



Helpers increase food abundance in the territory of a cooperatively breeding fish

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Received: 4 September 2017 / Revised: 21 January 2018 / Accepted: 24 January 2018 / Published online: 6 March 2018
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Abstract

In cooperatively breeding or eusocial animals, increasing resources such as food is a major task of brood care helpers or workers. While such food acquisition has been shown in several animal taxa, evidence is absent in fishes. Here, we provide the first evidence of increased food abundance caused by helpers in a cooperatively breeding fish. Helpers of the cichlid *Neolamprologus obscurus* excavate cavities by digging sand from under stones, which serve as shelter for the group members. We test whether these cavities additionally increase the abundance of benthic invertebrates in the territory. Stomach content analyses of wild-caught fish revealed that benthic invertebrates pose the main food resource of *N. obscurus*. Experimental assessments of daily benthic invertebrate immigration into artificial cavities demonstrate a significant increase in invertebrate prey abundance according to the size of the excavated stone area. Finally, by applying correlational and experimental approaches in the field, we show that helpers play a crucial role in the maintenance of the excavated cavities. In combination, these results demonstrate that helpers increase the abundance of benthic invertebrates inside the territory of breeders in *N. obscurus*. Our results provide the first evidence of increased food abundance through helpers in fishes. Such foraging system may resemble those described in other species living in highly social groups, and appears to be a ubiquitous mechanism underpinning the maintenance of complex societies in animals.

Significance statement

Evidence of elaborate food acquisition such as farming or trap building is only known from a limited number of animal taxa. The cichlid *Neolamprologus obscurus* is a highly social fish, where all group members create and maintain cavities under stones, which serve as shelters. These fish feed on benthic invertebrates, which hide inside such cavities during daytime. We show that the cavities of *N. obscurus* additionally increase the food abundance in their territory. Behavioral observation and experiment in the field revealed that group members increase the excavated cavities in their territory, and food abundance increases according to the size of excavated cavities. Our results provide the first evidence of food acquisition by group members in fishes.

Keywords Cichlid · Cooperative foraging · Group living · *Neolamprologus obscurus* · Helper effect · Helping behavior

Communicated by V. Schluessel

This article is a contribution to the Topical Collection From Sensory Perception to Behavior—Guest Editors: Theo C. M. Bakker, Horst Bleckmann, Joachim Mogdans, Vera Schlüssel

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00265-018-2450-5>) contains supplementary material, which is available to authorized users.

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Introduction

Many animals live in highly complex social systems, such as families or cooperatively breeding groups (Koenig and Dickinson 2016; Griesser et al. 2017). Members of these groups gain direct fitness benefits, for example due to increased predator protection or higher foraging efficiency (Choe and Crespi 1997; O’Riain and Faulkes 2008; Koenig et al. 2016; Taborsky 2016). Furthermore, by living in groups with relatives, they receive indirect fitness benefits when the individuals increase the reproductive success of related individuals (Brown 1987; Cockburn 1998). However, living in such complex groups is assumed to be costly, for example due to increased competition for resource (West et al. 2002). One of the factors balancing the costs and benefits of living in

complex social groups is the availability of food resources. Consequently, food availability plays an important role in shaping the structure of family groups and cooperative societies (Creel and Macdonald 1995; Whitehouse and Lubin 2005; Sorato et al. 2016).

