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Original Article

Experimental predator intrusions in a cooperative breeder reveal threat-dependent task partitioning

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In cooperatively breeding species, nonbreeding individuals provide alloparental care and help in territory maintenance and defense. Antipredator behaviors of subordinates can enhance offspring survival, which may provide direct and indirect fitness benefits to all group members. Helping abilities and involved costs and benefits, risks, and outside options (e.g., breeding independently) usually diverge between group members, which calls for status-specific differentiated behavioral responses. Such role differentiation within groups may generate task-specific division of labor, as exemplified by eusocial animals. In vertebrates, little is known about such task differentiation among group members. We show how breeders and helpers of the cooperatively breeding cichlid *Neolamprologus savoryi* partition predator defense depending on intruder type and the presence of dependent young. In the field, we experimentally simulated intrusions by different fish species posing a risk either specifically to eggs, young, or adults. We used intrusions by harmless algae eaters as a control. Breeders defended most when dependent young were present, while helper investment hinged mainly on their body size and on the potential threat posed by the respective intruders. Breeders and helpers partitioned defense tasks primarily when dependent young were exposed to immediate risk, with breeders investing most in antipredator defense, while helpers increased guarding and care in the breeding chamber. Breeders' defense likely benefits helpers as well, as it was especially enhanced in the treatment where helpers were also at risk. These findings illustrate that in a highly social fish different group members exhibit fine-tuned behavioral responses in dependence of ecological and reproductive parameter variation.

Key words: **brood care, division of labor, lamprologine cichlid, *Neolamprologus savoryi*, task sharing, territory defense.**

INTRODUCTION

Predation risk is a major selective force promoting group living (Caro 2005; Beauchamp 2014). For potential prey, the main benefits of living in groups are increased predator detection probabilities, confusion, and risk dilution effects, as well as shared antipredator defense (Gaston 1978; Krause and Ruxton 2002; Townsend et al. 2014; Lehtonen and Jaatinen 2016). Predation may also be an important driver in the evolution of social systems, as it selects for delayed dispersal and cooperative defense to protect offspring (Taborsky 1984; Clutton-Brock et al. 1999; Heg et al. 2004; Yagi and Hasegawa 2011; Sorato et al. 2012; Tanaka et al. 2016). Cooperative defense includes shared vigilance, which allows other group members to reduce their investment in being alert without increasing the risk of predation (Yasukawa and Cockburn 2009), as well as joint mobbing and predator attacks (Arnold et al. 2005; Jungwirth et al. 2015; Groenewoud et al. 2016). Benefits of group defense have been suggested to promote the transition to eusociality by favoring morphological specializations, enhancing efficient defense of the brood or territory against predators (Grüter et al. 2012; Wcislo and Fewell 2017).

The efficiency of cooperation among group members strongly depends on the partitioning of different tasks among individuals and their associated costs and benefits (Oster and Wilson 1978; Ridley and Raihani 2008; Chittka and Muller 2009; Rubenstein and Abbot 2017). Investment may depend on an individual's age, sex, body condition and social status (Oster and Wilson 1978; Heinsohn and Legge 1999; Arnold et al. 2005; Bruintjes and Taborsky 2011). Different investment abilities and associated costs and benefits can select for specializations in defense behavior, and hence for a task-specific division of labor (Queller and Strassmann

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1998; Clutton-Brock 2002; Griffin and West 2003). For example, in the cooperatively breeding cichlid *Neolamprologus pulcher*, variation in body size and perceived risk favors task partitioning among group members (Taborsky and Limberger 1981; Bruintjes and Taborsky 2011; Groenewoud et al. 2016). Under unmanipulated conditions in the field, smaller helpers of this species invest mainly in territory maintenance while larger helpers primarily engage in territory defense (Groenewoud et al. 2016).

The defense of a territory or brood is costly as it does not only demand time and energy (Taborsky and Grantner 1998), but also increases the risk of injury or death for the defending individual (Balshine-Earn et al. 1998; Heinsohn and Legge 1999; Heg et al. 2004). Costs of predator defense are assumed to be higher for smaller and unexperienced individuals as they are more vulnerable and have less energy reserves to spend (Johnsson et al. 1999; Garvy et al. 2015). Antipredator investment is supposed to be influenced by these costs as well as by potential benefits, such as protecting related individuals or own offspring (Bruintjes et al. 2011), or the chance of inheriting the territory (Balshine-Earn et al. 1998). Group members should therefore adjust their defense behavior in relation to 1) their individual costs and benefits, 2) the presence of dependent young, and 3) the type and behavior of the intruder. Here, refined discrimination of predators and an appropriate response to the reproductive state of the group can enhance the individual's fitness prospects. Evidence for such fine-tuned adjustments comes, for example, from cooperatively breeding meerkats, which perform different kinds of warning calls depending on the predator type and threat, and which show increased sentinel behavior in the presence of young (Manser 2001; Santema and Clutton-Brock 2013). However, studies experimentally demonstrating the adjustment of defense behavior to the predator type and the reproductive state of the group are underrepresented in the literature thus far (but see Manser 2001; Desjardins, Stiver, et al. 2008; Yasukawa and Cockburn 2009; Bruintjes and Taborsky 2011; Santema and Clutton-Brock 2013; Zöttl, Frommen, et al. 2013; Tanaka et al. 2018).

