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Helpers increase the reproductive success of breeders in the cooperatively breeding cichlid *Neolamprologus obscurus*

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Abstract

In cooperatively breeding animals, individuals other than breeders assist in raising young. While it is generally assumed that such helpers increase the reproductive success of breeders, positive effects can be cryptic and difficult to detect. Furthermore, measuring the effect of helpers in the wild is often difficult because multiple factors such as breeder's individual quality or experience may affect their reproductive success. Thus far, best examples for fitness benefits of helpers come from a small number of long-term data sets in cooperatively breeding birds and mammals. In contrast, little is known about helpers' effect on the reproductive success of other cooperatively breeding taxa, e.g., fishes. Here, we investigated the effect of helpers in the cooperatively breeding cichlid *Neolamprologus obscurus*. We analyzed field data collected during three years to elucidate the effect of helpers on reproductive success of breeders, while considering differences in the quality of breeders and size of their territories. As proxy for reproductive success, we measured the number of juveniles in the respective territory. Our results show that the number of juveniles increased with the number of helpers, while neither breeders' quality nor the size of the territories had a significant effect. These findings increase our understanding of the beneficial effects of helpers in cooperatively breeding fishes, helping us to understand the evolution of such complex social system in general.

Significance statement

In cooperatively breeding animals, individuals other than breeders assist in raising young. An increased reproductive success of breeders is the ultimate measure of benefits caused by helpers. However, such relationship is rarely demonstrated in cooperatively breeding fishes. We show that the number of helpers positively correlates with the reproductive success of breeders in the cooperatively breeding cichlid *Neolamprologus obscurus*. Our results contribute to the understanding of the evolution of cooperative breeding animals.

In memory of Hirokazu Tanaka, who deceased before the final submission of this article.

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Introduction

In cooperatively breeding animals, individuals other than breeders assist in raising young (Brown 1987; Solomon and French 1997; Koenig and Dickinson 2016). How such seemingly altruistic behaviors evolved has been investigated for many decades (Skutch 1935; Brown 1987; Cockburn 1998; Boland and Cockburn 2002; Koenig and Dickinson 2004, 2016). Helpers are often offspring of the breeders that delayed their dispersal from their natal territory (Emlen 1995; Hatchwell and Komdeur 2000; Hatchwell 2009). In such cases, helpers may gain indirect fitness benefits through helping to raise related young (Emlen and Wrege 1989; Komdeur 1994; Russell and Hatchwell 2001; Hatchwell 2009; Nam et al. 2010; Preston et al. 2016). Indeed, family formation is an

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important precondition for the evolution of cooperative breeding (Drobniak et al. 2015; Burkart et al. 2017; Griesser et al. 2017). However, besides such indirect benefits, helpers may gain direct fitness benefits by staying in the territory of breeders, e.g., through group protection (Kokko and Ekman 2002; Bergmüller et al. 2005) or by inheriting the territory of the breeders (Woolfenden and Fitzpatrick 1984; Stacey and Ligon 1987; Balshine-Earn et al. 1998; Field and Leadbeater 2016). Such multiple benefits exceed the cost of helping, leading to the evolution of cooperative social systems (Choe and Crespi 1997; Solomon and French 1997; Koenig and Dickinson 2004; Heg and Bachar 2006; Lubin and Bilde 2007; Duffy and Macdonald 2010; Taborsky 2016).

Costs and benefits of cooperative breeding also apply for breeders, which benefit from the presence of helpers in several ways. Helpers can reduce the workload of breeders (*load-lightening effects*) or additively benefit the offspring, for example by additional provisioning, which will increase the survival or growth of offspring (*additive effects*) (Crick 1992; Hatchwell 1999; Heinsohn 2004; Johnstone 2011; Tanaka et al. 2018a). These benefits are expected to increase the current and/or future reproductive success of breeders. Indeed, such positive helper effects on reproductive success of breeders are the most adaptive and clear expectation of helping behavior (Brouwer et al. 2005; Doerr and Doerr 2007; Canestrari et al. 2008; Cockburn et al. 2008). However, helpers sometimes pose costs for breeders. For instance, helpers and breeders might compete for resources such as food (Creel and Creel 2015), or helpers might reduce the reproductive success of breeders via reproductive parasitism (Mulder et al. 1994; Dierkes et al. 1999). Indeed, the effect of helpers on breeder's reproductive success is not always straight forward in some species (Magrath and Yezerinac 1997; Legge 2000; Eguchi et al. 2002), or difficult to detect due to concealed helper effects such as reduced female egg investment (Russell et al. 2007; Canestrari et al. 2011).