In cooperative breeding animals, helpers often engage in acquiring food in order to provide nutrition to others. While such food acquisition by group members is found in a range of animal taxa (e.g., insects: Choe and Crespi 1997, spiders: Avilés 1997; Lubin and Bilde 2007, birds: Brown 1987; Koenig and Dickinson 2004, mammals: O’Riain and Faulkes 2008; Stiner et al. 2009), it is not described from any fish species. The cooperatively breeding cichlid *Neolamprologus obscurus* provides a unique opportunity to investigate food acquisition by group members. These fish feed on benthic invertebrates, especially shrimp (Konings 1998). Under natural conditions, these invertebrates are active during the night and move up into the water column in large swarms. Before dawn, they sink back to the ground, where they hide in crevices and under stones during the day (Yuma et al. 1998; Fryer 2006). *N. obscurus* creates cavities by excavating sand under stones (Supplementary Fig. S1). These cavities serve as hiding and breeding substrate. Individuals seldom leave these excavated areas (Tanaka et al. 2015) and are highly dependent on prey items they find in and nearby this place. Compared to non-shrimp feeding cooperative breeders, which inhabit the same habitat, the amount of sand removal is larger in *N. obscurus* (Taborsky 1984; Heg et al. 2005; Tanaka et al. 2015; Groenewoud et al. 2016), and the excavated cavities of *N. obscurus* are deeper (HT personal observation). These observations suggest that the cavities of *N. obscurus* may not only function as shelters but may also be important for gaining food resources. Breeders of *N. obscurus* accept up to ten helpers of both sexes in their territory, but usually the number of the helper is small (median and quartiles = 1, 0, 3, $N=189$, HT, unpublished data). Helpers engage in brood care such as defense against con- and heterospecific competitors and predators, including egg and fry predators (Tanaka et al. 2015, 2016). Importantly, they assist breeders in maintaining the excavated cavities by constant removal of sand and debris (Tanaka et al. 2018), indicating that helpers extend the excavated cavities of the breeders. This might not only improve the quality of the shelter as hiding or breeding habitat, but might also increase the food abundance in the territory. Such structure for acquiring food resources has thus far only been shown in a few social animals (e.g., social spiders: Avilés 1997; Whitehouse and Lubin 2005; Tizo-Pedroso and Del-Claro 2007, humans: Bar-Oz et al. 2011), and to the best of our knowledge, it has never been reported in any fish species.

Here we test the hypothesis that helpers of *N. obscurus* contribute to increase the abundance of food resources by increasing the size of the excavated cavities under natural conditions. First, we experimentally tested whether the

excavated cavities function as food trap. For this, we assessed whether benthic invertebrate abundance increases with the size of the excavated stone area by creating artificial cavities of different sizes and counting the number of invertebrates migrating into the cavities on the next day. Second, we examined the stomach contents of wild-caught fish in order to confirm the main diet of this species. Third, we examined the effect of helpers on extending the excavated cavities by analyzing the relationship between the size of the excavated stone area and the number of helpers, using 3-year field data. Finally, we conducted a helper removal experiment to experimentally verify the effect of helpers on the size of the excavated stone area.

Methods

Study site

The study was conducted in a large colony of *N. obscurus* (Tanaka et al. 2015, 2016) at the southern tip of Lake Tanganyika at Nkumbula Island near the city of Mpulungu, Zambia (8°45.2’S, 31°05.2’W). The underwater landscape of this site is a steep sandy slope with partially exposed stones, and *N. obscurus* is found at this site through depths of 5 to 13 m. Data were collected by SCUBA diving. It was not possible to record data blindly because our study involved observing focal animals in the field.

Assessment of benthic invertebrate’s abundance

It is impossible to measure the amount of shrimp inside the excavated cavities of *N. obscurus* under natural condition, as the shrimp will leave the cavities or hide deep in the sediment when disturbed. Therefore, we artificially created excavated cavities and measured the daily immigration of benthic invertebrates to assess the relationship between the size of the excavated cavities and the amount of daily benthic invertebrate immigration. We prepared three different-sized plastic boxes with a small (170 cm²), medium (315 cm²), or large (600 cm²) area size and put layers of stones from the natural habitat into these boxes in order to simulate artificial excavated cavities. The boxes could be closed with a lid in order to prevent shrimp from escaping during handling. Stones were put to the same height in each of the three boxes. Between 13:00 to 14:00 h, we placed these three boxes simultaneously into the studied population at 6–10 m depth. On the next morning between 10:00–11:00 h, we carefully covered each box with the lid, put them into separate plastic bags, and brought them up to the surface. Here, the boxes were opened and their content was poured into a plankton net. All stones were carefully washed above the plankton net to collect all benthic invertebrates that adhered to the stones. The collected invertebrates

from the respective box were put into separate bottles and preserved in 4% Formalin. After the fixation, we noted down the taxonomic group of the benthic invertebrates and counted their numbers using a stereo microscope in the laboratory. This procedure was repeated on six nights between October 13 and 30 2011.

