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Punishment controls helper defence against egg predators but not fish predators in cooperatively breeding cichlids

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Helping behaviour in some cooperative breeders is apparently maintained by a combination of coercion and reciprocity. In such pay-to-stay systems, alloparental brood care of subordinate group members functions as a service to dominants, which tolerate subordinates based on how much help they provide. Cooperative territory defence is a key task of cooperative breeders, but it is unknown how territory defence by subordinates is socially regulated. Diverse costs and benefits associated with defending the territory against different threats suggest that these defence behaviours may be maintained through divergent selection regimes, and they might be regulated through different social processes. In the cooperatively breeding cichlid fish *Neolamprologus pulcher*, unrelated subordinates help defend the territory against egg predators even if they do not participate in reproduction and therefore do not suffer direct or indirect fitness costs through predators of eggs. This behaviour has therefore been interpreted as altruistic service to dominants. Subordinates also defend the group territory against predators of juveniles and adults, which might at least partly reflect their own direct fitness interests and could be maintained through mutualistic interactions among group members. Here, we directly compared the regulation of these two types of defence behaviours and tested whether they are enforced by breeders. We prevented subordinates from defending the territory against egg predators or predators of adults and observed whether they received more aggression in response to this treatment. We found that subordinates received more aggression from breeders after withholding defence against egg predators, but not after withholding defence against fish predators. This suggests that territory defence against egg predators by helpers is enforced by breeders and hence subject to negotiations and trading, whereas defence against fish predators is probably based on mutualistic fitness benefits.

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Evolutionary theory explains traits of individuals as means to compete for limited resources (Darwin, 1859). Yet some traits appear to be altruistic, favouring other individuals at an immediate cost to the actor. Many altruistic traits can be explained by kin selection, mutualistic benefits or coercion, but some seem to be based on a reciprocal exchange of same or different commodities resembling human trade (Lehmann & Keller, 2006). In such reciprocal relationships, traits that benefit others are selected for through benefits obtained from others in return (Taborsky, Frommen, & Riehl, 2016; Trivers, 1971). Evolutionarily stable reciprocal altruism thus requires a contingency between benefits received and benefits given, which may simply be a consequence of certain population structures (generalized reciprocity; Boyd & Richerson, 1989; van Doorn & Taborsky, 2012; Hamilton & Taborsky, 2005a; Nowak & Roch, 2007; Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005; Rankin & Taborsky, 2009). Alternatively, the trait may be expressed differentially towards individuals that are likely to reciprocate received benefits (direct reciprocity; Axelrod & Hamilton, 1981; Carter & Wilkinson, 2013; Rutte & Taborsky, 2008).

Drawing a clear line between the four fundamental mechanisms generating evolutionarily stable levels of cooperation (mutualism, kin selection, enforcement and reciprocity; Lehmann & Keller, 2006) is often difficult and can be misleading, because more than one of these mechanisms may be involved concomitantly (Carter, 2014; Carter, Schino, & Farine, 2019; Taborsky et al., 2016). Two distinctions are especially problematic to make. First, it may be difficult to distinguish reciprocity from mutualistic interactions. While it is easy to show that a trait benefits others, it is much harder to show that the trait is contingent on predictable return benefits (reciprocity; Clutton-Brock, 2002). The trait may instead

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have been selected for selfish benefits and may provide advantages for others as a mere by-product (mutualism; Brown, 1983). Second, the evolution of reciprocity and coercion may not be easily separated from each other, as reciprocal exchanges usually occur between partners with different negotiating power (Quiñones, Doorn, Pen, Weissing, & Taborsky, 2016). Power asymmetries may provide opportunities for the more dominant partner to demand a service from the subordinate (coercion; Cant, 2011). This does not prevent reciprocity from evolving (Johnstone & Bshary, 2007, 2008), but it highlights the importance of considering the asymmetry in negotiating power when aiming to understand the mechanisms underlying reciprocal exchanges (Phillips, 2018).

All four mechanisms mentioned above are probably involved in the evolution of alloparental care in cooperative breeders. This breeding system is characterized by philopatry and reproductive skew and has been observed in a wide range of group-living birds, mammals, fishes and insects (Choe & Crespi, 1997; Koenig & Dickinson, 2004, 2016; Solomon & French, 1997; Taborsky & Wong, 2017). Subordinate group members typically delay dispersal and help to raise the offspring of dominants and, therefore, are called helpers. Dominants benefit from the services of helpers through increased offspring survival and reduced workload (Brouwer, Heg, & Taborsky, 2005; Johnstone, 2011). For example, when helpers are present, dominants may lay smaller eggs (Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007; Taborsky, Skubic, & Bruintjes, 2007), increase their reproductive rate (Taborsky, 1984) or survive longer (Langmore, Bailey, Heinsohn, Russell, & Kilner, 2016; Russell et al., 2007).

The pay-to-stay hypothesis of cooperative breeding explains the evolution of helping behaviour through an interplay of coercion and reciprocity. It asserts that the alloparental care behaviour of subordinates functions as rent payment to dominants, which differentially tolerate subordinates in their territory based on how much help they provide (Gaston, 1978; Hamilton & Taborsky, 2005b; Hellmann & Hamilton, 2018; Kokko, Johnstone, & Wright, 2002). Helping behaviour is thus believed to have acquired the function of reducing aggression from dominant individuals, similar to submissive displays (Bergmüller & Taborsky, 2005; Taborsky & Wong, 2017). Subordinates may benefit in many ways from being tolerated by territory owners, proximately through resource access or reduced predation risk and ultimately through reproductive participation, queuing for dominance and increased survival (Bruintjes, Bonfils, Heg, & Taborsky, 2011; Grinsted & Field, 2017; Groenewoud et al., 2016; Heg, Bachar, Brouwer, & Taborsky, 2004; Hellmann et al., 2015; MacLeod, Nielsen, & Clutton-Brock, 2013; Taborsky, 1984, 1985; see Taborsky et al., 2016 for a review). Other theories of cooperative breeding focus on the direct fitness benefits of helping behaviour (Clutton-Brock, 2002; Kingma, 2017). One renowned example is the sentinel behaviour of Arabian babblers, *Turdoides squamiceps*, which is apparently selected by increasing the survival of the sentinel, yet also reduces predation risk for other group members as a by-product (Wright, Berg, De Kort, Khazin, & Maklakov, 2001). Alloparental care and group territoriality in cooperative breeders may similarly reflect mutualistic interactions, for example through group augmentation effects (Kingma, Santema, Taborsky, & Komdeur, 2014; Kokko, Johnstone, & Clutton-Brock, 2001).