For cooperative breeding to be evolutionary stable, benefits of both breeders and helpers should outweigh the respective costs in their lifetime (Alexander 1974; Bourke 2011; Shen et al. 2017). Therefore, it is essential to comprehend the benefits of breeders in order to understand the evolution and maintenance of cooperative breeding in animals. Effects of helpers on the reproductive success of breeders are often challenging to assess in cooperatively breeding animals. This is because reproductive success of breeders is expected to correlate not only with the number of helpers but also with territory quality or the experience of breeders (reviewed in Cockburn 1998). Additionally, breeders owning a territory of high quality or that are in good body condition might be able to produce or recruit more helpers, which makes it difficult to disentangle these factors directly affecting the reproductive success of breeders. Multifactorial analysis incorporating the effect of breeder's quality or territory quality (Ridley 2007; Awata et

al. 2010), or experimental removal of helpers from the group (Brouwer et al. 2005; Tanaka et al. 2018a), has been applied to disentangle these multiple correlations. Such analyses often apply paired comparison or mixed-model/hierarchical-models to compare the same breeding individuals and territory in sequential years with and without helpers (Legge 2000; Magrath 2001; Eguchi et al. 2002; Russell et al. 2003; Woxvold and Magrath 2005; Doerr and Doerr 2007; Canestrari et al. 2008; Cockburn et al. 2008). While such approaches are powerful, especially in long-lived species that can be followed over several years, they are less feasible when tracing the same group or individual is difficult across the years, e.g., due to high mortality (e.g., Heg et al. 2005b; Jungwirth and Taborsky 2015; Tanaka et al. 2016) or due to difficulties studying individuals without disturbing the nest or burrow (Sumbera et al. 2003; Diesel and Schubart 2007; Tanaka et al. 2015).

In fishes, cooperative breeding is described for about 25 lamprologine cichlids endemic to Lake Tanganyika (Taborsky and Limberger 1981; Yamagishi and Kohda 1996; Kohler 1998; Awata et al. 2005; Heg et al. 2005a; Heg and Bachar 2006; Tanaka et al. 2015; Taborsky and Wong 2017). In many of these species, groups contain unrelated helpers. Here, direct fitness benefits for the helpers play an important role in the evolution and maintenance of cooperative breeding (Awata et al. 2005; Dierkes et al. 2005; Groenewoud et al. 2016; Taborsky 2016; Dey et al. 2017; Tanaka et al. 2018c), which is different from other animal taxa (Koenig and Dickinson 2004; Lubin and Bilde 2007; Duffy and Macdonald 2010; Lukas and Clutton-Brock 2012; Chak et al. 2017; Griesser et al. 2017; but see Riehl 2013). This makes lamprologine cichlids a unique model to investigate alternative pathways to the evolution and maintenance of cooperative breeding. Thus far, one species of this taxonomic group (i.e., *Neolamprologus pulcher*) has been intensively studied in this context (reviewed in Wong and Balshine 2011; Taborsky 2016). However, our knowledge of other cooperative breeding fishes is limited, which makes it difficult to understand the general factors leading to the evolution of cooperative breeding (Tanaka et al. 2018c). This shortcoming is unfortunate, as it prevents the comparison of the evolution of complex social system within and between different taxonomic groups. We aim at increasing our knowledge of breeder's benefits of having helpers using the cooperatively breeding cichlid *Neolamprologus obscurus*.

Neolamprologus obscurus is a cichlid fish that has recently been reported as cooperatively breeding (Tanaka et al. 2015, 2018a, b, topical collection on From sensory perception to behavior). This small benthic fish inhabits sandy to rocky habitats of Lake Tanganyika (Konings 1998), in which breeder females form a breeding unit with up to 10 subordinate helpers (hereafter termed "group"), which all show helping behavior (Tanaka et al. 2018a). Breeder males might be monogamous or monopolize several of such female groups (Tanaka et al. 2015). *N. obscurus* excavate cavities under