Stomach content analysis

To investigate the stomach contents of *N. obscurus*, we caught 38 fish of various body sizes (22.4–50.4 mm standard length (SL)) between October 13 and 30 2011 at 6–10 m depth. Right after catching, we put the fish into a plastic bag and quickly sacrificed them by adding an overdose of eugenol diluted in ethanol into the bag. Afterwards, approximately 1 ml of 39% formalin was injected to the stomach of the fish to preserve all undigested food items. Then, fish were brought to the laboratory in the field station in Mpulungu. Here, we measured the body sizes of the fish to the nearest 0.05 mm, dissected the fish, and assessed the stomach contents under a stereo microscope. The stomachs of 12 individuals were empty; thus, stomach contents of 26 individuals were used in the subsequent analyses. For the analyses, we used a modified version of Hynes' points method (Hynes 1950): first, the fullness of each stomach was estimated on a five step scale ranging from 0 (empty), over 1/4, 1/2, 3/4, to 1 (full). Next, points corresponding to the fullness (0, 4, 8, 12, and 16, respectively) were assigned to the stomach of each individual. A 3/4 full stomach, for instance, would receive 12 points. Next, the stomach contents were sorted out into five food categories: shrimp, aquatic insects (i.e., mainly benthic insect larvae), mollusks, limnetic invertebrates (i.e., copepoda, ostracoda, and other plankton), and unidentified matters. We regarded shrimp, aquatic insects, and mollusks as benthic invertebrates. The relative volumes of each diet category were judged by eye and the given points were allocated to each diet category according to the relative volume of each diet categories. For instance, if a stomach that was assessed as 12 points contained the same amount of shrimp and aquatic insects, the shrimp and aquatic insects received 6 points each. During the assessment, two of the authors (HT and MK) assessed several stomach samples twice in order to confirm that our assessment was reliable. Finally, we calculated the proportion of each diet category found in the stomach by dividing the total points of each diet category from all individuals by the sum of the total points from all diet categories.

Group composition and territory size

Group composition and territory size assessment was conducted in three separate years: from September 3 to November 27, 2010, September 18 to November 29, 2012, and August 20 to

December 17, 2013. We installed 20 × 8 m (2010), 10 × 6 m (2012), or two 8 × 4 m (2013) grids at different depths of the same population using strings attached to the ground (see Tanaka et al. 2016 for detail). We subdivided the grid into 0.5 × 0.5 m (2010 and 2012) or 1 × 1 m (2013) cells using strings to easily map the territories. A topographic map including the stone composition of the study site was either drawn underwater on water resistant paper (2010), or video recorded using a Canon G15 digital camera and subsequently drawn on a personal computer using Adobe illustrator CS2 (2012 and 2013).

In each year, we first identified all individuals found inside the grid area using the natural stripe patterns on their bodies (Tanaka et al. 2015), and recorded the relationship between group members and their social rank by observing each individual for 10–15 min. We used aggressive behaviors, social behaviors, and/or submissive behaviors to assess their social ranks (see Tanaka et al. 2015 for more detail for each behavior shown by fish of different social rank). We counted all helpers in the respective territory. Fish start participating in helping activities from above 17 mm SL and were thus defined as helpers following Tanaka et al. (2016). Breeding males of *N. obscurus* usually guard the territories of several females and seldom engage in habitat maintenance. Therefore, we noted the breeding males for the respective territories, but lay no strong focus on analyzing their behavior.

