand manipulation, the number of digging behaviours as well as the number of entries into the breeding chamber were monitored for all individuals for 15 min. Digging behaviour was defined as the uptake of sand, debris, small stones, or snail and mussel shells with the mouth underneath rocks, which were then transported outside the shelter area (Taborsky, 1984; Tanaka, Kohda, et al., 2018). After these 15 min baseline observations we filled a 100 ml plastic syringe with 30 ml of fine sand taken from the lake bottom at least 1 m from the respective territory. The

sand was slowly injected into the breeding chamber. In pilot studies, this amount proved to be enough to induce digging behaviour, while at the same time never filling up the breeding shelter by more than ca. 20%; this kept it functional as a protective hiding place from predators. Afterwards, we measured the time until the first individual started digging out the sand. In one trial digging did not occur within 30 min, so the trial was terminated. In all other trials, we took the same measures as described for the baseline measure from the first digging onwards for 15 min and noted whether digging was initiated by the breeding female, breeding male or helper. The presence of young was recorded and checked during the mapping of the colony, as well as at the end of each experimental trial and 6–8 days after the experiments.

Ethical Note

Data collection caused minimal disturbance to the animals and followed the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching, and the regulations of the 'Zambian prevention of cruelty to animals' act.

Statistical Analyses

All statistical analyses were conducted using R 3.1.1 (R Core Team, 2014). We fitted linear models (LM), generalized linear models (GLM) and generalized linear mixed models (GLMMs) using the packages 'lme4' (Bates, Maechler, & Bolker, 2013, pp. 1–7) and 'glmmADMB' (Fournier et al., 2012). LMs were checked for deviation from normality, and GLMMs were checked for overdispersion and zero-inflation (Fournier et al., 2012). We removed nonsignificant interactions from the models and only report significant interaction terms (Engqvist, 2005).

Group structure

First, we analysed whether there was a relationship between female body size and group size. We fitted a GLM with quasi-Poisson error distribution using the number of helpers per female as the response variable and female body size as a predictor. To test whether the number of helpers influenced the reproductive success of female breeders, independently of female quality, we fitted a binomial GLM with presence or absence of young as the response variable and number of helpers as well as female body size as predictors. We also analysed whether larger females had larger helpers. When a female had more than one helper, we selected the largest one and regressed helper body size on female body size using an LM.

Visits to breeding chamber as a measure of brood care

We used entries to the breeding chamber that were not followed by digging behaviour as a proxy for brood care (Balshine-Earn et al., 1998; Balshine et al., 2001; Stiver, Dierkes, Taborsky, Gibbs, & Balshine, 2005; Tanaka, Frommen, Engqvist, et al., 2018). For this purpose, we subtracted the number of entries followed by digging from the total number of times a fish entered the breeding chamber in 15 min. To test whether differences in entries to the breeding chamber depended on the number of helpers and the presence of young, we fitted two GLMMs with a negative binomial error distribution, one for the dominant females and one for the helpers. Both models included the number of breeding chamber entries as the response variable, and the presence of young, manipulation (before, after), and the number and SL of either breeder females or helpers as predictors. Territory identity was fitted as a random effect to account for repeated measurements of the same group. Models for helpers were additionally corrected for zero-inflation.

Digging

We analysed differences in the number of digging events in 15 min before and after the manipulation using a GLMM with a negative binomial error distribution correcting for zero-inflation. The number of digging events was set as a response variable and manipulation (before, after) was fitted as a predictor. We included class (breeder or helper) and territory identity as random effects to account for repeated observations of the same group. Of 33 breeder males, only five showed any digging, and these dug at a low frequency (median = 2, range 1–23). Therefore, breeder males were excluded from further analysis. Prior to manipulation digging occurred at a low rate, probably because sand had been removed from the shelters according to need before our observations. Therefore, all further analysis focused on the data after the experimental manipulation. We analysed whether digging was initiated earlier in the presence of dependent young and of helpers. By applying Grubb's (1969) outlier test we identified two significant outliers that were removed from the data. We then fitted an LM with time until the first digging event shown by any individual as the response variable, and the presence of young as well as the number of helpers as predictors. We also tested whether the female's workload was related to the number of helpers, the presence of dependent young and her SL. We fitted a GLM assuming a negative binomial error distribution using digging frequency of dominant females as the response variable and the presence of dependent young, the number of helpers and the female's body size as predictors. To test whether the effect of helper number on workload changed with the presence of young we included an interaction between these factors. The workload of helpers was analysed in the same way. As we measured the behaviour of all helpers of a given territory, we included territory identity as random effect to account for repeated measurements of the same group. Finally, we analysed whether the overall digging investment per territory was related to the occurrence of helpers to distinguish between additive and load-lightening effects. We fitted a GLM with a negative binomial error distribution and included the total number of digging events as the response variable, and presence or absence of helpers as a predictor with two levels.