several stones (see Tanaka et al. 2015, 2018b, topical collection on From sensory perception to behavior, for a detailed description). These cavities are connected to each other, forming the groups' shelter. Shelters have a threefold function: they serve as spawning substrate (Tanaka et al. 2015) and shelter from predation threat for all group members (Tanaka et al. 2016). Moreover, the cavities serve as traps for collecting benthic invertebrates, which are the main food resource of *N. obscurus* (Tanaka et al. 2018b, topical collection on From sensory perception to behavior). Helpers perform territory defense, which leads to load-lightening effects for the breeder female (Tanaka et al. 2018a). In addition, helpers maintain excavated shelters by frequent sand removal and additively increase the size of shelters, which will increase the space for hiding from predators and the food abundance in the territory of breeders (Tanaka et al. 2018b, topical collection on From sensory perception to behavior). While these results suggest benefits of helpers for breeders, direct evidence for increased reproductive success of breeders remains elusive.

Here, we investigated the effect of helpers on the reproductive success of breeders in *N. obscurus*. By using a large data set obtained during three field seasons, we first describe the number of helpers and juveniles found in 189 groups. Second, we investigated the relationship between group structure and the body size of the breeder female. Finally, we investigate the effect of the number of helpers, breeder female's body size, and size of the shelter on the reproductive success of breeder female. As fishes show unlimited growth, body size is a good proxy for age (Dierkes et al. 2005). Older breeders are usually expected to be more experienced than younger individuals are (Cockburn 1998). Therefore, we used body size of breeder female as a proxy of experience of breeders. Additionally, the size of the excavated shelter area influences the food abundance in the territory (Tanaka et al. 2018b, topical collection on From sensory perception to behavior) and may increase predator protection for all group members including juveniles, as seen in closely related cooperative breeders (Balshine et al. 2001). Therefore, we took the size of the shelter into account in our analysis.

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 consists of a steep sandy slope with partially exposed stones. *N. obscurus* lives at this site through depths of 5 to 13 m. Data were collected by SCUBA diving. As data were

taken in the wild, it was not possible to apply blinding methods.

Group composition and shelter size

Measurements of group composition and territory assessments were conducted in three years: from September 3rd to November 27th 2010, September 18th to November 29th 2012, and August 20th to December 17th 2013. We indicated grids measuring 20×8 m (2010), 10×6 m (2012), or two times 8×4 m (2013) at different depths of the same population using strings attached to the ground (see Tanaka et al. 2016 for details). We subdivided these grids into squares measuring 0.5×0.5 m (2010 and 2012) or 1×1 m (2013) 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 Abode 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 and recorded the relationship between group members and their social rank by observing each individual for 10–15 min. Individuals below 17 mm standard length (SL) usually hide inside the shelters, protected by breeders and helpers (Tanaka et al. 2016). Fish start participating in helping activities from above 17 mm SL, while there are no other obvious developmental differences occurring at this size (Tanaka et al. 2016). Therefore, we regarded fish larger than 17 mm SL as helpers and those below 17 mm SL as juveniles, following established protocols (Tanaka et al. 2016, 2018a, b, topical collection on From sensory perception to behavior). We counted all helpers and juveniles in the respective territory. Molecular analysis and long-term field observation revealed that juveniles delay their dispersal and stay in the natal territory (Tanaka et al. 2015; Tanaka et al. 2016). Furthermore, breeder turnover is rare in this species (Tanaka et al. 2016). Therefore, we used the number of juveniles as a proxy of female reproductive output. Breeder males of *N. obscurus* usually guard the territories of several females and seldom engage in habitat maintenance. Therefore, we noted the breeder males for the respective territories, but did not focus on them during the analysis. In 2010, all groups found within the grid served as focal groups ($N = 47$). In 2012 and 2013, we randomly 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.

N. obscurus usually excavate their cavities under stones (see Tanaka et al. 2015; Tanaka et al. 2018b, topical collection on From sensory perception to behavior, for a detailed description). These cavities are connected to each other, forming the groups' shelter. To estimate the area of the excavated shelter in each breeder female's territory, we first

assessed the territory borders by tracing the swimming tract of the respective female. We observed breeder females of all focal groups for 30 min (in 2010), or 20 min (in 2012 and 2013). The swimming tract was indicated 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 excavated stones of each territory on the topographic map. Stones were regarded as excavated if breeders or helpers dug out sand from under a stone or entered the existing cavity. Subsequently, we calculated the surface size (cm^2) of the excavated shelter inside the home range of each breeder female using imageJ (Rasband 2014), and used this measure as a proxy of shelter size (Tanaka et al. 2015; Tanaka et al. 2018b, topical collection on From sensory perception to behavior).