In 2010, all groups found within the grid served as focal groups ($N=47$). In 2012 and 2013, we haphazardly selected focal groups ($N=37$ in 2012; $N=105$ from two grids in 2013), which sums up to a total of 189 groups from three years. To estimate the size of the excavated cavities in the territory of each breeding female, we first assessed the territory by tracing the swimming tract of the respective female. We observed breeding females of all focal groups for 30 min (in 2010), or 20 min (in 2012 and 2013). The swimming tract was directly mapped on the topographic map underwater (2010), or recorded using a Canon G15 digital camera and subsequently mapped on a personal computer using Adobe illustrator CS2 (2012 and 2013). Furthermore, we recorded the extent of the excavated stone area within each territory on water resistant paper (2010), or on a personal computer (2012 and 2013). Each excavated area consisted of several stones (typically diameter 10–30 cm, see Supplementary Fig. S1 for an example and Tanaka et al. 2015 for a detailed description). The area was regarded as part of the excavated cavity if breeders or helpers dug out sand from under stones or entered the already existing cavity. Subsequently, we calculated the size (cm²) of the excavated stone area inside the home range of each breeding female using image J (Rasband 2014) and used this measure as a proxy of excavated cavity size.

After the observations, all fish in the focal groups were caught using gillnets, hand-nets and 30% clove oil diluted in ethanol. In 2012, we measured the body size of the caught fish

underwater to the nearest 0.5 mm SL and released them back to their territory. In 2010 and 2013, the caught fish were anesthetized and euthanized using an overdose of the anesthetic FA100 (10% solution of eugenol; Tanabe Seiyaku Inc.). In the laboratory, we measured their SL to the nearest 0.05 mm. We also confirmed the sex of each individual by dissecting the fish and inspecting the gonads. Euthanized fish were then used for subsequent analyses (data shown in Tanaka et al. 2015, 2016; HT unpublished data).

Helper removal experiment

To experimentally test whether helpers increase the excavated cavities of the breeding female, we conducted a helper removal experiment and compared the size of the excavated stone area before and after the helper removal. We conducted the study in a depth of 9–13 m outside the grid area from November 15 to December 17, 2013 and from July 28 to December 23, 2015. We haphazardly chose 36 territories, which at least contained two helpers. All focal groups were marked by placing numbered stones near to the excavated area. In order to calculate the size of the excavated stone area before the helper removal, we took a digital picture from right above by using a Canon G15 digital camera. The picture also contained a 50 × 50 cm square metal frame as a size standard. On the next day, we carefully caught one helper from each territory. In 18 out of 36 groups, we released the captured helper after 5 min as a control treatment. All released helpers were accepted in their original group. One week after the helper removal, we again took a digital picture of the excavated stones in all of the territories, in order to calculate and compare the size of the excavated stone area before and after the experiment. The size of the excavated stone area was calculated from the digital pictures using the software image J (Rasband 2014).

Statistical analysis

Data analyses were conducted using R version 3.1.1 (R Core Team 2014). We fitted linear mixed models (LMMs), generalized linear models (GLMs), or generalized linear mixed-effect models (GLMMs) using the packages lme4 (Bates et al. 2011) or lmerTest (Kuznetsova et al. 2014). Normality was checked from the residuals of the applied models. All reported test statistics were derived from two-tailed testing.

To investigate the relationship between the size of the simulated excavated cavities and the amount of immigrated benthic invertebrates, we fitted a LMM with Gaussian error distribution and identity link. We set the number of invertebrates as response variable, and the size of the artificial excavated stone area as explanatory variable. We added the date of the experiment as a random factor to account for non-independency of data collected during the same night.

To compare the amount of the respective prey categories found in the fish's stomach, we fitted a GLMM applying a Poisson error distribution with log link. We set the points of the respective categories from the stomach contents as response variable, and prey category (shrimp, aquatic insect, mollusks, limnetic invertebrates, and unidentified matters) as explanatory variable. We set "Shrimp" as a reference category. Identity of the respective fish was included as random factor. Additionally, we investigated whether the amount of shrimp in the stomach was related to the body size of the fish by fitting a GLM with Poisson error distribution with log link. For this, we set the individual points of the shrimp from the stomach contents as response variable, and body size of the respective fish as explanatory variable.