RESULTS

Group Structure

The breeding system of the main focal colony ranged from monogamous pairs to polygynous territories, in which dominant males defended one to six female groups (see Fig. 1). Each dominant female defended her own subterritory containing up to four helpers (median = 1; see Fig. 1). Helpers were allowed to enter the breeding shelter of the respective dominant female and engaged in direct egg care (Josi et al., 2019a), shelter maintenance and defence against conspecific and heterospecific intruders. In addition, we found one male association consisting of a dominant male and a large subordinate male without any breeding females or helpers. Such large subordinate males were also tolerated in monogamous or polygynous breeding clusters and were usually slightly larger than the dominant female, but smaller than the breeder male (Josi, Taborsky, & Frommen, 2019b). These subordinate males either defended their own home range within the breeder male's territory or they visited the different females of the respective dominant male (see Fig. 1). Occasionally, solitary males without overlapping home ranges to any other individual were found at the study site (see Fig. 1).

Helper number was related to female size, with large females having more helpers in their territory (GLM: $N = 46$, $\beta \pm SE = 0.11 \pm 0.04$, $t = 2.695$, $P = 0.01$; Fig. 2a). The body size of

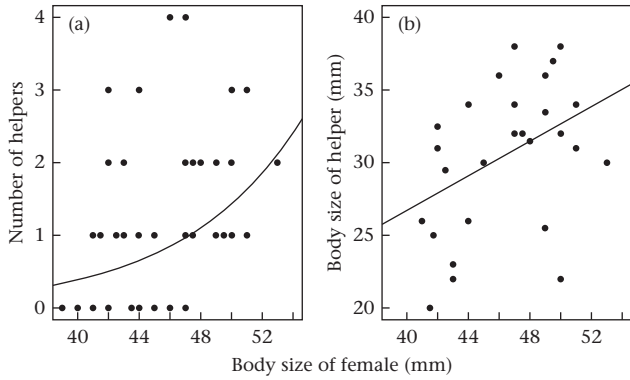


Figure 2. (a) The number of helpers in a territory and (b) the body size of the largest helper per group in relation to female body size. The solid lines indicate the model-predicted regressions. Model parameter estimates are given in the Results.

the largest helper in the group was positively associated with female body size ($F_{1,25} = 4.98, P = 0.027$; Fig. 2b). Further, the breeders' probability of having reproduced successfully was positively associated with the number of helpers, independently of female body size (GLM: $N = 46, \beta \pm SE = 0.63 \pm 0.34, \chi^2 = 3.98, P = 0.046$; Fig. 3); the effect of female body size even pointed in the opposite direction, although this effect failed to reach statistical significance ($\beta \pm SE = -0.17 \pm 0.1, \chi^2 = 3.02, P = 0.08$; median difference of female body size between groups: 1 mm).

Visits to Breeding Chamber as a Measure of Brood Care

In total, we sampled 51 female groups belonging to 33 different male harems. After the addition of sand, females mainly entered the breeding chamber for digging, as the number of entries that did not serve for digging declined significantly (Table 1). Breeder females showed more shelter-visiting behaviour in the presence of young, whereas their visit rates were independent of body size and the number of helpers (Table 1).

The number of visits of helpers to the breeding chamber was comparable before and after the manipulation (Table 1). Helpers entered the breeding chamber more often if dependent young were

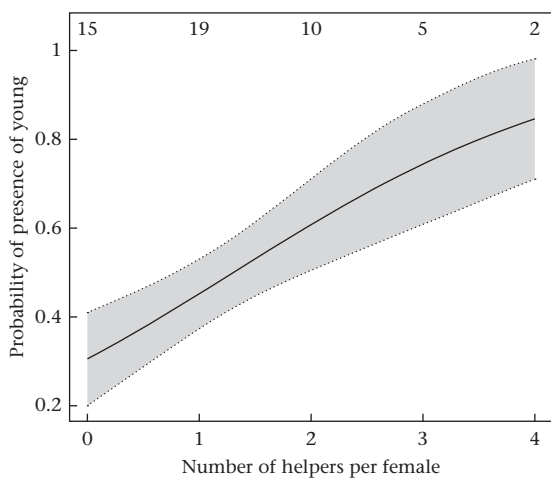


Figure 3. The likelihood of having dependent young in a territory in relation to the number of helpers. Model-predicted logistic regression line (black) and the estimated standard error range (grey) are shown for the presence of young in relation to the number of helpers per group. Sample sizes for each helper number are indicated at the top.