Fish sampling

After the observations, all females, helpers, and juveniles in the focal groups were caught using gillnets, hand-nets, and 30% clove oil diluted in ethanol as mild anesthetic. In 2012, we measured the standard length of the caught fish to the nearest millimeter underwater and released them back to their respective 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.), and their SL measured to the nearest 0.05 mm in the laboratory. Euthanized fish were used in subsequent analyses (see Tanaka et al. 2015, 2016).

Statistical analysis

Data analysis was conducted using R version 3.1.1 (R Core Team 2014). We fitted mixed-effect regression models using the lme4 package (Bates et al. 2011). When inspecting the helper numbers, we found one group in which 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 reflects a state in transition, for example because a neighboring territory collapsed due to the death of the breeder female. Therefore, we excluded this group and used 188 groups for all of the analyses, except for the description of the number of helpers and juveniles (see "Results" and Fig. 1). Still, the main results (the analysis of reproductive success of breeders) did not change when including this data point (GLMM: number of helpers, $\beta \pm SE = 0.28 \pm 0.07$, $z = 3.88$, $p = 0.0001$; body size of breeder female, $\beta \pm SE = -0.005 \pm 0.027$, $z = -0.19$, $P = 0.85$; size of excavated shelter, $\beta \pm SE = 0.0002 \pm 0.0005$, $z = 0.37$, $P = 0.71$). We checked collinearity among the covariates by calculating the variance inflation factor (VIF) in all models that included more than two explanatory variables. We found that the VIF was below 2
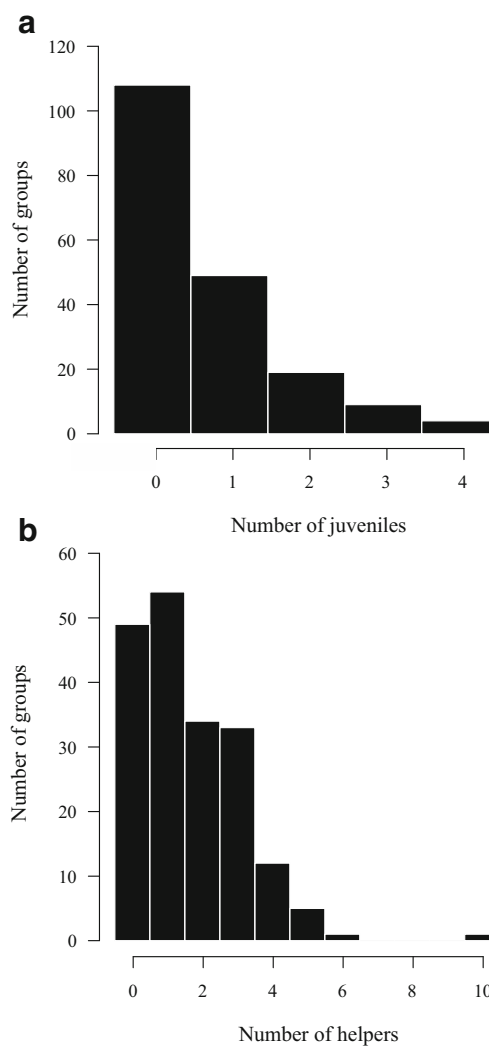
Fig. 1 The number of **a** juveniles and **b** helpers observed in 189 groups of *N. obscurus* during three field seasons

in all cases, which indicates that the covariates did not suffer from collinearity (Zuur et al. 2010). All tests were two-tailed. SD of random factors is shown in Table 1.

To investigate the relationship between the body size of the breeder female and the number of helpers in their groups, we fitted a generalized linear mixed-effect model (GLMM) with Poisson error distribution and log link. We set the number of helpers as response variable and the body size of the breeder female as explanatory variable. We added the study year and the ID of the breeder male as separate random factors.

Table 1   SD of the random effects year, breeding male, and breeding unit

Model	Year	Breeding male	Breeding unit
Number of helpers	0.06312	2.59×10^{-4}	–
Number of juveniles	–	1.13×10^{-5}	0.606

To investigate the effect of helper number, body size of the breeder female, and shelter area on the reproductive success of the breeder female, we fitted a GLMM with Poisson error distribution and log link. We set the number of juvenile as response variable and the helper number, the body size of the breeder female, and shelter area as explanatory variables. We added the study year, the ID of the breeder male, and the ID of the breeding group as separate random factors. To improve model convergence, we removed the random factor "study year," which had the lowest variance of the three random factors in the final model.