To understand the relative importance of reciprocity, coercion and mutualism in the evolution of helping, it is necessary to investigate the regulation of specific helping behaviours. The reason for this is that different behaviours classified as helping fulfil different functions and may be associated with considerably different costs and benefits for both subordinates and dominants (Grantner & Taborsky, 1998; Josi, Taborsky, & Frommen, 2020; MacLeod et al., 2013; Mulder & Langmore, 1993; Taborsky, 2016). Detailed knowledge about the regulation of different helping behaviours may allow us to find general principles in the evolution of alloparental care. Known variation in costs and benefits between different alloparental care behaviours can be used to derive testable predictions about the decision rules involved in their regulation and the selective forces that form and maintain them. For a number of reasons, cooperatively breeding cichlids such as *Neolamprologus pulcher* offer a unique opportunity for these types of studies. First, the costs and benefits associated with various helping behaviours have been determined (Taborsky & Grantner, 1998). Second, experimental studies are more practical in cichlids than in birds or mammals, since important factors such as relatedness, environmental conditions, group composition and the behaviour of group members can easily be manipulated in aquaria and in the wild (Taborsky, 2016). The negotiation rules applied in such groups are increasingly well understood, but experimental studies that investigate the regulation of specific helping behaviours are scarce (Balshine-Earn, Neat, Reid, & Taborsky, 1998; Bergmüller, Heg, & Taborsky, 2005; Bergmüller & Taborsky, 2005; Bruintjes & Taborsky, 2008; Fischer, Zöttl, Groenewoud, & Taborsky, 2014; Heg & Taborsky, 2010; Naef & Taborsky, 2020a; Quiñones et al., 2016; Taborsky, 1985; reviewed in ; Taborsky & Wong, 2017).

A previous study of the social cichlid *N. pulcher* suggested that the helper's territory maintenance behaviour (digging out shelters) reduces the aggressive behaviour of dominants towards the helper, as predicted by the pay-to-stay hypothesis. In contrast, the helper's defence behaviour against egg predators was associated not with these appeasement effects but with a compensatory response, as helpers intensified their defence efforts against egg predators after a period of experimental prevention (Naef & Taborsky, 2020a). This compensatory response has also been described for defence against conspecific intruders (Bergmüller & Taborsky, 2005) and for direct egg care (Schreier, 2013). It has been suggested that its function is to prevent punishment by breeders through pre-emptive appeasement (Bergmüller & Taborsky, 2005), which implies that helpers would be punished if prevented from showing this compensatory response. However, a compensatory response could also result from an intrinsic and purely selfish regulation of territory defence. It is therefore unclear whether reciprocity and coercion are involved in regulating territory defence of subordinate group members as predicted by the pay-to-stay hypothesis, or whether this behaviour represents a mutualistic interaction between group members.

An intriguing aspect of cooperative territory defence is that the evolutionary forces maintaining it may depend on the particular challenge, because different intruder types may be associated with different defence abilities, and with varying costs and benefits of defence for different types of group members (Desjardins, Stiver, Fitzpatrick, & Balshine, 2008; Taborsky, 1984, 1985; Taborsky, Hert, Siemens, & Stoerig, 1986). Here we compared the regulation of defence against two different types of intruders for which costs and benefits of defence diverge substantially: egg predators and predators of adults (i.e. fish predators). Subordinates gain no direct fitness benefit from defending the territory against egg predators, but this behaviour is frequently observed in this species (Bruintjes & Taborsky, 2011; Weber, 2012). It may thus be interpreted as being altruistic, because it is beneficial to breeders (Weber, 2012), but costly to helpers (Grantner & Taborsky, 1998). In contrast, defending the territory against fish predators may entail direct fitness benefits for helpers through deterring the predator and, perhaps, also signalling the helper's own strength to the predator. This behaviour might thus reflect a selfish tendency that creates benefits for breeders as a by-product. These differences suggest divergent regulatory mechanisms: defence against egg predators by helpers might be part of the negotiation process between subordinates and breeders that characterizes the pay-to-stay process, whereas defence against fish predators by helpers may not be part of this cooperative exchange, but may reflect a mutualistic interaction.

To test these predictions, we presented groups of *N. pulcher* either with intruding egg predators or with fish predators and prevented the focal helper from defending the territory. The expected compensatory response was experimentally suppressed in one treatment and allowed in the other. To keep the total time that helpers can defend constant between treatments, both treatments included a phase during which defence was prevented and another phase during which defence was possible. We systematically varied the sequence of these two phases. In the treatment where defence was first prevented and then allowed, helpers had the opportunity to compensate. In the treatment where defence was first allowed and then prevented, they could not. We predicted that helpers would not show any compensation and would not be punished if prevented from defending against fish predators, whereas punishment and/or compensation should occur if the defence against egg predators were experimentally inhibited. We added a third pair of treatments where the same manipulations were applied in the absence of any intruder, to control for potential effects of our experimental procedure (Figs. 1 and 2).