The cooperatively breeding lamprologine cichlids of Lake Tanganyika are exposed to a large diversity of predators, with different species being specialized in feeding either on adult fishes (Kohda et al. 1997; Heg et al. 2004), juveniles (Taborsky 1984), free swimming young (Ochi et al. 2007), or eggs (Bruintjes and Taborsky 2011; Josi et al. 2019). Consequently, these cichlids are expected to show fine-tuned behavioral responses to variation in predation risk (Zöttl, Frommen, et al. 2013; Fischer et al. 2014). All cooperatively breeding lamprologines establish territories containing shelters underneath rocks or in crevices, which serve to protect group members from predation and as breeding substrate (e.g., Taborsky and Limberger 1981; Tanaka et al. 2016; Josi et al. 2019). These cichlids show substantial defense effort against conspecific and heterospecific intruders, including different predator species (e.g., Groenewoud et al. 2016). *Neolamprologus savoryi* belongs to these cooperatively breeding cichlids, living in small groups in sandy and rocky habitats (Heg et al. 2005). Breeder males defend territories, in which one to several breeding females defend smaller independent subterritories. Breeder females are smaller than breeder males, and they may be assisted by helpers of various sizes and both sexes (Josi, Taborsky, et al. 2020). Brood care helpers are allowed to enter the breeding chamber and do so more often in the presence of young (Josi, Taborsky, et al. 2020). They may also defend a private shelter inside the female's subterritory, which serves as an additional lair (Josi, Taborsky, et al. 2020). Some male helpers are larger than the breeder females and either defend their own subterritory within the territory of a breeder male, or patrol between the females contained in the harem (D. Josi, personal observation). Helpers engage in egg care (Josi et al. 2019) and territory maintenance (Josi, Taborsky, et al. 2020), and benefit from protection within the group. Reproduction is highly skewed toward breeders but may involve large helpers as well (D. Josi, D. Heg, T. Takeyama, D. Bonfils, D. A. Konovalov, J.G. Frommen, M. Kohda, and M. Taborsky, unpublished data). Furthermore, helpers contribute to defending the territory against intruders. They attack intruders either by performing overt physical aggression (ramming and biting) or by showing threat displays (restrained aggression). Such costly behaviors are not shown by all helpers and toward all intruders alike (Heg et al. 2005; Garvy et al. 2015). Therefore, studying territory defense offers a great opportunity to understand fine-tuned behavioral adjustments of group members in dependence of risk and demand.

We aim at elucidating potential task sharing and division of labor among group members as well as individual investment strategies in relation to the costs and benefits of collaborative defense. To this end, we experimentally simulated predator intrusions into territories of *N. savoryi* using different stimulus species that pose a risk either to adults, young or eggs. Moreover, we used a harmless algae-eating species as a control. We hypothesize that tasks differing in risk, such as taking care of offspring inside the breeding chamber or exhibiting antipredator defense, are partitioned differently among group members in relation to the associated costs and benefits. We predict that (i) task partitioning of breeders and helpers of different sizes is strongest if dependent young are exposed to immediate risk. Here, the young need to be protected in the breeding chamber while at the same time the predator needs to be kept at bay. We further predict that (ii) the respective tasks of group members depend on social class, body size (which determines efficiency) and potential fitness costs and benefits. Therefore, breeders and large helpers are predicted to invest more in defense, especially when dependent young are present, as they are 1) more efficient in defense and 2) more likely to get direct fitness benefits through reproductive participation. In haremic mating systems, breeder females may receive less paternal investment with an increasing number of female breeders contained in the harem (Desjardins, Fitzpatrick, et al. 2008; Jungwirth et al. 2016). Currently, it is unclear if breeder males allocate their investment preferably toward females/groups in larger need. We predict that (iii) male harem owners strategically support those females in the harem that currently have dependent young.

METHODS

Study site and colony structure

Our study site is located at the southern tip of Lake Tanganyika (8°46.849′ S, 31°04.882′ E) at Kasakalawe point, Zambia. Here, the bottom of the lake is sandy, with occasional rocks up to approximately 40 cm in diameter (see Heg et al. 2008). The focal colony was located at a depth of 9.5–11.5 m and at least 50 m away from any other *N. savoryi* colony. The study was conducted from September to November 2016 and 2017, respectively. Data were collected by SCUBA diving. Across the colony, we established a 10 × 10 m grid subdivided into 1 m^2 cells. The grid was then video recorded from above. Videos were processed using Adobe Illustrator CS2 in order to establish a topographic map of all stones (Josi et al. 2019; Josi, Taborsky, et al. 2020). The map was printed on waterproof paper. Each individual of *N. savoryi* larger than 15 mm living within the colony was observed for 20 min, and the respective home ranges were directly drawn on the waterproof map using a pencil. Based on these home ranges, all male territories were identified, and the main shelters/breeding chambers of all breeder females were marked using numbered stones, allowing to recognize female subterritories. Group compositions were assessed by observing the social interactions between individuals, such as submission and allowance to enter the breeding chamber (Josi et al. 2019; Josi, Taborsky, et al. 2020). Observations of similar-sized cooperatively breeding cichlids revealed that individuals smaller than 15 mm rarely show helping behavior (Taborsky and Limberger 1981; Heg et al. 2004; Groenewoud et al. 2016; Tanaka et al. 2016). Accordingly, we defined these individuals as dependent young (see also Josi, Taborsky, et al. 2020). At least 4 days before the experiment started, all individuals larger than 15 mm of each group were caught using fence nets. The standard length (SL) of all fish was measured to the nearest mm in situ using a measuring board. The sex of each fish was determined by close inspection of the genital papilla. Reliable sexing was only possible for individuals larger than 20 mm, which was the case for approximately half of all helpers.