To investigate the relationship between the size of the excavated cavities and the number of helpers, we fitted a GLMM with gamma error distribution and log link. We set the size of the excavated stone area as response variable, and the number of helpers and the body size of the breeding females as explanatory variables. Breeding males of *N. obscurus* usually guard the territories of several females and seldom engage in territory maintenance. To take any potential effects of breeding males into account, we incorporated the ID of the breeding male as well as the study year as separate random factors, respectively. In one group the number of helpers ($N=10$) was nearly twice as high as in any other group we ever encountered (HT, personal observation). This group most likely reflected a state in transition, for example due to a collapse of a neighboring territory by the death of the breeding female. Therefore, we did not include this territory for the analysis, and 188 groups were used in all analyses.

To investigate the change in the size of the excavated cavities before and after helper removal, we fitted a GLMM with gamma error distribution and log link. We set the size of the excavated stone area as response variable. The interaction term of period (before or after helper removal) and treatment (control or experiment) served as explanatory variable. In addition, we set body size of the breeding female as explanatory variable and group ID as random factor. As the interaction turned out to be significant, we fitted two separate GLMMs with gamma error distribution and log link in order to test how the size of the excavated stone area was changed in our control and in the experiment. For the model analyzing the control treatment, we set the size of the excavated stone area as response variable, and included period (before helper removal or after helper removal) as an explanatory variable. For the model analyzing the experimental treatment, we also tested whether body size of the removed helpers affected the change in excavated stone area size. For this, we set the size of the excavated stone area as response variable, and an interaction term of period (before helper removal or after helper removal) and body size of removed helpers as an explanatory variable. Group ID was incorporated as a random factor in both of the

models. We set “before helper removal” (for the term “period”) as a reference category to compare the behavioral difference between before and after the helper in all of the models.

Data accessibility The datasets analyzed during the current study are available in the figshare repository, DOI: <https://figshare.com/s/e457c5bd0f907545d28a>

Results

The daily immigration of benthic invertebrates increased with the size of the simulated excavated stone area (Fig. 1, LMM: $\beta \pm SE = 0.038 \pm 0.007$, $t = 5.30$, $P < 0.0001$). On average, 81.5% of the stomach content of *N. obscurus* consisted of benthic invertebrates, especially shrimp (shrimp 51.7%, aquatic insect 24.7%, mollusks 5.1%, limnetic invertebrates 7.9%, and unidentified matters 10.7%). The amount of shrimp found in the stomach was larger compared to all other food items (Table 1). We found no effect of the fish’s body size on the relative amount of shrimp found in the stomach (GLM: $\beta \pm SE = 0.000 \pm 0.009$, $z = 0.007$, $P = 0.99$).

The size of the excavated stone area inside the territory of the breeding female significantly increased with the number of helpers and the body size of the female (Fig. 2, GLMM: number of helpers, $\beta \pm SE = 0.197 \pm 0.002$, $z = 82.1$, $P < 0.0001$;

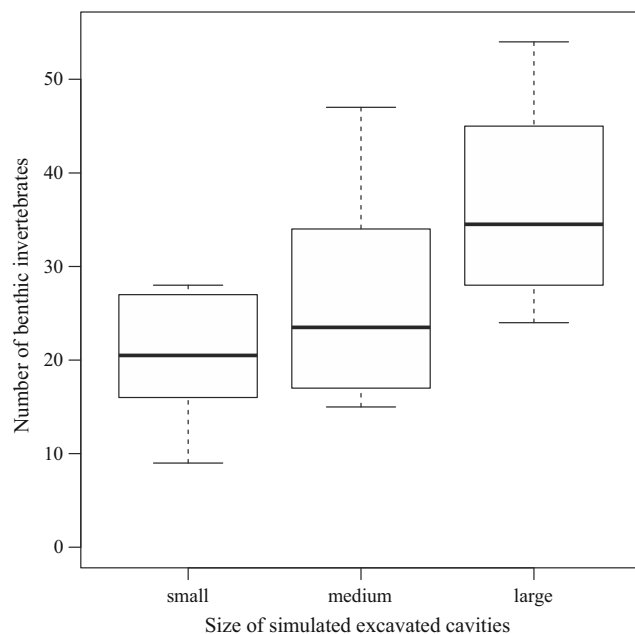


Fig. 1 The relationship between the size of the excavated stone area and the number of immigrated benthic invertebrates. The amount of immigrated prey items linearly increased with increasing simulated area size (see results for details). Depicted are medians, first and third quartiles and ranges