METHODS

Study Species

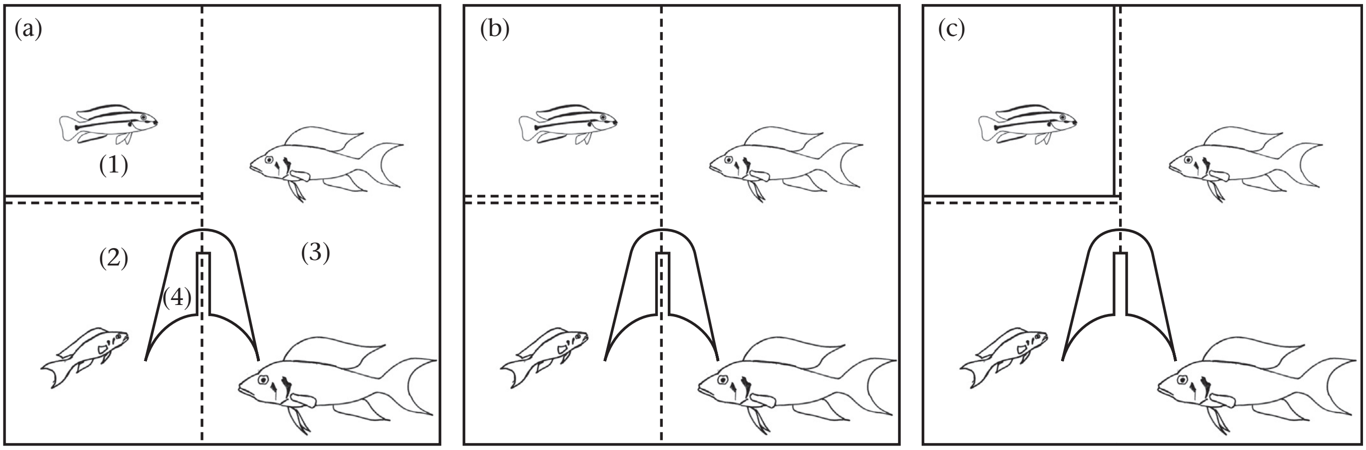
Neolamprologus pulcher is a cooperatively breeding, small cichlid fish endemic to Lake Tanganyika, Africa (Brichard, 1978; Duftner et al., 2007; Poll, 1986). Groups consist of a breeding pair and up to 30 immature and mature helpers of both sexes, and exhibit a size-based dominance hierarchy (Balshine et al., 2001; Taborsky, 1984; Taborsky & Limberger, 1981). They inhabit diverse habitats along the shore of the lake and form colonies of up to 200 groups (Heg, Heg-Bachar, Brouwer, & Taborsky, 2008; Jungwirth, Josi, Walker, & Taborsky, 2015). Helpers are often not related to the other group members, as their relatedness to other group members declines with age due to group membership dynamics (Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005; Stiver, Dierkes, Taborsky, Lisle Gibbs, & Balshine, 2005). Reproductive skew is generally high in this species, and reproductive parasitism by female helpers in the main breeding shelter is rare (Heg & Hamilton, 2008; Taborsky, 2009, 2016).

Telmatochromis vittatus is a cichlid fish similar in size to *N. pulcher* (Brichard, 1978) that is abundant in *N. pulcher* habitats (Heg et al., 2008). It feeds opportunistically on eggs and fry (Bruintjes & Taborsky, 2011; Konings, 2019; Ochi & Yanagisawa, 1998; Weber, 2012) and is expelled from *N. pulcher* territories by both dominant and subordinate group members, even though it is no direct threat to subordinates. Defence against *T. vittatus* by nonbreeding, unrelated subordinate group members has therefore been interpreted as altruistic helping behaviour that primarily benefits the dominant breeders (Bruintjes & Taborsky, 2011; Kasper, Colombo, Aubin-Horth, & Taborsky, 2018; Weber, 2012).

Lepidiolamprologus elongatus is a large solitary cichlid (Brichard, 1978) and one of the most common predators of adult *N. pulcher*, being abundant in *N. pulcher* colonies (Balshine et al., 2001; Groenewoud et al., 2016; Heg et al., 2004, 2008; Taborsky, 1984).

Experimental Animals

All experimental animals were obtained from our laboratory stock populations originating from Kasakalawe Point, Zambia. We used 108 *N. pulcher* as focal subjects, four *T. vittatus* as egg predators and four *L. elongatus* as predators of adults. The *N. pulcher* stock was kept in separate-sex groups of about 30 individuals in 400-litre tanks without breeding shelters. This simulates aggregations of wild individuals that are too small to take over a breeding position (Taborsky, 1984; Taborsky & Limberger, 1981). The *T. vittatus* stock was kept in 200-litre tanks with breeding shelters, in mixed-sex groups of about 30 individuals, and *L. elongatus* were kept in pairs in 400-litre tanks, with the two pair members separated by transparent perforated partitions to allow for olfactory and visual communication while preventing aggressive interactions. As *L. elongatus* is a solitary species except when breeding in pairs (Brichard, 1978; M. Taborsky, personal observations), this housing



Defence against egg predator prevented

Defence against egg predator allowed

Test phase

Figure 1. Tank set-up as seen from above and experimental procedure, using the example of the treatment with an egg predator where defence compensation was possible ('EP+', see Fig. 2). Dotted lines depict transparent partitions with holes; solid lines depict opaque partitions. (a) The general tank set-up. (1) Intruder presentation compartment, (2) helper compartment, (3) breeder compartment, (4) shared breeding shelter. The gap in the top of the shelter accommodates a transparent partition to separate the helper from the breeders during the manipulation phase of the experiment. This is the situation 'EP_N', where an egg predator (T. vittatus) is presented in the intruder compartment and the helper is prevented from defending. (b) This is the situation 'EP_Y', where defence behaviour of the helper has been made possible by replacing the opaque partition between helper and intruder compartments with a transparent one. (c) During the test phase, the intruder compartment is sealed off from the group with opaque partitions and the separation between helper and breeder compartments is removed to allow all group members to use the entire territory. This also corresponds to the situation outside experimental trials.