Experimental manipulation

Data were collected from a total of 37 breeder female subterritories that belonged to 15 different breeder males (median females per male = 2, range = 1–5). Thirty-two subterritories were sampled in 2016 and five in 2017. Each male harem contained at least one breeder female defending dependent young. In total, 19 subterritories contained dependent young. Twenty-six of the females had at least one helper (median = 2, range = 1–5), whereas there were no helpers present in 11 female territories. In total, we collected behavioral observations of 70 helpers. In a randomized sequence, we presented four different fish stimuli and an empty control in each breeder female's territory: (i) *Lepidiolamprologus elongatus* (predator of fish, $n = 11$ individuals, SL = 7.7–10.9 cm, mean = 8.54 cm; Heg et al. 2004, 2008; Hellig et al. 2010; Groenewoud et al. 2016), (ii) *Gnathochromis pfefferi* (predator of young, $n = 10$ individuals, SL = 5.6–7.7 cm, mean = 6.81 cm; Ochi et al. 2007; Heg et al. 2008), (iii) *Telmatochromis vittatus* (predator of eggs, $n = 10$ individuals, SL = 3.5–5.1 cm, mean = 4.4 cm; Ochi and Yanagisawa 1999; Bruintjes and Taborsky 2011), (iv) *Xenotilapia spilopterus* (nonpredatory herbivore cichlid, $n = 12$ individuals, SL= 5.4–7.8 cm, mean = 6.59 cm; Heg et al. 2008). We attempted to keep size variation of stimulus fish small and therefore used only adult individuals. The risk of being predated by *L. elongatus* decreases with the prey's body size (Heg et al. 2004; Groenewoud et al. 2016) and is highest for juveniles (<15 mm) and helper sized individuals (<40 mm). *Gnathochromis pfefferi* only poses a risk to juveniles < 15 mm and not to helpers. *Telmatochromis vittatus* is a facultative predator of eggs, which only poses a threat to eggs. *Xenotilapia spilopterus* was chosen because these fish are neither space nor food competitors and do not pose a risk to any group member (Heg et al. 2008). Additionally, we presented (v) an empty tube once in each territory as control for the manipulation itself. The five stimuli were presented in a unique order for each group. Individuals of each stimulus species were caught outside of the colony and were used for several presentations to reduce potential stress caused by catching (median = 3 times, range = 1 – 14). After the presentation, the SL of each stimulus fish was measured, and they were marked using VIE-tags to avoid inadvertent recaptures (see Jungwirth et al. 2019 for tagging procedure). Stimulus fish were presented in a cylindrical acrylic glass tube (length: 14 cm, diameter: 9 cm) that was closed with a net so that the focal groups perceived both visual and olfactory cues of the stimulus. The tube was placed in front of the entrance of the breeding chamber and the diver recorded videos of each treatment for 5 min with a handheld camera. Before the experiment started, the diver remained motionless for at least 2 min in front of the territory to acclimatize the focal group to his presence (cf. Groenewoud et al. 2016).

Data collection

The video recordings were analyzed using the software BORIS (Friard and Gamba 2016). During the video analyses, different group members were identified by using a combination of individual body sizes, natural color marks, the respective home ranges, and group compositions. The ethogram used for the analyses was slightly modified from versions used in closely related congeners (Taborsky 1984; Balzarini et al. 2014; Tanaka et al. 2015). We counted all restrained (fast approach, fin spread, S-bend, tail beat, opercula spread, and head down display) and overt (bite, ram) aggressions shown by group members that were directed toward the presented stimulus fishes. All measured aggressive behaviors are clearly distinct from any other behaviors (e.g., evasion or submission). Due to the low frequency of some behaviors, we combined overt and restrained aggressions into a single aggression value for statistical analyses (Heg et al. 2005; Garvy et al. 2015; Tanaka et al. 2018). Additionally, the time each group member spent in the breeding chamber was recorded. As a measure of stimulus activity, the time the respective stimulus fish was actively moving in the tube was measured. Group members showed no aggressive behaviors toward the empty tube control, which was therefore not further analyzed.

Ethical note

Data collection caused minimal disturbance to the animals. The study complies with the regulations of the "Zambian prevention of cruelty to animals" act and followed the ASAB (2018) guidelines for the treatment of animals in behavioral research and teaching.

Data analyses

All statistical analyses were performed using R 3.5.1 (R Core Team 2018). We used the packages glmmADMB (Fournier et al. 2012) to run generalized linear mixed-effect models (GLMM) and lme4 (Bates et al. 2015) to run linear mixed-effect models (LMM) and binomial GLMMs. Error distributions and the correction for zero-inflation of GLMMs were chosen based on differences of Akaike Information Criterion (AIC) values using the function "AICtab" from the R-package bbmle (Supplementary Table S1; Bolker and R Development Core Team 2017). For the top models, we inferred the parameter significance based on likelihood ratio tests of deviances assuming a χ^2 distribution. Furthermore, GLMMs were tested for overdispersion. Post-hoc analysis of significant interactions among two factors were analyzed with the R-package phia (De Rosario-Martinez 2015), which allows testing specific contrasts of interest of the respective model by using the function "testInteractions." P values of these post-hoc analyses were based on a Wald χ^2 test.

Aggression toward stimulus fish

First, we tested if social classes (i.e., breeders and helpers) differed in their contribution to defense across treatments. We fitted a GLMM with a negative binomial error distribution and log link function. We included a constant zero-inflation value to account for zero inflated data (Supplementary Table S1a). We used the total number of aggressive behaviors of breeders and helpers as response variable. Social class, treatment, and activity of the stimulus fish were set as explanatory variables. We included the time each individual was outside the breeding chamber as a log offset term to account for differences in presence time between individuals. Additionally, we include harem ID as random effect to account for repeated observations of the same harem, and stimulus ID to account for the repeated use of the same stimulus fish for some territories. To test for differences in aggression between breeders and helpers across treatments, the interaction among social class and treatment was included. Two post-hoc tests were conducted on the interaction to compare 1) the investment of breeders and helpers in each treatment and 2) the investment between the treatments within each social class.