Table 1 Results of the GLMM comparing the amount of the stomach items

Explanatory variables	Mean effect size \pm SE	z-value	P
Intercept	1.18 \pm .13	8.85	< 0.0001
Diet category			
Shrimp	Reference		
Aquatic insect	-0.74 \pm .18	-4.06	< 0.0001
Mollusks	-2.32 \pm .35	-6.72	< 0.0001
Limnetic invertebrates	-1.88 \pm .28	-6.63	< 0.0001
Unidentified matters	-1.58 \pm .25	-6.32	< 0.0001

body size of breeding female, $\beta \pm SE = 0.046 \pm 0.002$, $z = 29.3$, $P < 0.0001$).

The helper removal experiment revealed a significant difference in the excavated stone area size between control and experiment treatment 1 week after the helper removal (Fig. 3, Table 2). The size of the excavated stone area in the control treatment did not change before and after the helper removal (GLMM: period, $\beta \pm SE = 0.004 \pm 0.009$, $z = 0.50$, $P = 0.62$), while the size of the excavated stone area in the experimental treatment decreased after helper removal. This decrease was larger when removed helpers were of large body size (Supplementary Fig. S2, GLMM: period \times body size of removed helper, $\beta \pm SE = -0.04 \pm 0.001$, $z = -54.0$, $P < 0.0001$).

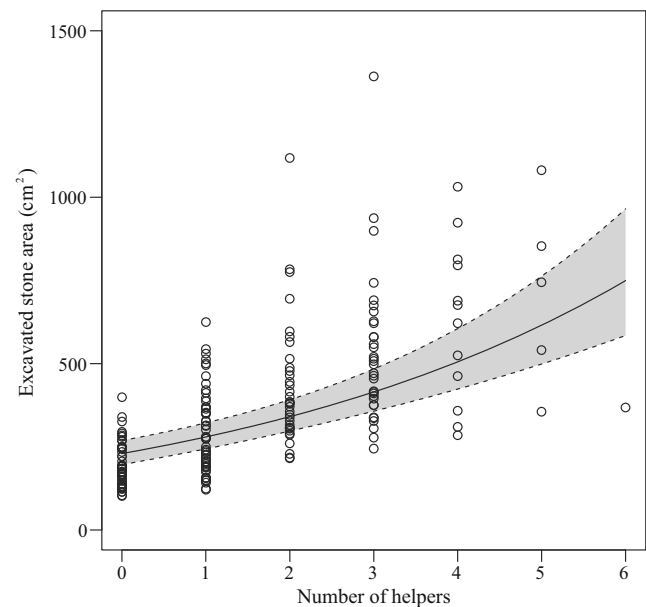


Fig. 2 The relationship between the number of helpers and the size of the excavated stone area. The excavated area exponentially increased with increasing number of helpers. The line indicates the relationship predicted by a GLMM with 95% confidence intervals, dots represent single data points

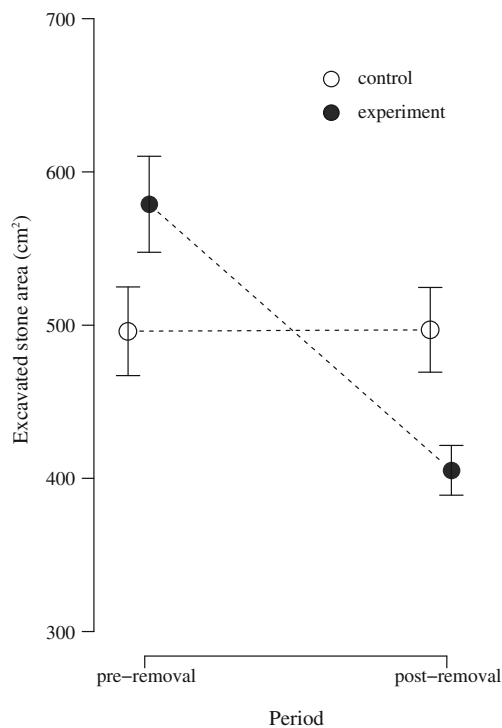


Fig. 3 Changes in the excavated stone area before and 1 week after the helper removal experiment. While the excavated stone area decreased when helpers were removed it remained constant in the control treatment (see results for details). Depicted are means \pm SE, black dots indicate experimentally treated groups, white dots show the result of the control