Table 1

Visit rates of breeding females and helpers to the breeding chamber with respect to the presence of young, the number of helpers and body size

	Estimate \pm SE	Z	P
Female entries to breeding chamber			
Intercept	1.5712 \pm 0.136		
Manipulation before	0.4022 \pm 0.114	3.53	<0.001
Presence of young	0.3287 \pm 0.168	1.96	0.049
Number of helpers	-0.0584 \pm 0.082	-0.71	0.47
Body size	-0.0257 \pm 0.026	-1.01	0.32
Helper entries to breeding chamber			
Intercept	0.9002 \pm 0.251		
Manipulation before	-0.0199 \pm 0.146	-0.14	0.89
Presence of young	0.6994 \pm 0.26	2.69	0.007
Number of helpers	-0.2627 \pm 0.126	-2.09	0.036
Body size	0.0328 \pm 0.02	1.68	0.09

Significant P values are shown in bold.

present (Table 1, Fig. 4a). Furthermore, individual helpers entered the breeding shelter less often if other helpers were present in the territory (Table 1). There was no relationship between helper body size and the number of entries to the breeding chamber (Table 1).

Digging

The digging rate after the experimental manipulation was significantly higher than the baseline observation (GLMM: $\chi^2 = 34.226, P < 0.001$). After sand was added to the breeding chamber, groups with dependent young tended to start digging earlier than groups without young ($F_{2,45} = 3.05, P = 0.088$; Fig. 4b). Digging was initiated once by a breeding male in a territory with dependent young lacking helpers. In all other cases, the breeder female initiated digging. Time to initiate digging was not significantly related to the presence of helpers ($F_{2,45} = 0.148, P = 0.7$). Breeder females dug more in the presence of young (Table 2, Fig. 5a). Furthermore, they showed lesser digging effort the more helpers were present in the group, suggesting load-lightening effects (Table 2, Fig. 5a). The latter result did not vary significantly with the presence of young (young*number of helpers: $N = 46, \chi^2 = 2.47, P = 0.12$). The total number of digging events per territory did not differ significantly between territories with or without helpers, suggesting a lack of additive effects (GLM: $N = 51, \chi^2 = 1.52, P = 0.22$). Female investment was related to their body size, with smaller females digging more than larger ones (Table 2, Fig. 5b). Helpers did not adjust their amount of digging to the

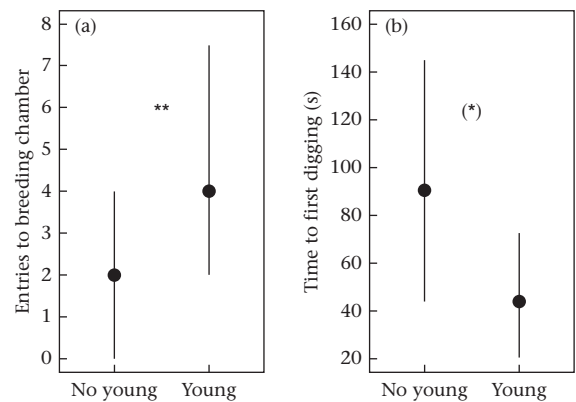


Figure 4. (a) The number of entries of helpers to the breeding shelter and (b) the time (s) elapsed until a group member (in all but one case the breeding female) initiated digging in relation to the presence of young. Dots indicate medians; vertical bars show interquartile ranges. (*) $P < 0.1$; ** $P < 0.01$.