For all subsequent analyses, we fitted separate models for breeders and helpers. To test if the aggression shown by breeders was related to the presence of young or helpers and whether it changed depending on the treatment, we fitted a GLMM with negative binomial error distribution and a log link function. We used the total number of aggressive behaviors as response variable, and treatment, presence of helpers (yes/no) and young (yes/no), as well as breeder sex (female/male), as explanatory variables. We included harem ID as random effect to account for a given breeder male being measured in each of his female groups. Stimulus ID was set as an additional random factor and the time outside the breeding chamber was set as a log offset term. The top model included a constant zero-inflation value to account for zero inflated data (Supplementary Table S1b). We tested for the interactions between the presence of helpers or young and treatment. In case of a significant interaction term, we conducted a post-hoc analysis to investigate the pairwise difference across treatments.

Only a proportion of helpers attacked the stimulus fishes (16% in the predator of fish treatment, 26% in the predator of young treatment, 51% in the predator of eggs treatment, and 13% in the herbivore control treatment). However, those that attacked did so at high frequencies (Figure 1b). Therefore, aggression of helpers was analyzed by using GLMMs with a binomial error distribution and logit link function. The occurrence of aggressive interactions (yes/no) was used as response variable and treatment, presence of young, number of helpers, and body size of helpers were used as explanatory variables. Group ID nested within harem ID was included as random effect to account for repeated observations of the same group within a harem. The interaction between treatment and presence of young (yes/no) was included. Because of a significant interaction term between the presence of young and treatment, we conducted a post-hoc analysis to investigate the pairwise difference across treatments.

Time spent in the breeding chamber

In addition to predator defense, helpers take care of the offspring inside the breeding chamber (Josi et al. 2019). As helpers (but not breeders) reduced their defense behavior in the presence of young when confronted with a predator of young (see Results), we tested whether this reduction was associated with an increase in the time spent protecting the offspring inside the breeding chamber. Therefore, we fitted an LMM for helpers in the predator of young treatment, which consisted of time in the breeding chamber during the 5 min observation as response variable and the presence of young and SL of the helpers as explanatory variables. Group ID nested within harem ID was included as random effect.

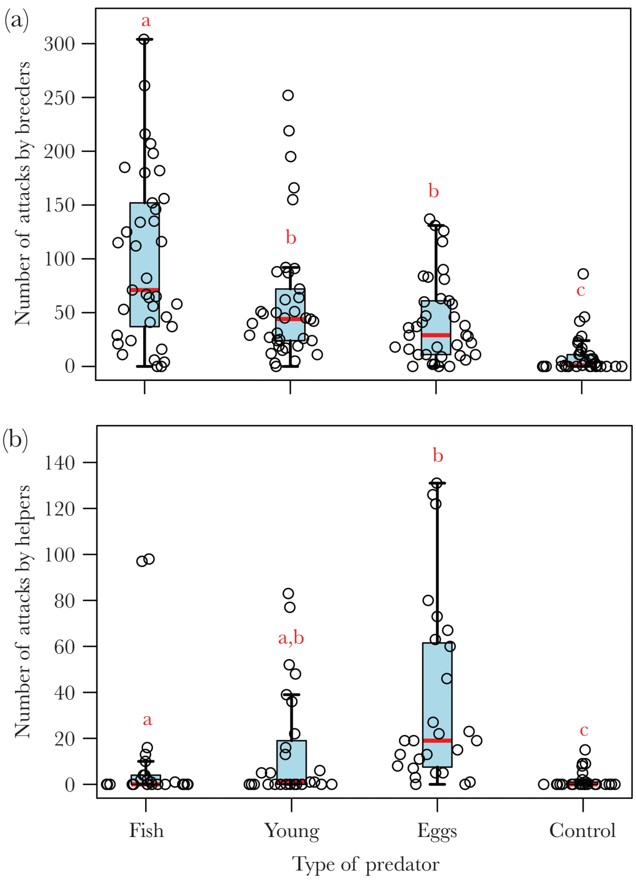

Figure 1

The breeders' (a) and helpers' (b) defense effort in relation to the different predator treatments. Red lines depict medians, blue boxes the interquartile range (IQR), and whiskers the value of the respective quartile (Q1 or Q3) ± 1.5 times the IQR. Circles show the density distribution of the original data points. Different superscripts indicate significant differences within each panel.

Differential male investment within harems

Polygynous breeder males are assumed to allocate their investment toward females in larger need, that is, those that are currently breeding (Jungwirth et al. 2016). To test for differences in male investment between different females within the harem, we used a subset of data that included all haremic breeder males monopolising at least one breeder female with young and one without. The count of aggressive behaviors of breeder males was set as response variable in a GLMM with negative binomial error distribution, a log link function and a constant zero-inflation value to account for zero inflated data (Supplementary Table S1c). We included the presence of young (yes/no), the presence of helpers (yes/no), and the activity of the stimulus fish as explanatory variables. Treatment and harem ID were added as random effects. In this data set, males were almost always present in the territory (mean value across treatment ranged between 286 and 292 s out of 300 s). Therefore, we did not include an offset term.