Discussion

Foraging is an important aspect of group living and social organization in animals. While animals show a great diversity in their way to acquire food resources, e.g., farming (Chapela et al. 1994; Aanen et al. 2002; Silliman and Newell 2003; Hata and Kato 2006; Biedermann et al. 2009), tool use (Mann and Patterson 2013; Sanz et al. 2013; Rutz et al. 2016) or trap building (Foelix 1996; Scharf and Ovadia 2005; Bar-Oz et al. 2011), knowledge of such elaborate food acquisition is only known from a limited number of animal taxa. In this study, we investigated whether helpers contribute to increase the food abundance in the territory of the cooperatively breeding cichlid *Neolamprologus obscurus*. The stomach contents analysis revealed that most of the fish's diet consists of benthic invertebrates, especially shrimp, demonstrating that invertebrates are an important food resource for these fish. By creating artificial cavities, we show that the amount of invertebrates increase according to the size of the excavated cavities. Finally, both correlational and experimental field data revealed a strong link between the size of the excavated stone area and the number of helpers in the respective territory. Taken together, these results suggest that helpers in *N. obscurus* extend and maintain the excavated cavities and

by doing so, contribute to an increase in food abundance inside the territory of breeding females. Although fishes show great divergence in acquiring food resource, such as algae cultivation (Hata and Kato 2006) or tool use (Mann and Patterson 2013), this study is, to the best of our knowledge, the first to report evidence of joined food acquisition by group members in fishes.

Compared to non-shrimp feeding cichlids, shrimp feeders in Lake Tanganyika have large home ranges in which they search for prey (Hori 1987; Ochi 1993; Yuma 1994; Matsumoto and Kohda 2007; Kohda et al. 2008; Ochi et al. 2017; but see Yanagisawa 1987). In contrast, *N. obscurus* defends only small territories (Tanaka et al. 2015), and the excavated cavities facilitate the fish to efficiently acquire food within their limited home range. The function of these excavated cavities may resemble the webs of social spiders, which live in groups and share the trapped prey among group members (Kullmann 1972; Kraft 1979; Buskirk 1981). In these spiders, individuals gain benefits through group living by cooperating with related group members (Bilde and Lubin 2001; Schneider and Bilde 2008; Yip and Rayor 2014) or reducing per capita silk expenditure for constructing webs (Evans 1998). At the same time, individuals inflict costs on each other by living together, which will balance their group size (Bilde et al. 2007; Yip et al. 2008). In *N. obscurus*, these costs and benefits are still elusive, but most likely shaping the social system of this species in a comparable way. Excavating sand is supposed to be highly costly for these fish, both in terms of time and energy they spend (cf. Taborsky and Grantner 1998). Sand usually enters the cavities continuously from the edges of the excavated area. Relative edge length of the excavated cavities decreases with increasing absolute size of the excavated stone area, as edge length increases with first power whereas size of the excavated cavities increase with third power. Therefore, fish living in groups may be able to increase and maintain considerably larger excavated cavities per capita compared to solitary living fish. Consequently, group living enables *N. obscurus* to efficiently increase the prey abundance in their territory and may in turn increase the body condition and future reproductive success of breeders and/or helpers, suggesting a clear benefit of group living.