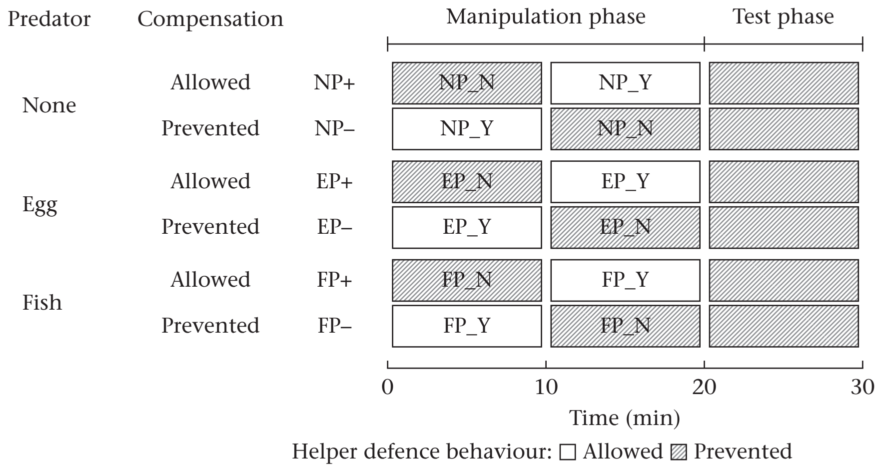


Figure 2. Example of the sequence of six treatments to which each experimental group was exposed. Each row represents one 30 min treatment, composed of three consecutive 10 min periods (shown as boxes). The first two periods ('Manipulation phase') differed with respect to the type of predator presented, and whether or not the helper was allowed to defend the territory (white boxes: defence allowed; hatched boxes: defence prevented). The sequence of the two manipulations determined whether the helper had the opportunity to compensate for lost defence opportunities or not (compensation allowed/prevented). The last period ('Test phase') was identical for all treatments. Each box thus corresponds to one data point, i.e. one 10 min recording in which behaviours were counted. Treatment names are composed of the type of predator that was presented and whether or not the helper could compensate for lost defence opportunities (NP: no predator; EP: egg predator; FP: fish predator; '+': compensation possible; '–': compensation prevented). Manipulation phase: '_N': defence by helper prevented; '_Y': defence by helper allowed. The procedure for treatment 'EP+' is shown in detail in Fig. 1.

set-up can prevent social stress. All aquaria were maintained at an average temperature of 26 °C, with a 13:11 h light:dark cycle. Fish were checked daily and fed with dry food 5 days a week, and with frozen plankton on 1 day a week. All aquaria contained air-driven biological filters. All animals were returned to their respective stock tanks after the experiments.

Breeding Groups

We created 36 groups of three unrelated individuals each: a breeding male (5.4–6.5 cm standard length, SL), a breeding female (4.5–5.5 cm SL) and a sexually mature female helper (3.5–4.5 cm SL). Groups of this composition occur in the wild (Balshine et al., 2001; Dierkes, Taborsky, & Achmann, 2008) and show natural behaviour when created in the laboratory (Dierkes, Taborsky, & Kohler, 1999; Taborsky, 1984). The three group members were selected to have a size difference of at least 10 mm to each other to facilitate the formation of a clear dominance hierarchy. The fish were caught from aggregation tanks and assigned to groups according to their size and sex. All fish were put in the experimental tank on the same day (day 0), but the dominant male and female were initially contained in isolation nets to allow the helper to take possession of the shelter provided. The dominant female was released on day 1 and the dominant male on day 2. Upon release from the isolation nets, the fish usually engaged in aggressive interactions, but had established a clear dominance hierarchy by day 3. Groups were considered stable if the helper was accepted in the breeding shelter and ritualized aggression–submission interactions indicated a clear dominance hierarchy. On day 7, 26 stable groups were randomly selected for the experiment. The other groups were discontinued, and their members transferred back to their home tanks. Manipulations and observations took place on days 9–14.

Aquarium Set-up

We used 200-litre tanks that were divided in half with a transparent, perforated partition. The breeding groups established in these compartments thus had visual and olfactory contact with the group in the other half of the tank. This situation induces territory defence behaviour, which greatly reduces within-group aggression and increases group stability (Bruintjes, Lynton-Jenkins, Jones, & Radford, 2016; Fischer, Bohn, Oberhummer, Nyman, & Taborsky, 2017; Taborsky, 1985). Each group's territory was divided into three compartments with transparent perforated partitions: one for presenting an intruder, one for the helper and one for the breeders (Fig. 1). The divisions that defined the intruder compartment were fixed to the tank, but the division between helper and breeder compartments was only inserted during experimental manipulations according to need. A flowerpot half, which is the breeding shelter this laboratory population of *N. pulcher* is used to, was cut and placed in such a way that half of the shelter was in the helper compartment and the other half in the breeder compartment (see Naef & Taborsky, 2020a).

Design

Our experiment followed a within-subject design, where each of the 26 groups was exposed to six 30 min treatments that differed with respect to two crossed factors: 'intruder species' and 'compensation'. 'Intruder species' distinguishes the type of predator that was presented to the group: either no predator (control), an egg predator (*T. vittatus*) or a fish predator (*L. elongatus*). 'Compensation' refers to whether the helper could compensate for a period of induced idleness in defending the group territory, which was achieved by blocking the helper's view of the intruder. Where compensation was possible, defence behaviour by the helper was first prevented for 10 min (view of intruder blocked) and then allowed for 10 min (view of intruder available); where compensation was prevented, defence was first allowed and then prevented. This two-part, 20 min manipulation phase was followed by a 10 min test phase that was identical for all treatments (see Fig. 1 for a depiction of the experimental procedure and Fig. 2 for an overview of treatments). Treatments were recorded on 6 consecutive days, each group at a specific time of day. The two treatments with the same intruder species but different levels of compensation were recorded on consecutive days in random order, with the same intruder specimen for a specific group. The order of treatment pairs with the same intruder species was balanced across groups, with each order being tested four times (24 groups/six possible permutations of intruder species order). In seven groups, either the helper or the dominant female was evicted from the group before all treatments were recorded. These groups were discontinued, and the treatments already recorded were discarded, resulting in a total of 19 groups for which data on all treatments were collected. This comprises the total data set used in the analyses.