RESULTS

Breeder—helper comparison

Overall, aggression of all group members against intruders increased with increasing activity of the presented stimulus fish (Table 1, (a)). Breeder and helper aggression significantly differed across treatments, exemplified by a significant social class*treatment interaction (Table 1, (a)). The first post-hoc analysis revealed that breeders defended significantly more than helpers in the predator of fish treatment (Table 1, (b)) and herbivore control (Table 1, (b)). Furthermore, there was a marginal difference in the predator of young treatment, where breeders tended to defend more than helpers (Table 1, (b)). No difference in defense was found in the predator of eggs treatment (Table 1, (b)). The second post-hoc analysis (of the same initial model) across treatments revealed that the predator of fish received significantly more aggression by the breeders than all other stimulus fishes, whereas there was no difference between aggression levels against predators of young and predators of eggs (Table 1, (c); Figure 1a). The herbivore control fish received less aggression than all other stimulus fish (Table 1, (c)). The same post-hoc comparisons for helpers revealed that predators of eggs received most aggression from them, followed by the predators of young and fish (which received comparable amounts of aggression) and the empty control (Table 1, (c); Figure 1b).

Breeder defense

The breeders' aggression against intruders increased by 35% when dependent young were present, although this tendency was not statistically significant (Table 2, (a); Figure 2a). This trend did not depend on intruder type (treatment × presence of young: df = 3; $\chi^2 = 3.36$; $P = 0.34$). Aggression further increased with the activity of the stimulus fish (Table 2, (a)). Breeder males showed 52.6% less aggression than females (Table 2, (a)).

Breeder aggression toward intruders differed between treatments depending on the presence of helpers (Table 2, (a)). The post-hoc analysis of this interaction indicated that when helpers were present, breeders attacked predators of fish more often (Table 2, (b) and Figure 2b). There was a similar, nonsignificant trend in the same direction in the herbivore control (Table 2, (b)). Such effect was not shown in the predator of young treatment (Table 2, (b)) and in the predator of eggs treatment (Table 2, (b)).

Helper defense

The helpers' likelihood to defend against an intruder increased with their body size (Table 3, (a); Figure 3a). It neither changed

Table 1

Results of the comparisons of different reactions of group members to the presented intruders. (a) Estimates of the GLMM and the interaction between social class (breeder/helper) and the treatments. Two post-hoc comparisons on this interaction revealed (b) that investment differed between breeders and helpers and (c) that both (breeders and helpers) changed their investment depending on predator types. Aggressive behaviors within each treatment are shown as mean ± SE. Sample sizes are shown within parentheses for table (b) and in a separate column in table (c). Significant *P* values (<0.05) are highlighted in bold and marginally significant *P* values (<0.1) in italic digits

(a) Overall investment (model summary)

	Estimate		SE	df	χ^2	*P*
Intercept	2.827	±	0.169			
Activity	0.284	±	0.066	1	500.6	**<0.001**
Social class × treatment				3	30.58	**<0.001**

(b) Breeder–helper comparison (post-hoc)

Predator types		Breeder mean ± SE		Helper mean ± SE	df	χ^2	*P*
Fish	*L. elongatus*	49.6 ± 6.2 (74)	—	3.6 ± 1.8 (68)	1	45.3	**<0.001**
Young	*G. pfefferi*	30.4 ± 4.4 (74)	—	5.8 ± 1.9 (70)	1	3.65	*0.056*
Eggs	*T. vittatus*	21.3 ± 3.3 (74)	—	14.0 ± 3.3 (70)	1	0.05	0.83
Control	*X. spilopterus*	4.9 ± 1.6 (70)	—	0.7 ± 0.3 (69)	1	7.87	**0.005**

(c) Investment (post-hoc)

Predator type	Mean ± SE	*N*		Predator type	Mean ± SE	*N*	df	χ^2	*P*
Breeder									
Fish:	49.6 ± 6.2	74	—	Young:	30.4 ± 4.4	74	1	11.84	**<0.001**
Fish:	49.6 ± 6.2	74	—	Control:	4.9 ± 1.6	70	1	38.01	**<0.001**
Fish:	49.6 ± 6.2	74	—	Eggs:	21.3 ± 3.3	74	1	14.06	**<0.001**
Young:	30.4 ± 4.4	74	—	Control:	4.9 ± 1.6	70	1	6.99	**0.008**
Young:	30.4 ± 4.4	74	—	Eggs:	21.3 ± 3.3	70	1	0.02	0.89
Control:	4.9 ± 1.6	70	—	Eggs:	21.3 ± 3.3	70	1	5.64	**0.02**
Helper									
Fish:	3.6 ± 1.8	68	—	Young:	5.8 ± 1.9	70	1	1.01	0.31
Fish:	3.6 ± 1.8	68	—	Control:	0.7 ± 0.3	69	1	3.95	**0.046**
Fish:	3.6 ± 1.8	68	—	Eggs:	14.0 ± 3.3	70	1	6.39	**0.01**
Young:	5.8 ± 1.9	70	—	Control:	0.7 ± 0.3	69	1	5.04	**0.02**
Young:	5.8 ± 1.9	70	—	Eggs:	14.0 ± 3.3	70	1	1.56	0.21
Control:	0.7 ± 0.3	69	—	Eggs:	14.0 ± 3.3	70	1	8.77	**0.003**

Table 2

Results of the analyses of the investment of breeders in relation to the presence and absence of helpers and/or young. (a) Shown are the estimates of the GLMM and the interaction between helper presence (yes/no) and the different treatments. Breeder females are the reference for the factor sex. Based on this significant interaction, the post-hoc comparison (b) revealed that for certain predatory types, breeder investment changes depending on the presence or absence of helpers. Aggressive behaviors within each treatment are shown as means ± SE. Sample sizes are shown in parentheses. Significant *P* values (<0.05) are highlighted in bold and marginally significant *P* values (<0.1) in italic digits