In family groups, parents and offspring may compete over resources in their territory. Therefore, the conflict among family group members has been suggested to shape life-history adaptations, such as a slow pace of life (Covas and Griesser 2007). Additionally, specific ecological conditions such as predictable access to food resource will set the precondition for the evolution of family living (Griesser et al. 2017). Groups of *N. obscurus* mainly consist of related individuals (Tanaka et al. 2015) and are relatively small compared to other cooperatively breeding cichlids (Heg et al. 2005; Heg and Bachar 2006; Awata et al. 2010; Groenewoud et al. 2016;

Table 2 Results of the GLMM comparing the excavated stone area before and after the helper removal experiment

Explanatory variables	Mean effect size \pm SE	z-value	P
Intercept	3.88 \pm 0.51	7.60	< 0.0001
Body size of breeding female	0.06 \pm 0.01	4.50	< 0.0001
Observation period			
Before helper removal	Reference		
After helper removal	0.004 \pm 0.033	0.13	0.89
Treatment			
Control	Reference		
Experiment	0.15 \pm 0.06	2.61	0.009
Observation period \times treatment			
Before helper removal \times control	Reference		
After helper removal \times experiment	-0.35 \pm 0.05	-7.49	< 0.0001

Taborsky 2016). One explanation for this pattern might be the conflict over food among group members, which is well investigated in cooperatively foraging animals (Caraco and Wolf 1975; Creel and Creel 1995; Baird and Dill 1996; Whitehouse and Lubin 2005; Yip et al. 2008). For instance, individual of African wild dogs gain benefits through group living via increased mean prey mass, hunting success and the likelihood of catching multiple prey (Creel and Creel 1995, 2002). However, these benefits are not evenly allocated among adult group members, leading to a high adult mortality rate in larger groups (Creel and Creel 2015). Our stomach contents result revealed that small as well as large individuals prey on benthic invertebrates, suggesting that helpers and breeders may potentially compete for food in the territory. Group members show a clear dominance hierarchy, with the breeding female being most dominant (Tanaka et al. 2015). This social position of breeding females might allow them to control the food intake of helpers by preventing access to some cavities and in turn improve their own food intake. This mechanism might keep the group size of *N. obscurus* small. This may also be reflected in their life history. As predicted by theory (Covas and Griesser 2007), *N. obscurus* produce small numbers of eggs (HT unpublished data), which can be a way to keep competition between offspring low. Comparable conflicts over food resources are also observed between sexually matured male *N. obscurus*. Here, dominant males tolerate matured single males inside their territories and frequently visit the excavated cavities of these males, where most food resources will be found (Tanaka et al. 2015). Single males in turn attempt to prevent this intrusion. These observations further emphasize that foraging is an important driver shaping the social system of *N. obscurus*.

In summary, we provide the first evidence of food acquisition by helpers in fishes, which is a novel aspect potentially determining the structure and maintenance of the cooperative system of *N. obscurus*. Such foraging system may be

comparable to the behavior found in other highly social animal taxa, and appears to be a ubiquitous mechanism underpinning the maintenance of complex social societies. Future study will reveal the cost and benefits of food acquisition in this fish species.

Acknowledgments We thank all Hasli members, especially Jon Andreja Nuotclà for fruitful discussions. We also thank Tetsumi Takahashi, Masaya Morita, Kazutaka Ota, Michio Hori, and the staff of the Lake Tanganyika Research Unit, Mpulungu, Zambia, especially Harris Phiri, Danny Sinyinza, Taylor Banda, Ruben Shapola, and Henry Simpembwa for supporting our studies in the field. We appreciate Michio Hori for valuable advice on examining stomach contents of the cichlids, and Vera Schluessel and two anonymous reviewers for valuable comments on an earlier version of the manuscript. We are grateful to the organizers of the 12th Topical Meeting of the Ethological Society for encouraging us to submit this paper.

Funding This work was financially supported by JSPS KAKENHI (25304017, 23570033 and 4501) to MK. During manuscript preparation, HT was funded by a SNF grant (31003A_166470) to JGF.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

Ethical approval The study was carried out in the field in agreement with and approved by the Zambian Department of Fisheries: Ministry of Agriculture and Cooperatives. Data collection were in accordance with the current laws of the Republic of Zambia and followed the ASAB/ABS (2012) guidelines for the treatment of animals in behavioural research and teaching.

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