Experimental Procedure

On the evening of the day before each trial started, the intruder compartment was sealed off from the focal group with solid opaque partitions, and the predator used in the respective treatment was introduced. The predator thus had at least 12 h to acclimatize to the new environment. In a pilot study we found this to be sufficient for achieving natural behaviour of both predator species used in this experiment. The partitions used to conceal the intruder during this period were not perforated, to minimize passive water exchange and thus prevent the group from recognizing the predator by smell before the start of the treatment.

The focal group was allowed to habituate to the recording situation for 10 min before the start of each treatment. At the start of this habituation phase, the group was visually separated from the group in the neighbouring compartment of the same tank with solid opaque partitions to prevent interactions between them during the experiment, and the cameras were installed in the tank. The experimental partition that would later manipulate defence behaviour of the helper was also inserted between the helper and intruder compartments at this point. An opaque partition was used to prevent defence behaviour of the helper by restricting its view of the predator, and a clear partition was used if defence behaviour was allowed. These partitions had holes that lined up with the holes in the fixed partition between helper and intruder compartments to allow passive water exchange and olfactory recognition of the predator. Note that this experimental partition did not affect intruder visibility or passive water exchange at this point, as the intruder remained sealed off from the group with solid opaque partitions throughout the 10 min habituation phase. The purpose of inserting the experimental partition now rather than later was to minimize and standardize the necessary manipulations after the habituation phase.

After the habituation phase, we gently guided the helper to the helper compartment and inserted the transparent partition between helper and breeder compartments. The partitions that sealed off the intruder compartment were then removed, revealing the predator to the breeders, but leaving the experimental partition previously inserted between helper and intruder compartment in place, such that the helper could either participate in defence or not, depending on the treatment. The group was then left undisturbed and was recorded for 10 min (first part of the manipulation phase, Fig. 1a). After this first 10 min recording, the experimental partition between helper and intruder compartments was switched: if an opaque partition had been used in the first period, a transparent partition was now inserted and vice versa. The group was again left undisturbed and was recorded for another 10 min (second part of the manipulation phase, Fig. 1b). After this second 10 min recording, the transparent partition that separated the helper from the breeders was removed, allowing the helper to use the entire territory and interact physically with the breeders. The intruder compartment was sealed off, thus re-establishing the situation from before the start of the treatment. The group was again left undisturbed and was recorded for 10 min (test phase, Fig. 1c).

Behavioural Observations

All 30 min treatment sessions were recorded with two small action-cameras (SJCAM M10) at a resolution of 720p, a frame rate of 30 fps and a bit rate of 6554 Kb/s, compressed as mpeg-2. One camera was placed in front of the aquarium (bottom edge in Fig. 1), and the other in the water, facing the helper and intruder compartments (right edge in Fig. 1). This ensured that all parts of the territory, including the inside of the shelter, were always visible. We used a clapperboard to synchronize the two video streams, and combined them in a Matroska container file using the open-source programs FFmpeg (FFmpeg Developers, 2016) and Audacity (Audacity Team, 2016). To avoid observer bias, the three 10 min parts of each treatment were extracted from the original recordings and stored as individual files with uninformative names. This ensured that the observer was blind to all independent variables when scoring the test phase. During the manipulation phase, the experimental manipulations (e.g. the presence of an intruder) were inevitably visible. To avoid sequence effects, the videos were analysed in random order. Behaviours were scored using the free software BORIS (Friard & Gamba, 2016). We recorded all behaviours of the helper and all behaviours of the breeders that were directed at the helper. The ethogram included aggressive displays (operculum spread, fin spread, lateral display, head down display), overt aggression (biting, ramming), submissive displays (tail quivering and backwards approach), affiliative behaviour (bumping) and territory maintenance (digging; see Taborsky, 1984). Displays were recorded as events with duration and the other behaviours as point events. All behaviours were eventually analysed as counts. Overt aggression and aggressive displays by the helper towards the intruder were combined as defence behaviour and those of both breeders towards the helper as breeder aggression (see Naef & Taborsky, 2020a).

Data Analysis

We used raw frequencies of behaviours (aggressive behaviours of breeders to helpers, submissive displays of helpers and defence behaviours of helpers) per time (the entire 10 min recording period) as dependent variables. All dependent variables followed a negative binomial distribution and were analysed with generalized linear mixed models with negative binomial error distribution using the package glmmADMB (Fournier et al., 2012; Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016). Data from the test phase were analysed with intruder species (no predator, egg predator or fish predator) and compensation manipulation (compensation prevented or allowed) as fixed factors and group ID as a random factor. Defence behaviour by the helper during the manipulation phase was analysed in the same way, as each treatment included exactly one recording during which defence was possible. Social interactions during the manipulation phase were analysed with intruder species and the manipulation of defence behaviour (defence prevented or allowed) as fixed factors, and treatment nested within group ID as random factors to account for the fact that the manipulation phase of each treatment comprised two recordings, one in which defence was prevented and one in which it was possible. The interactions between fixed factors and a variable to account for sequence effects were initially included in all models and dropped if they were not significant. For breeder aggression we performed post hoc analyses of pairwise differences and accounted for multiple testing using the Holm–Bonferroni procedure (Holm, 1979). We report back-transformed estimates and P values. Graphs were produced using ggplot2 (Wickham, 2016). All data processing was done using RStudio (RStudio Team, 2015).

Ethical Note

Experiments were approved by the Veterinary Office of the Kanton Bern (licence number 74/15). Throughout the experiment, all animals were checked daily for aggressive interactions. Individuals that were evicted from the group or received excessive aggression from group members were immediately removed from the group and transferred back to their original tank. No injuries or fatalities occurred during the experiment. Stock tanks of all three species involved were also checked daily, and individuals suspected to be under physical or social stress were temporarily isolated to stabilize the situation. To reduce the total number of animals used in experiments, the individuals used in this study have been used in experiments before and will continue to be used in future experiments. This does not constitute excessive stress, as experimental manipulations are mostly restricted to transferring animals between tanks to achieve specific social contexts. This corresponds to the natural situation of these species with high group turnover.