Results

Eighty-one out of 189 breeding groups contained at least one juvenile individual. The mean number of juveniles found in these breeding groups was 1.58 (Fig. 1a, median, quartiles = 1, 1, 4, range = 1–4, $N = 81$). On average, groups contained 1.64 helpers per (Fig. 1b, median, quartiles = 1, 0, 4, range = 0–10, $N = 189$), and the body size of the breeder females was positively correlated with the number of helpers (Fig. 2, GLMM: $\beta \pm SE = 0.115 \pm 0.019$, $z = 6.01$, $p < 0.0001$, $N = 188$). The number of juveniles significantly increased with the number of helpers, but was neither significantly correlated with size of the shelter nor breeder's body size (Fig. 3, Table 2).
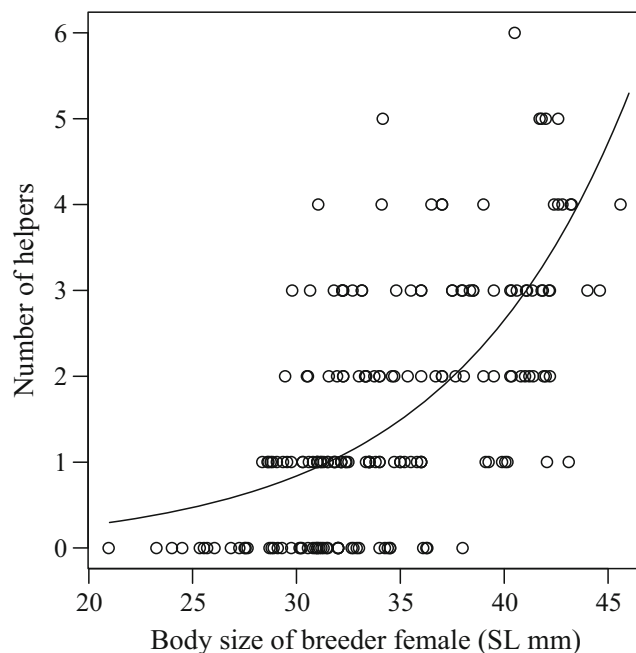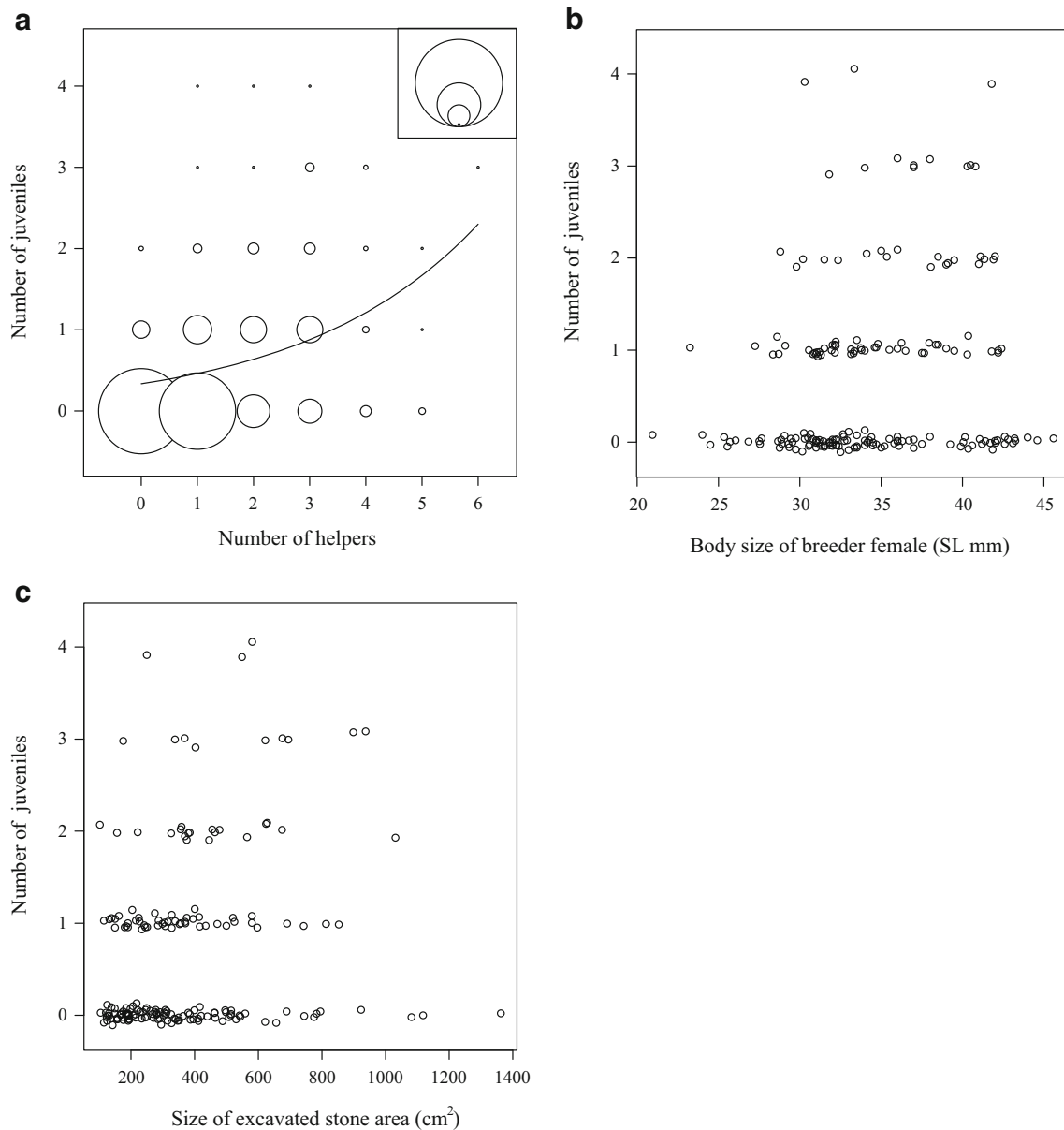