Table 2

Digging behaviour after the experimental manipulation (addition of sand to breeding chamber) in relation to body size, the presence of young and the number of helpers

	Estimate \pm SE	Z	P
Female investment			
Intercept	2.74002 \pm 0.16		
Body size	-0.1164 \pm 0.035	-3.32	<0.001
Presence of young	1.05291 \pm 0.23	4.574	<0.001
Number of helpers	-0.2828 \pm 0.113	-2.51	0.012
Helper investment			
Intercept	-10.351 \pm 3.933		
Body size	0.365 \pm 0.126	2.89	0.004
Number of helpers	-0.178 \pm 0.703	-0.25	0.8

Variables were removed from the model if dropping them resulted in a model with a minimum difference of two Akaike information criterion values. Results are from the final models. Significant *P* values are shown in bold.

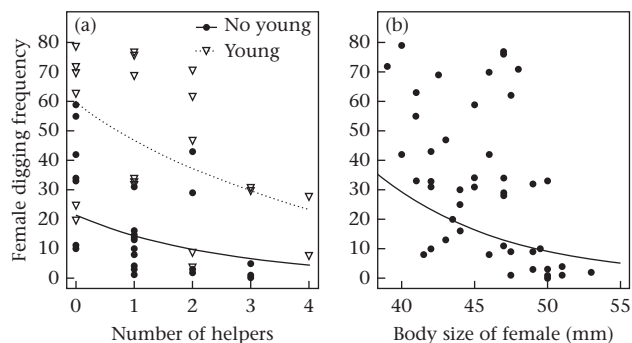


Figure 5. (a) The investment in digging (number of diggings per 15 min) by breeder females in relation to the number of helpers either with or without the presence of young. (b) Investment in digging by females in relation to their body size. The solid and dashed lines indicate the model-predicted regressions. Model parameter estimates are shown in Table 2.

presence of young or to the number of other helpers, but large helpers dug more than smaller ones (Table 2).

DISCUSSION

Studies of the behaviour of helpers and its consequences are usually confined to direct brood care, even though in many species helpers may provide important additional services to dominant breeders and their offspring (Koenig & Dickinson, 2016). For instance, they may contribute to territory defence and maintenance, which may benefit breeders even in the absence of dependent young. Investigating such behaviours is therefore important to reveal the costs and benefits of accepting helpers in general. Our results indicate that in the cooperatively breeding cichlid *N. savoryi*, breeder females exhibited increased brood care and shelter digging in the presence of young. Their reproductive success was positively related to the number of helpers (Fig. 3). When our experimental manipulation increased the need for additional digging, helper presence affected female breeder investment levels in a manner consistent with a load-lightening effect.

Large females showed less digging effort than smaller ones (Fig. 5b). This might be due to a higher digging efficiency of larger females owing to their larger buccal cavity. However, larger females also need larger breeding chambers, which may diminish such efficiency benefits. Furthermore, females benefited from helpers independently of their body size, as with increasing helper number females invested less (Fig. 5a). This reduction in investment with more helpers was independent of the presence of young, even though the latter generally caused increased investment by breeder

females. The highest workload reduction was gained by large breeder females, as they had more and larger helpers in their territories (Fig. 2a and b), which dug more (Table 2, Fig. 5b). It remains to be experimentally tested whether large females had more large helpers because they were older and had therefore defended their territory containing helpers for longer than smaller females or because they were more efficient at recruiting helpers. A field observation suggested that breeding females might actively recruit helpers prior to egg laying (Josi et al., 2019a). Also, in the congener *N. pulcher*, acceptance of helpers in the territory depends on the demand (Taborsky, 1985; Zöttl, Frommen, & Taborsky, 2013). However, in *N. savoryi* this seems to be rather rare, as helpers are more related within than between subgroups, and immigration rates are generally low (Josi et al., 2019).

Subordinate helpers can provide important contributions to the survival of young and significantly increase the reproductive success of dominant breeders (Brouwer, Heg, & Taborsky, 2005; Canestrari, Marcos, & Baglione, 2008; Tanaka, Kohda, et al., 2018). In our study species, a potential increase in reproductive success due to brood care helpers, as suggested by the positive association between helper number and the occurrence of offspring, might be caused by helpers actively joining in brood care, territory maintenance (such as digging) and defence against predators. Such an increase in the reproductive success of breeders as a result of helpers has been suggested in other cooperatively breeding cichlids (*J. ornatus*: Awata et al., 2005; *N. pulcher*: Balshine et al., 2001; *N. obscurus*: Tanaka, Kohda, et al., 2018) and confirmed experimentally (*N. pulcher*: Taborsky, 1984; Brouwer et al., 2005). These benefits can outweigh potential costs of having helpers, such as increased competition for food (Creel & Creel, 2015), shelter (Balshine et al., 2001) or reproduction (Bruintjes, Bonfils, Heg, & Taborsky, 2011; Dierkes, Taborsky, & Kohler, 1999; Hellmann et al., 2015).