RESULTS

Breeder Aggression During the Manipulation Phase

Helpers received less aggression from breeders during the manipulation phase when a fish predator was present than when no intruder was present (estimate = 0.362, $P < 0.001$; Fig. 3). When an egg predator was present, breeder aggression tended to depend on whether or not the helper was able to defend against it, although not significantly so (interaction egg predator*defence prevented: estimate = 1.49, $P = 0.087$). A post hoc analysis confirmed that breeder aggression was reduced in all treatments with an intruder present, except when the intruder was an egg predator and the helper could not defend, compared to the control situation with no intruder where the helper could not defend (see Fig. 2 for abbreviations of treatment names; NP_Y: estimate = 1, $P = 0.982$; NP_N: reference treatment; EP_Y: estimate = 0.59, $P = 0.022$; EP_N: estimate = 0.877, $P = 0.978$; FP_Y: estimate = 0.363, $P < 0.001$; FP_N: estimate = 0.465, $P < 0.001$; P values corrected for multiple testing).

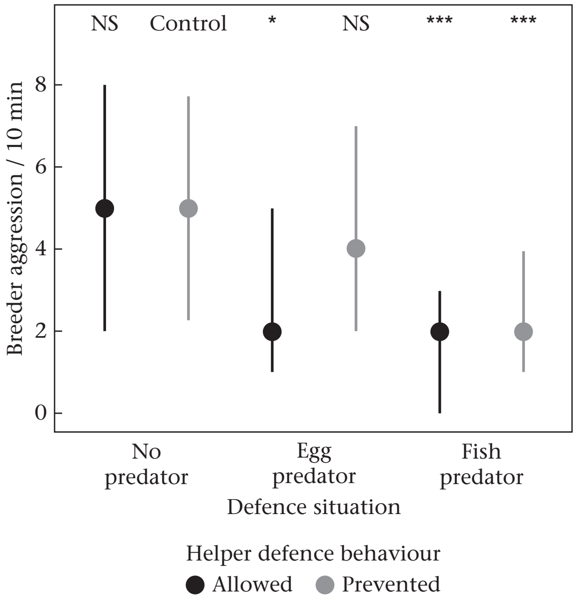


Figure 3. Aggression of breeders towards the helper during the manipulation phase, depending on the defence situation, i.e. which predator was presented and whether the helper could defend or not. Medians and interquartile ranges are shown. Differences to the control, adjusted for multiple testing, are shown: *$P < 0.05$; ***$P < 0.001$.

Breeder Aggression During the Test Phase

Breeders performed more aggression towards subordinates during the test phase in treatments with an egg predator (estimate = 1.23, $P = 0.032$; Fig. 4), but not in treatments with a fish predator (estimate = 0.922, $P = 0.422$), compared to control treatments with no predator. There was no significant interaction between intruder species and compensation treatment (egg predator*compensation prevented: estimate = 1.17, $P = 0.404$; fish predator*compensation prevented: estimate = 1.23, $P = 0.29$).

Helper Defence During the Manipulation Phase

Subordinates defended more against the egg predator than against the fish predator (estimate = 6.66, $P < 0.001$; Fig. 5). The amount of defence was not influenced by the compensation treatment (estimate = 1.02, $P = 0.922$), and there was no significant interaction between intruder species and compensation treatment (estimate = 0.911, $P = 0.823$).

Helper Submission During the Manipulation Phase

Helpers showed less submission during the manipulation phase of treatments with a fish predator (estimate = 0.494, $P < 0.001$), but not in treatments with an egg predator (estimate = 0.992, $P = 0.964$), compared to control treatments with no predator. Preventing helper defence increased their submission overall (estimate = 1.41, $P = 0.018$), but there was no significant interaction

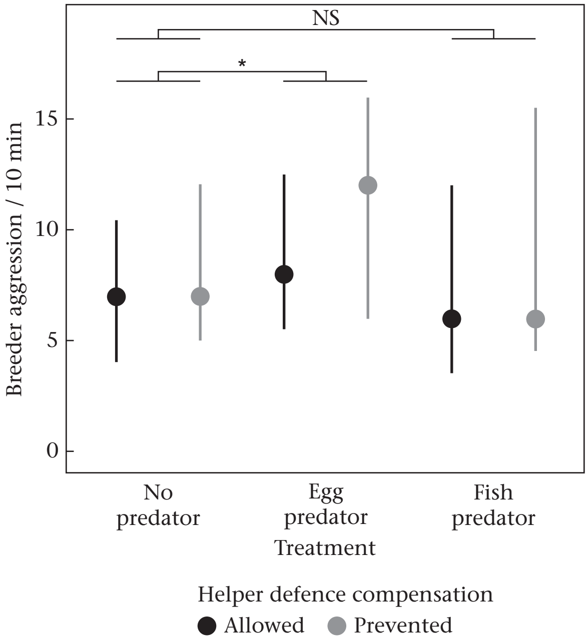


Figure 4. Aggression of breeders towards the helper during the test phase, depending on treatment, i.e. which predator was presented and whether the helper could compensate for lost defence opportunities or not. Medians and interquartile ranges are shown. Effects of presenting different predator species, compared to the control with no predator, are shown: *$P < 0.05$.

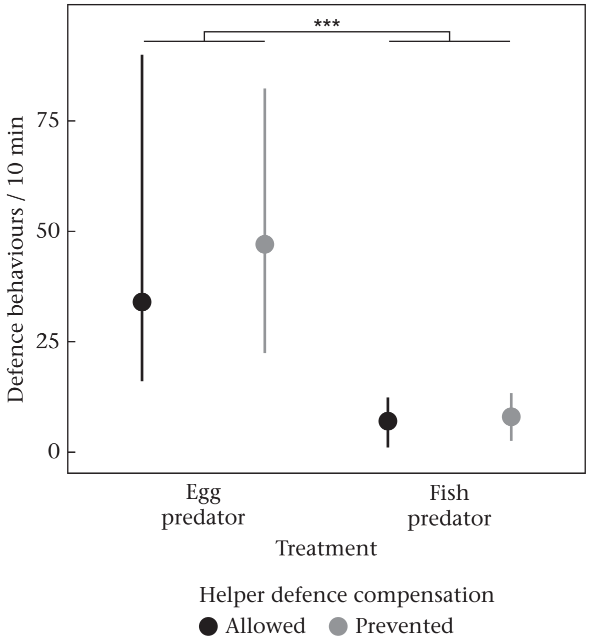


Figure 5. Defence behaviours of the subordinate during the manipulation phase, depending on predator species and compensation treatment, i.e. whether the helper could compensate for previous idleness or not. Medians and interquartile ranges are shown. Significant difference in defence behaviours against the two predator species is shown: $^{***}P < 0.001$.

between intruder species and defence prevention (egg predator*defence prevented: estimate = 1.01, $P = 0.987$; fish predator*defence prevented: estimate = 1.13, $P = 0.745$).