Fig. 2 The relationship between the number of helpers and the body size of the breeder females. The line indicates the regression derived from the GLMM (see text for details). $N = 188$ groups

Discussion

An increased reproductive success of breeders is an expected benefit of helping behavior in cooperatively breeding animals. While such relationship is frequently shown in cooperatively breeding birds, mammals, and invertebrates, evidence in fishes is rare (but see Balshine et al. 2001; Brouwer et al. 2005; Awata et al. 2010). Furthermore, reproductive success of breeders often correlates with several other factors such as breeder's quality or territory quality (Brown et al. 1982; Cockburn 1998; Cockburn et al. 2008), making it difficult to disentangle the causality between these factors. Using an extensive set of field data, we show that the presence of helpers is the best predictor for explaining the number of juveniles in a breeding female's territory, while the effects of female quality and size of the shelters had low explanatory power. While load-lightening and additive effects of helpers are reported in *N. obscurus* (Tanaka et al. 2018a, b, topical collection on From sensory perception to behavior), these results describe first evidence of positive helper effects on breeder's reproductive success in this species.

An increased number of helpers may benefit breeder females in several ways. First, helpers reduce the workload of breeder females during territory defense and parental care, which is beneficial for the female in terms of saving energy and time (Tanaka et al. 2018a). As a consequence, females might be able to invest more resources into reproduction as well as increasing foraging activities (Tanaka et al. 2018a). Second, helpers in *N. obscurus* extend the excavated shelter area, which increase protection from predators and food abundance in the territory (Tanaka et al. 2018b, topical collection on From sensory perception to behavior). Increased food resources benefit not only the offspring but also improve breeder's body condition (HT, unpublished data), leading to an increase in reproductive success or survival of females later in their life. Third, an increased number of helpers may directly increase the survival of offspring, for example by defending eggs and offspring against predators, cleaning the eggs, and providing them with oxygen-rich water (Tanaka et al. 2015). Indeed, breeder females adjust the shelter visits during egg and juvenile stage when they have more helpers in their territory. This suggests that helpers are beneficial in terms of brood care, as it is the case in other cooperatively breeding cichlids (*N. pulcher*: Balshine et al. 2001; Zöttl et al. 2013; *N. savoryi*: D. Josi et al., unpublished data).