(a) Breeder investment (model summary)

	Estimate		SE	df	χ^2	*P*
Intercept	2.290	±	0.218			
Activity	0.230	±	0.060	1	14.72	**<0.001**
Young present	0.237	±	0.134	1	3.13	*0.077*
Sex	−0.630	±	0.144	1	19.19	**<0.001**
Helper present × treatment				3	12.25	**0.007**

(b) Breeder investment in presence or absence of helpers (post-hoc)

Predator types		Helpers mean ± SE		No helpers mean ± SE	df	χ^2	*P*
Fish	*L. elongatus*	57.3 ± 7.4 (51)	—	31.7 ± 10.2 (22)	1	9.16	**0.002**
Young	*G. pfefferi*	27.7 ± 8.2 (53)	—	31.4 ± 5.2 (20)	1	0.07	0.78
Eggs	*T. vittatus*	23.5 ± 6.8 (53)	—	20.5 ± 3.8 (20)	1	0.06	0.81
Control	*X. spilopterus*	6.2 ± 2.1 (51)	—	1.2 ± 0.6 (18)	1	3.21	*0.07*

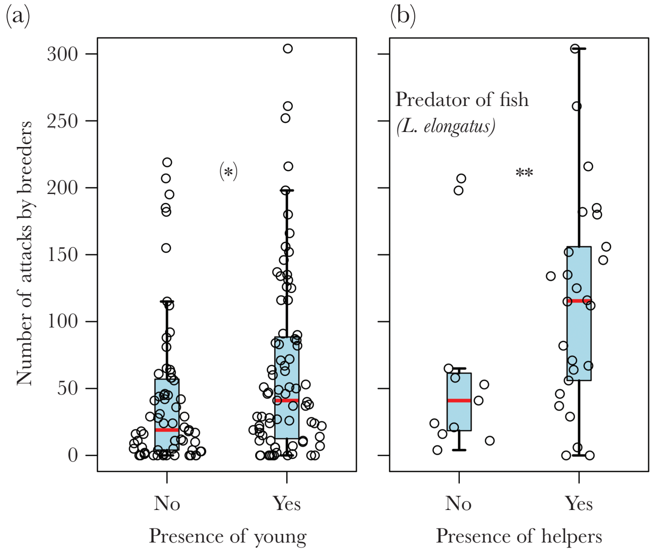

Figure 2

(a) The breeders' defense effort in relation to the presence of dependent young. (b) The breeders' defense effort in dependence of the presence of helpers. Red lines depict medians, blue boxes the interquartile range (IQR), and whiskers the value of the respective quartile (Q1 or Q3) ± 1.5 times the IQR. Circles show the density distribution of the original data points. (*) indicates $P < 0.1$; ** indicates $P < 0.01$.

with the number of other helpers in the group (Table 3, (a)), nor with the activity of the stimulus fish (Table 3, (a)).

There was a marginally significant interaction between the presence of young and treatment (Table 3, (a)). The post-hoc analysis of this interaction indicated that in the presence of young, the helpers' probability to attack decreased by 33.86% in the predator of young treatment (Table 3, (b); Figure 3b). There was a trend in the same direction (−27.42%) in the predator of eggs treatment (Table 3, (b)). In all other treatments, there was no difference in defense between the presence or absence of young (Table 3, (b)).

Time spent in breeding shelter

If exposed to a predator of young, helpers tended to spend more time in the breeding chamber when dependent young were present in the group ($n = 49$) compared with their absence ($n = 20$; Table 4; Figure 3c). The time helpers spent in the breeding chamber decreased with increasing body size (Table 4) and was not affected by the activity of the stimulus fish (Table 4).

Differential male investment within harems

Male breeders ($n = 13$) did not defend more in subterritories that had dependent young present (Table 5). Additionally, the presence of helpers and breeder male size had no significant influence on the allocation of antipredator defense of males within their harems (Table 5). Increasing activity of the stimulus fish significantly enhanced the males' defense behavior (Table 5).

DISCUSSION

Defense against predators is an essential component of brood care. In cooperative breeders, the guarding of young represents an important helping task that may enhance offspring survival and yield direct and indirect fitness benefits to all group members (Brouwer et al. 2005). In this study, we experimentally investigated how breeders and helpers partition defense against predator threats as a function of predator type and the presence of dependent young. Our results indicate task sharing among group members when dependent young are present. Breeders invested mainly in direct territory defense while helpers increased their presence in the breeding chamber if young were at immediate risk. They furthermore contributed to defense depending on their body size and intruder type.

An accurate assessment of predators threatening different classes of group members is important for efficient and successful defense of offspring, mating and social partners, and the territory. Our results indicate that breeders adjusted their investment to the respective threat level in relation to the presence of young and helpers. Breeders were most aggressive against the fish predator, followed by attacks toward predators of young and eggs, which received similar

Table 3

Results of the analyses of the helpers' investment (attack probabilities) in relation to their size, the number of other helpers, and the presence or absence of young. (a) The estimates of the GLMM are shown and the interaction between presence of young (yes/no) and the different treatments. Based on this interaction, the post-hoc comparison (b) revealed that for certain predatory types, the helpers' attack probability changed depending on the presence or absence of young. The model-predicted attack probabilities within each treatment are shown as means ± SE. Sample sizes are shown in parentheses. Significant *P* values (<0.05) are highlighted in bold and marginally significant *P* values (<0.1) in italic digits

(a) Helpers' attack probability (model summary)

	Estimate		SE	df	χ^2	*P*
Intercept	−1.622	±	0.655			
Activity	0.137	±	0.152	1	0.83	0.86
Body size	0.101	±	0.020	1	31.07	**<0.001**
Helper number	−0.024	±	0.138	1	0.03	0.36
Young present × treatment				3	7.6	*0.055*