Helper Submission During the Test Phase

Helper submission during the test phase did not differ between treatments (interaction egg predator*compensation prevented: estimate = 0.869, $P = 0.555$; interaction fish predator*compensation prevented: estimate = 1.1, $P = 0.689$; preventing compensation: estimate = 1.08, $P = 0.454$; egg predator: estimate = 0.953, $P = 0.69$; fish predator: estimate = 1.03, $P = 0.777$).

DISCUSSION

In accordance with our prediction, experimentally preventing helpers from defending the territory resulted in punishment by breeders only in treatments where the territory was challenged by an egg predator. This was evident in both the test and the manipulation phases of our experiment. This suggests that the defence of *N. pulcher* helpers against egg predators is at least in part enforced by breeders. In contrast, helpers apparently defended against fish predators without their help being enforced. During the test phase, after a period of experimentally induced idleness in defending the group territory, helpers received significantly more aggression in treatments in which an egg predator had been present than in treatments with no predator present, while aggression was not increased in treatments in which a fish predator had been present (significant main effect of egg predator treatment). During the manipulation phase, breeders were generally less aggressive towards the helper when a predator was present than in the no predator control. Presumably, when a predator was present the breeders' attention was focused on the predator and their time was occupied with defending the territory, resulting in reduced aggression towards the helper. However, when the intruder was an egg predator, this effect disappeared if the helper was idle because of experimental prevention of defence (interaction effect between egg predator treatment and defence prevention); the post hoc analysis showed that aggression levels in this situation were not distinguishable from the control situation. This suggests that the aggression-reducing impact of the egg predator presentation was rendered ineffective if the helper did not attack the egg predator.

We predicted that helpers would be able to avoid punishment during the test phase if given the opportunity to compensate for induced idleness in attacks against predators. However, we did not find such an effect (nonsignificant interaction between egg predator treatment and compensation during the test phase). The amount of defence by helpers during the manipulation phase suggests that they did not show the expected compensatory response, either in treatments with egg predators or in treatments with fish predators (nonsignificant interaction between intruder species and defence manipulation). This seems puzzling because the present experiment was performed using a similar experimental set-up as in a previous study (Naef & Taborsky, 2020a), in which a strong compensatory response was observed. A plausible explanation for this discrepancy could be that the compensatory response found in previous studies was indeed the result of direct, physical enforcement by breeders (Bergmüller & Taborsky, 2005; Fischer et al., 2014; Naef & Taborsky, 2020a), while breeders were not able to enforce such compensation in a similar way in the present experiment, owing to a crucial difference in the experimental procedure. Both in the previous experiment using egg predators as intruders (Naef & Taborsky, 2020a) and in the experiment using conspecifics as intruders (Bergmüller & Taborsky, 2005), defence compensation was observed in a situation where helpers and breeders could freely interact. In contrast, in the present experiment the helper was separated from the breeders by a transparent partition when a compensatory response was possible (see Fig. 1b). Helpers may not have perceived the threat of punishment strongly enough in this situation due to the barrier, which prevented physical contact between group members. In the absence of physical aggression, breeders may not be able to force helpers to compensate for previous idleness. In line with this interpretation, helpers showed no compensation for previously prevented egg care when the breeders were confined behind transparent barriers, but compensated when breeders were free swimming in an experiment manipulating the helpers' egg care behaviour (Schreier, 2013).

We also analysed submissive displays of helpers to breeders as the pay-to-stay hypothesis predicts helping behaviours to be functionally similar to submissive displays. Submissive displays have evolved to signal to the aggressor that further attacks are not useful because their opponent has already surrendered (Kaufmann, 1983), and thus function to reduce aggression in dominants. Helping behaviours are believed to have acquired a similar appeasement function in cooperative breeders such as *N. pulcher* (Bergmüller & Taborsky, 2005). We therefore expected that helpers would react to the aggressive behaviours of breeders with submissive displays in situations where appeasement by helping was not possible. This was indeed the case in a previous experiment where helpers were punished for refraining from digging out a shared shelter because of experimental prevention, after which they showed more submission towards the breeders (Naef & Taborsky, 2020a). However, even though in the present study helpers were apparently punished for not defending the territory against egg predators, they did not respond by increasing their submissive displays during the test phase. This might suggest that submissive displays are ineffective to compensate for prevented defence behaviour, while they may serve this purpose when helpers need to compensate for withheld help in digging out a shared shelter (Naef & Taborsky, 2020a). Nevertheless, in our experiment submissive displays during the manipulation phase are difficult to interpret because our set-up prevented direct physical interactions between breeders and helpers, which probably affected the helpers' motivation to engage in submission. This is corroborated by the helpers’ diminished submission levels during the manipulation phase of treatments with a fish predator, which reflected the reduced aggression they received from breeders during those periods.

In combination with previous studies on social cichlids, our results show that the regulation of helping behaviour in cooperative breeders may involve sophisticated social regulatory processes, which can be highly behaviour specific. This implies that the underlying regulatory mechanisms may be maintained through different selection mechanisms. Our results suggest that in *N. pulcher*, the helpers' defence against egg predators is enforced by breeders, reflecting the interplay of coercion and reciprocal trading predicted by the pay-to-stay hypothesis (Hellmann & Hamilton, 2018; Quiñones et al., 2016). This is similar to the regulation of the helpers' participation in digging out the breeding shelter (Naef & Taborsky, 2020a) and providing oxygen to eggs by direct brood care (Schreier, 2013). On the other hand, the helpers’ territory defence against fish predators does not seem to be enforced in this manner and is probably selected by direct fitness benefits to the helper, together with positive side-effects on other group members (by-product mutualism; Taborsky, 2016).