A previous study on *N. obscurus* found a positive relationship between the number of juveniles and female body size (Tanaka et al. 2015). However, our current results suggest that the body size of the breeder female loses predictive power when including the number of helpers to the analysis. Still, there might be additional effects of female body size, such as

Fig. 3 The relationship between the number of juveniles and **a** the number of helpers and between **b** the body size of breeder females and **c** the size of the excavated shelter area. Different circle sizes in (**a**) indicate overlapping data points, the legend in the top right box indicates $N = 40$,

20, 10, and 1 (shown as dot), respectively. Plots in (**b**) and (**c**) are jittered to avoid overlap of data points. The line in (**a**) indicates the regression from the results of the GLMM (see text and Table 2 for details). $N = 188$ groups

an increased fecundity or higher experience of larger (and thus older) females in raising fry, which were masked by the strong

Table 2 Result of GLMM investigating the effect of the number of helpers, body size of female, and shelter area on the reproductive success of breeder female. $N = 188$ groups

Explanatory variables	$\beta \pm SE$	z	P
Intercept	-0.77 ± 0.90	-0.86	0.39
Number of helpers	0.34 ± 0.10	3.51	0.0004
Body size of female	-0.02 ± 0.03	-0.52	0.60
Shelter area	0.0002 ± 0.0006	0.30	0.76

effect of helper number. Similarly, the size of the excavated shelter that serves as hiding place from predators as well as feeding area had no significant effect on juvenile number. One possible explanation might be that the positive effects of a large shelter do not translate in direct reproductive success, but instead have long-term effects, such as increased female survival or longevity. Future studies will reveal the complex interplay between territory quality, breeder's body size, and lifetime reproductive success in *N. obscurus*.

The number of helpers increased with the body size of the breeder female. This may be due to two non-mutually exclusive reasons. First, as the offspring delay dispersal from their

natal territory (Tanaka et al. 2015, 2016), larger (and thus older) females will have more time to gain helpers in their territory. Second, as hierarchies are strongly size based in highly social fishes, the body size of the largest individual should determine the body size of the second rank individual and so on (Buston 2003; Heg et al. 2004; Wong et al. 2008). Consequently, the body size of breeder females will determine the number of helpers, leading to groups of larger females containing more helpers. Such body size-dependent group structuring is reported in other highly social fishes, including cooperatively breeding cichlids (e.g., Heg et al. 2004, 2005a; Heg and Bachar 2006).

Overall, breeding groups contained only small numbers of juveniles. Furthermore, juveniles in a given territory differed strongly in their body size. This might be explained not only due to the natural growth difference between juveniles in a group but may also be caused by females' spawning repeatedly in a short time frame. While it is difficult to assess the number of spawned eggs as well as the spawning interval directly in the field due to the small and cryptic breeding shelters, dissection of adult females revealed small numbers of matured eggs with various stages of immature eggs in the ovaries (HT, unpublished data). Even when considering that *N. obscurus* is a small cichlid species, such egg numbers are exceptionally low compared to other fishes of the same tribe (range from 10 to > 1500, Yanagisawa 1987; Gashagaza 1991). An explanation for such low egg numbers might be that in this highly philopatric species (Tanaka et al. 2016) competition for food, space or hierarchy between subordinates, but also between subordinates and breeders, is assumed to be high (Tanaka et al. 2018b). Indeed, aggression is highest between individuals that are similar in size in the cooperatively breeding lamprologine *N. pulcher* (Ligocki et al. 2015; Balzarini et al. 2017). In this species, aggressive interactions impair anti-predator behaviors (Hess et al. 2016). Thus, costs of within-group aggression in *N. obscurus* might overrule the benefits of having many subordinates around. Producing only small number of offspring at a time might be a female's strategy to initially lower the risk of within-group conflict.

In conclusion, we describe positive helper effects on the reproductive success of breeders in the cooperatively breeding cichlid *N. obscurus*. Our results thus contribute to the further understanding of the evolution of cooperative breeding in fishes, which is a hitherto understudied taxonomic group.

Compliance with ethical standards

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

Ethical approval   The study complies with the current laws of the Republic of Zambia and was carried out in agreement with the Department of Fisheries: Ministry of Agriculture and Cooperatives, following the Zambian prevention of cruelty to animals act. There was no further ethical approval required. Data collection followed the ASAB/ABS (2012) guidelines for the treatment of animals in behavioural research and teaching.

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