(b) Helpers' attack probability in presence or absence of young (post-hoc)

Predator types		Young mean ± SE		No young mean ± SE	df	χ^2	*P*
Fish	*L. elongatus*	0.15 ± 0.02 (47)	—	0.20 ± 0.04 (20)	1	0.24	0.63
Young	*G. pfefferi*	0.16 ± 0.02 (49)	—	0.50 ± 0.04 (20)	1	6.88	**0.009**
Eggs	*T. vittatus*	0.43 ± 0.03 (49)	—	0.70 ± 0.04 (20)	1	3.62	*0.057*
Control	*X. spilopterus*	0.16 ± 0.02 (49)	—	0.05 ± 0.02 (19)	1	1.4	0.24

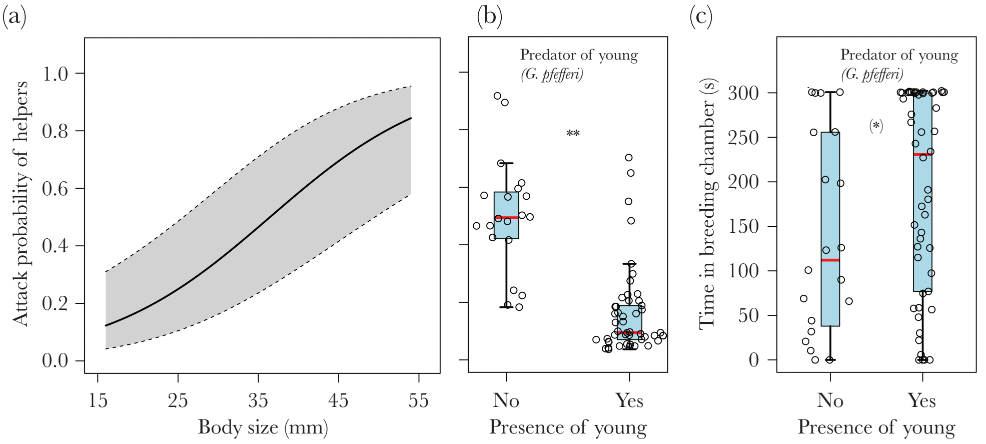

Figure 3

(a) The attack probability of helpers in dependence of body size. Larger helpers showed more antipredator defense (see text for statistical results). Shown is the model-predicted regression (black line) ± 95% confidence intervals (gray). (b) The attack probability of helpers against a predator of young (*G. pfefferi*) in dependence of the presence of small young. (c) The time helpers spent in the breeding chamber when a predator of young was presented, in dependence of the presence of young. Red lines depict medians, blue boxes the interquartile range (IQR), and whiskers the value of the respective quartile (Q1 or Q3) ± 1.5 times the IQR. Circles show the density distribution of the predicted (b) or original (c) data points. (*) indicates $P < 0.1$; ** indicates $P < 0.01$.

amounts of aggression (Figure 1a). All predators received significantly more aggressive attacks from breeders than the nonpredatory control fish. The fact that breeders adjust their investment to the respective threat level is further corroborated by the increased defense behavior in the presence of dependent young (Figure 2a). This effect did not change across treatments, indicating that any intrusion by heterospecifics might be harmful to their young. Breeders did defend differently across treatments, though, in dependence of helper presence. When helpers were present, breeders attacked the fish predator at a higher frequency (Figure 2b), suggesting enhanced protection for helpers. Such fine-tuned adjustments in defense effort against predators may be selected for in environments with a large diversity of predator types, as pertaining to our study population. Here, the fitness consequences of antipredator behavior for breeders depend strongly also on the presence of eggs, young, and helpers.

Costs and benefits associated with defending against predators differ between group members depending on an individual's social status, sex and body size, and on the reproductive state of the group. The helpers' participation in territory defense should hence vary with the presence of young (i.e., because they are helping kin and/or paying for being allowed to stay; Zöttl, Heg, et al. 2013) and the costs of attacking. Our results indicate that both apply in *N. savoryi*. The number of aggressive behaviors directed toward the fish predator was significantly lower in helpers compared to breeders, which corresponds to their higher risk of being injured or killed when attacking. Additionally, helpers tended to attack predators of young less often than the breeders did, and

Table 4

The time helpers spent in the breeding chamber (analyzed in minutes) during the presentation of the predator of young (*G. pfefferi*) in relation to helper size, the presence or absence of young (yes/no) and the activity of the predator (*n* = 69). Estimates of the GLMM are shown. Significant *P* values (<0.05) are highlighted in bold and marginally significant *P* values (<0.1) in italic digits

Time spent in breeding shelter

	Estimate		SE	df	χ^2	*P*
Intercept	2.409	±	0.351			
Activity	0.190	±	0.192	1	1.03	0.31
Young present	0.780	±	0.418	1	3.6	*0.058*
Body size	−0.109	±	0.020	1	25.58	**<0.001**

Table 5

Results of the differential male investment within their harem (*n* = 13) in relation to the presence or absence of helpers (yes/no) and young (yes/no), body size, and activity of the different predators. Estimates of the GLMM are shown. Significant *P* values (<0.05) are highlighted in bold digits

