



Differential responses to territory intrusions in cooperatively breeding fish

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In cooperatively breeding species, members of social groups will risk serious injury or even their lives by actively codefending the communal territory and young in the territory. However, individuals within the group vary in the intensity and frequency of defence. To date little is known about how sex, body size and social status interact with the degree of threat to influence defence activities. To this end, we experimentally manipulated the need for defence in wild groups of the cooperatively breeding cichlid, *Neolamprologus pulcher* by exposing social groups to four intruder types representing different forms of threat. Intruders were introduced singly (experiment 1) to assess the costs and benefits associated with defence and in tandem (experiment 2) to assess how individuals prioritize perceived threats. Dominant breeders defended more than subordinate helpers, females were more aggressive than males, and female breeders defended more than any other individual in the group. Individual body size, or the difference in body size between intruders and defenders, had no influence on the frequency of defence. Dominant male breeders defended most vigorously against threats to their dominance position, while dominant female breeders showed the highest defence rates to both threats to their position and the security of young to a similar degree relative to all others. Predators evoked the strongest defence responses by subordinate helpers, and conspecific intruders evoked the weakest responses relative to all other intruder types. The results suggest that both costs and benefits have shaped aggressive defence patterns in this cooperatively breeding teleost fish.

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Along the coastline of Lake Tanganyika, social groups of the small cichlid fish, *Neolamprologus pulcher*, jointly defend a breeding territory year round. In each social group, a dominant breeding pair is assisted in territory defence by other subordinate, sexually mature, but non-breeding individuals (Taborsky & Limberger 1981; Emlen 1996; Balshine-Earn et al. 1998; Fitzpatrick et al. 2006). For the individual defending, such joint defence behaviour is thought to have both high potential costs (time, energy, increased risk of injury or death) and significant benefits (increased reproductive success, maintenance of one's status and survival; Davies & Houston 1981; Taborsky 1984; Marler et al. 1995; Heg et al. 2005).

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Previous studies on cooperative breeders have mainly concentrated on examining the costs and benefits of two classes of cooperative behaviour: feeding of young (Komdeur 1994, 1996; Wright 1998; Wright & Dingemanse 1999; Komdeur et al. 2004) and sentinel behaviour (Clutton-Brock et al. 1999, 2001; Wright et al. 2001a, b; Clutton-Brock 2002; Bednekoff & Woolfenden 2003). However, the other class of costly cooperative behaviour, joint defence of the young and the territory, has been largely ignored. In this study, we examined this issue by manipulating the need for territory defence in wild groups of the small cooperatively breeding fish, *N. pulcher*.

We introduced four types of intruders: (1) a heterospecific predator species that threatened the survival of adults and young, (2) a heterospecific predator species that threatened only the survival of young, (3) a same-sex conspecific that could threaten an individual's position in the dominance hierarchy and (4) an opposite-sex

conspecific. We used these different intruders to test how the costs and the benefits of defence interact with an individual's social position, sex and size to influence their response to intruders (Houston et al. 1993; Bednekoff & Lima 1998; Lima & Bednekoff 1999; Manser 1999; Bednekoff 2001). We investigated whether the various intruder types elicited different responses from group members. Based on the costs and benefits of defence, we have outlined a series of sometimes contrasting predictions about how individuals might respond to intruders.

Specific Predictions Derived from the Benefits of Defence

Immediate Reproductive Benefits

In many cooperative breeders, helpers are closely related to breeders and so would enjoy indirect benefits from defence of young (for review see Queller & Strassmann 1998; Clutton-Brock 2002; Griffin & West 2003). In contrast, *N. pulcher* helpers are typically unrelated or only distantly related to the breeder (Hensel 2005; Stiver et al. 2005). Hence, breeders would be expected to benefit more from defence of young than helpers. Also, *N. pulcher* female breeders are commonly more closely related to young and helpers than are male breeders (Stiver et al. 2005) and smaller helpers are more closely related to both breeders than are large helpers (Hensel 2005). Therefore, we predicted that in *N. pulcher* (1) breeders would defend more than helpers, (2) females would defend more than males, and that (3) small helpers would defend more than large helpers. Since predators of adults and predators of young would pose a direct threat to survival, but conspecifics would not, we predicted that all individuals would defend more against the predators than against conspecific intruders.

Future Reproductive Benefits

Enhancing the survival of current young is only one benefit of defence. Another major benefit is maintaining the groups' territory and one's position in the dominance hierarchy (Magrath 2001; Griffin & West 2003; Komdeur 2006). In *N. pulcher*, breeders that lose their breeding position are unlikely to survive and so disappear from the population, whereas helpers can retain their social position in the group following a breeder replacement event (Balshine-Earn et al. 1998; Stiver et al. 2004, 2006; Fitzpatrick et al., unpublished data). Therefore, we predicted that breeders would defend their position in the dominance hierarchy (against a sex-matched conspecific intruder) to a greater extent than helpers. Also, as male *N. pulcher* breeders commonly have multiple reproductive opportunities (they can hold more than one breeding territory simultaneously, whereas females hold only one breeding territory, Limberger 1983; Desjardins et al. 2008), we predicted that female breeders would defend their breeding position to a greater extent than male breeders.