If specific behaviours of subordinates are enforced by dominants through threats of aggression, dominants must somehow monitor these behaviours individually, which may only be possible in small groups. This is corroborated by a field study of *N. pulcher* involving experimental manipulations of the presence and behaviour of helpers, which revealed punishment of idle helpers by breeders occurred only in small groups (Fischer et al., 2014). In large groups, other group members seem to exercise control over the contributions of individual helpers (see also Balshine-Earn et al., 1998). Apart from group size, several other conditions may also affect the motivation and outcome of negotiations between helpers and breeders. Subordinate naked mole-rats, *Heterocephalus glaber*, are prompted to work by the dominant female depending on the nutritional status of the colony (Reeve, 1992). In superb fairy-wrens, *Malurus cyaneus* (Mulder & Langmore, 1993), subordinates were punished for withholding defence against predators of young only during the breeding season, when the costs of predator intrusions for dominants were high, but not outside the breeding season. In cooperatively breeding paper wasps, *Polistes dominula*, dominants accepted a lower payment from subordinates if the latter's outside options were experimentally improved (Grinsted & Field, 2017), which resembles the environmental effects on the negotiation process demonstrated in our study species (Bergmüller et al., 2005). In this cichlid, neighbourhood conditions and local population structure were also shown to affect cooperative territory defence of helpers (Hellmann & Hamilton, 2014; Jungwirth et al., 2015).

Cooperative breeding provides a perfect example of the exchange of different commodities among social partners, which typically involves alloparental care of subordinates to the benefit of dominants, and in return toleration and often also protection of subordinates by dominants, which benefits the helpers by providing them with access to vital resources (see Taborsky, 2016 for a review). Trading of different commodities has been demonstrated also in other contexts (for a review see Taborsky et al., 2016). Examples include the exchange between access to food and hygienic behaviour in Norway rats, *Rattus norvegicus*, and chimpanzees, *Pan troglodytes* (de Waal, 1997; Schweinfurth & Taborsky, 2018), or between grooming and social support in various primates (Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010; see; Schino, 2007 for a review; Seyfarth & Cheney, 1984). In other cases social partners reciprocally exchange a single commodity, such as food for food in dogs, *Canis lupus familiaris*, rats and vampire bats, *Desmodus rotundus* (Carter & Wilkinson, 2013; Dolivo & Taborsky, 2015; Gfrerer & Taborsky, 2018; Schneeberger, Dietz, & Taborsky, 2012), or social hygiene in various mammals (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Hart & Hart, 1992; see; Schino & Aureli, 2008 for a review; Stopka & Graciasová, 2001). In *N. pulcher*, digging out a common shelter is reciprocally exchanged between social partners (Taborsky & Riebli, 2020). What is unique in this species, however, is that subordinates can trade several commodities for being tolerated in the territory and protected by dominants (Quiñones et al., 2016; Taborsky, 2016). Intuitively, two behaviours that both function as rent payment might be expected to be interchangeable; if the helper is prevented from showing one of them, it can make-up for it by showing more of the other. However, this intercommodity compensation was not found in *N. pulcher* in a previous experiment involving antipredator defence and shelter digging (Naef & Taborsky, 2020a). The results on defence against egg predators presented here and the previous results on digging out a shared shelter showed that both behaviours of helpers are in fact enforced by breeders. Still, they are apparently not traded against one another: a lack of egg predator defence was not compensated by more digging and vice versa (Naef & Taborsky, 2020a).

Cooperative breeding has been studied in a wide range of animal species including insects, fishes, birds and mammals (Choe & Crespi, 1997; Koenig & Dickinson, 2016; Solomon & French, 1997; Taborsky, 1994). It is becoming increasingly clear that cooperatively breeding animals may use sophisticated negotiation rules for trading commodities and services (Quiñones et al., 2016; Taborsky et al., 2016; Zöttl, Heg, Chervet, & Taborsky, 2013), which may reflect the simultaneous impact of different selection pressures involving relatedness, mutual immediate fitness benefits, coercion and reciprocity (Clutton-Brock, 2002; Taborsky et al., 2016). Cooperatively breeding cichlids are a unique model system to investigate such interactions, as they can be studied in near-natural situations in the laboratory, where important factors such as group composition, relatedness, ecological challenges and individual behaviours can be experimentally controlled and manipulated. This is hardly possible in most other cooperative animal species. In addition, the fitness consequences of many behaviours involved in cooperative interactions are well understood in this species (Jungwirth & Taborsky, 2015; see Taborsky, 2016 for a review). Subordinate group members are apparently forced to provide alloparental care services to dominants in order to obtain shelter and protection from abundant predators (the pay-to-stay process; Gaston, 1978). This cooperative system reacts in nuanced ways to various factors including the relatedness between cooperative partners (Zöttl et al., 2013), outside options of subordinates (Bergmüller et al., 2005), the behaviour of social partners (Taborsky & Riebli, 2020) and group size (Fischer et al., 2014). We have shown here that territorial behaviour of subordinate helpers reflects both coercive and mutualistic interactions, depending on the species of intruder. The four major evolutionary mechanisms for cooperative behaviour, reciprocity, coercion, mutualism and kin selection (Lehmann & Keller, 2006), thus differentially influence the trading of commodities in this model system of social evolution.

Author Contributions

J.N. and M.T. conceived and designed the study. J.N. carried out the experiments, collected the data and carried out the statistical analyses. J.N. wrote the first draft of the manuscript, which was revised by M.T. Both authors gave final approval for publication and agree to be held accountable for the work performed therein.

Data Availability

The complete data set and analysis code are available at Mendeley Data (Naef & Taborsky, 2020b).

Declaration of Interest

We declare no competing interests.

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