Differential male investment within harems

	Estimate		SE	df	χ^2	*P*
Intercept	2.353	±	0.703			
Activity	0.316	±	0.140	1	5.560	**0.018**
Young present	0.398	±	0.301	1	1.74	0.19
Helper present	0.202	±	0.340	1	0.35	0.55
Body size	0.065	±	0.044	1	1.970	0.16

they were less likely to attack these intruders if the breeder female had dependent young (Figure 3b). At first sight, this seems counterintuitive. However, in this treatment, helpers spent more time in the breeding chamber, which likely enhanced the guarding of young that are usually hiding in the shelter while the breeders attacked the intruder (Figure 3c). As a predator of young does not pose a risk to helpers and the response of helpers changed with the presence or absence of young, we assume that these helpers were not just hiding in the shelter but actively guarding the young. Additionally, helpers often have private shelters next to the breeding chamber, which could have been used for increasing protection instead. The importance of visits to the breeding chamber has further been suggested by a recent study of *N. savoryi* in a nonpredatory context. Here, both breeders and helpers increased breeding chamber attendance when dependent young were present (Josi, Taborsky, et al. 2020). This indicates that shelter visits are a good proxy for offspring care (cf. Stiver et al. 2005). Our results suggest that the presence of dependent young induced partitioning of protective tasks between breeders and helpers when they were challenged by predatory intruders posing an immediate risk for dependent young. While breeders invested most in direct territory defense, helpers increased their attendance and care for the young in the breeding chamber. Comparable task sharing, where the labor is divided among group members belonging to different life stages occurs in some eusocial insects (Oster and Wilson 1978; West and Purcell 2020), and has been shown also in a few other cooperatively breeding vertebrates (Clutton-Brock et al. 2004; Arnold et al. 2005; Bruintjes and Taborsky 2011).

In *N. savoryi*, division of labor among helpers is apparently size dependent. The probability to attack an intruding predator increased with increasing body size of helpers across all treatments (Figure 3a). In contrast, smaller helpers spent more time in the breeding chamber, where they guard and care for dependent young and eggs (Josi et al. 2019). Additionally, these smaller helpers might themselves gain protection in the shelter, indicating that tasks might be shared depending on individual risk. In the cooperatively breeding congener *N. pulcher*, tasks are shared differently among subordinate group members when two environmental challenges were presented simultaneously; large helpers specialized in digging sand out of the breeding shelter, whereas small helpers defended the breeding shelter against egg predators, which was explained by the size-specific efficiency of helpers (Bruintjes and Taborsky 2011). Comparable sharing of digging activity also occurs in *N. savoryi* (Josi, Taborsky, et al. 2020). In the present study, no sand was added to the breeding shelter. Therefore, the higher defense effort of large helpers might reflect their greater efficiency in this duty.

The attack probability of helpers was highest in the egg predator treatment (Figure 1b), which again might reflect efficiency. Here, the total number of helper attacks was comparable to that of the breeders. The egg predator *T. vittatus* is a small species that can be easily ousted by helper-sized *N. savoryi*. Furthermore, a recent study revealed that *T. vittatus* is strongly attacked in the presence of eggs (Josi et al. 2019). We do not know whether eggs were present in the breeding chamber during the experiment as checking for eggs would have destroyed the shelter. Still, as spawning in *N. savoryi* occurs regularly throughout the year, it is highly likely that this applied at least to some of the territories. Comparable context-specific effects on territory defense were also shown in *N. pulcher* (Desjardins, Stiver, et al. 2008; Zöttl, Frommen, et al. 2013), indicating that size-dependent sharing of defense might be a common pattern in cooperatively breeding cichlids.

Besides a higher defense efficiency, there are several other nonmutually exclusive explanations for sized-depended investment in defense. Large body size may imply a lower risk of injuries or death, leading to lower costs of aggression against larger intruders. In addition, large helpers are sexually mature. Therefore, the enhanced defense effort of large helpers in *N. savoryi* could be partly associated also with direct fitness benefits gained through shared reproduction (cf. Bruintjes et al. 2011). Finally, large helpers might have to pay a higher price to stay in the territory because of costs imposed on dominant breeders due to their potential participation in reproduction (Heg and Taborsky 2010; Quiñones et al. 2016).

In polygynous mating systems, females may suffer from reduced paternal care as compared to monogamous systems, and breeder males may allocate a greater investment toward females in larger need, for example, because they are currently breeding or have few or no helpers (Jungwirth et al. 2016). In line with this assumption, female *N. pulcher* paired to polygynous males received overall less paternal care effort than females paired to monogamous partners (Desjardins, Fitzpatrick, et al. 2008; Jungwirth et al. 2016). These findings were corroborated in our experiment, where breeder females with dependent young did not receive increased assistance from the breeder male, independently of whether the female had helpers or not. This indicates a potential sexual conflict over the mating pattern and harem size between males and females. Furthermore, competition for male support could be a source of potential conflict among breeder females within the harem. The strength and importance of such intrasexual and intersexual conflicts, and potential adjustments of male and female breeding strategies, would pose a challenging subject for future studies.

In summary, this study reveals fine-tuned task-dependent behavioral adjustments among different group members in a cooperatively breeding fish species, especially when risk for dependent young is high. In the presence of small offspring, breeders and helpers showed division of labor, with breeders taking over the main defense duties and helpers guarding the young in the breeding chamber. Our findings highlight the importance of incorporating ecological and reproductive parameter variation for understanding the function and maintenance of helping in cooperatively breeding species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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AUTHOR CONTRIBUTIONS

D.J., M.T., and J.G.F. conceived the study and organized funding; D.J. conducted the experiments; A.F. analyzed the video material; and D.J. and A.F. analyzed the data and wrote the first draft of the manuscript, which was revised by M.T. and J.G.F.; all authors approved the final version of the manuscript.

Data availability: Analyses reported in this article can be reproduced using the data provided by Josi, Freudiger, et al. (2020).

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