While especially large helpers in our study joined the female in digging out the breeding shelter, they did not adjust the amount of digging to the presence of dependent young, indicating that digging out the shelter may be important independently of the current reproductive state of the female. Large helpers of cooperatively breeding cichlids, including *N. savoryi*, often maintain their own shelter near the breeding shelter (Josi et al., 2019a). Such individual shelters remained unmanipulated in our experiment, suggesting that digging by large helpers mainly benefited the breeder female and her offspring. Still, the digging behaviour of helpers may provide mutualistic benefits to all group members, including the digging helper as well.

Importantly, both females and helpers increased their visit rates to the breeding chamber in the presence of dependent young (Table 1, Fig. 4a), suggesting increased investment in direct brood care. After sand was added, females reduced their brood care (measured as visits to the breeding chamber without digging) and entered the shelter mainly for digging. In contrast, helpers provided brood care at the same rate as before the manipulation. Individual helpers adjusted their brood care effort to the presence of other helpers, indicating that group members share the workload among each other. Such task sharing and division of labour among group members is also known from other cooperative breeders (Arnold et al., 2005; Bruintjes & Taborsky, 2011; Clutton-Brock et al., 2004; Heinsohn & Legge, 1999; Zöttl et al., 2016).

In many cooperatively breeding fishes helpers show a broad range of body sizes (Heg, Bender, & Hamilton, 2004b; Tanaka, Kohda, et al., 2018). Differently sized helpers are expected to specialize in various helping tasks, depending on their body size (Bruintjes & Taborsky, 2011; Groenewoud et al., 2016; Taborsky & Limberger, 1981), and the contributions of each helper to a certain task can then lead to fitness benefits shared by all group

members (Johnstone & Rodrigues, 2016; Kokko, Johnstone, & Clutton-Brock, 2001; Riehl & Frederickson, 2016). Our results indicate that large helpers invested more in digging than smaller ones, which could be explained either by energetic costs being lower for large helpers, by greater digging efficiency as large helpers have larger buccal cavities to carry away sand, or because they require larger shelters as protection for themselves, and therefore invested more in maintaining the breeding chamber. These potential explanations are not mutually exclusive. This pattern conforms to experimental field data from *N. pulcher*: contrary to observational data (Groenewoud et al., 2016), large helpers showed higher digging effort than smaller ones when the requirement to dig out the breeding shelter was experimentally induced in a similar way as in our study (Bruitntjes & Taborsky, 2011). A reason for the discrepancy between observational and experimental data might be that the experimental adding of sand resembles rather rare disastrous events in nature, during which wave action or strong currents can shift large amounts of sand. Such situations do occur at the depths at which these fish occur, due to heavy storms (M. Taborsky, personal observation). On such occasions, larger helpers are probably much more efficient in restoring the shelter quickly due to their larger buccal cavity. Smaller helpers may instead take over the regular removal of smaller amounts of sand from the shelter, as they spend much more time close to the shelter than large group members (see Bruitntjes & Taborsky, 2011; Groenewoud et al., 2016; Heg & Taborsky, 2010).

In cooperatively breeding fishes observations of direct brood care in nature, such as cleaning and fanning of eggs, are difficult as such behaviours usually occur only inside the breeding chamber (Josi et al., 2019a). Therefore, visits to the breeding chamber that are not accompanied by digging behaviour have been used as a proxy for brood care in previous studies (Balshine-Earn et al., 1998; Balshine et al., 2001; Stiver et al., 2005; Tanaka, Frommen, Engqvist, et al., 2018). Nevertheless, the reliability of this measure has not yet been validated. We have shown here that visit rates increased in the presence of dependent young, suggesting a brood care function. As this was true for breeder females and helpers, we suggest this may be used as a reliable proxy for brood care in future studies.

Conclusion

Overall, breeding groups of *N. savoryi* contained few helpers, but their presence and number lessened the workload of breeder females and were positively related to their reproductive success. Helper contribution to digging was independent of the presence of young, which underlines the importance of shelters independent of a direct brood care function. To fully understand the evolution of complex animal societies, data on cooperative tasks other than direct brood care are important to fully grasp the role of helpers and the benefits they can provide to dominant breeders.

Declaration of interests

None.

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