Specific Predictions Derived from the Costs of Defence

The costs of defence typically include increased energy expenditure and an increased risk of injury or death during aggressive encounters (Davies & Houston 1981; Taborsky 1984; Marler et al. 1995; Heg et al. 2005). Dominant breeders, because of their larger size, social status, and increased experience, may better absorb these costs of defence than subordinate helpers. Dominant individuals typically have more energy reserves than subordinate individuals (Brown 1946; Baker & Fox 1978; Ketterson 1979; Policansky 1983; Pravosudov et al. 1999, 2003) and thus may be better able to tolerate an escalated aggressive encounter (Jaeger 1981; Krebs 1982; Mathis 1991; Johnsson et al. 1999). In *N. pulcher*, breeders are almost always larger than helpers (Taborsky 1984; Balshine et al. 2001) and larger individuals are known to be more likely to threaten and drive off a predator (Piper & Wiley 1990; Fuiman & Magurran 1994; Clutton-Brock et al. 1999). Therefore, we predicted that, in *N. pulcher*, larger fish (breeders versus helpers and large versus small helpers) would defend more frequently and at a higher rate than smaller fish. Also based on this argument, male *N. pulcher* would be expected to defend more than females because males are typically larger than females (Balshine et al. 2001).

To assess how individuals prioritize defence against intruders representing different types of threat, we conducted a second experiment in which intruders were presented in pairs and we monitored which intruder received the most aggressive acts. This second experiment allowed us to assess precisely which intruder type each focal individual prioritized in terms of defence. We predicted that breeders (males and females) would defend against an intruder that threatened their lives over an intruder that threatened their breeding position and would defend more against a predator of young than against a conspecific intruder of the opposite sex.

METHODS

Study Species and General Field Protocols

Neolamprologus pulcher, endemic to Lake Tanganyika, Africa, lives in social groups consisting of a dominant breeding pair and 1–20 subordinate helpers (males and females) that assist in all aspects of care including territory/nest defence, territory/nest maintenance and direct brood care (Taborsky 1984; Balshine-Earn et al. 1998; Heg et al. 2005). Each social group is found on a small territory (median size 3150 cm²) that consists of clusters of rocks on sandy substrate that serve as either the breeding site (known as a brood chamber) and/or as shelters where fish hide from predators (Balshine et al. 2001). Territories are clustered in space into distinct subpopulations (Stiver et al. 2004, unpublished data). Group members actively defend their territory (Taborsky 1984; Balshine-Earn et al. 1998) against both conspecific and heterospecific intruders that cross into their territory boundaries (Taborsky 1984; Balshine et al. 2001; Heg et al. 2005). Such intruders

include other fish species that are predators of adults, predators of young as well as space competitors and conspecific neighbours (Konings 1998). Such territory defence can be a very important aspect of care (eggs and young are typically extremely close to the territory boundaries because the territories are so small).

For this study, observations were conducted from 2 February to 28 April in 2005 in Kasakalawe Bay, Lake Tanganyika (Zambia: 8°46'S; 31°46'E), using SCUBA. Further details of the study area, and general field methods are described elsewhere (see Balshine-Earn et al. 1998; Balshine et al. 2001; Fitzpatrick et al. 2006; Stiver et al. 2006). A total of 10 *N. pulcher* groups were selected for this study and four focal fish from each of these 10 groups were observed in each trial (breeding male, breeding female, a large helper and a small helper). The same 10 groups were used in experiment 1 and experiment 2. These group sizes ranged from four to nine individuals (mean: 5.7 ± 0.6 SE). In each group, we observed the dominant breeding male (mean body length, SL (standard length) = 5.8 cm, range 5.5–6.4 cm), the dominant breeding female (mean body length, SL = 5.1 cm, range 4.4–5.3 cm) and at least one small helper (mean body length, SL = 3.4 cm, range 2.0–4.3 cm) and one large helper (mean = 4.7 cm, range 4.4–5.4 cm).

In our study site, breeding males may hold the dominant position in one social group or several (Limberger 1983; Desjardins et al. 2008). All 10 groups used for these experiments were polygynous groups representing one territory of several controlled by each of the 10 breeding males observed. In our study area, polygynous males occupy the breeding position in two to six territories (mean \pm SE = 2.7 ± 0.1). Usually these are neighbouring territories that share a boundary, with a mean \pm SE distance between a male's territories within a single harem of 92 ± 7.1 cm (Desjardins et al. 2008). Polygynous males divide their time between groups in their harem and each group in a harem consists of one breeding female and her associated helpers. These individuals (a female and her helpers) do not interact with other females and helpers from other groups that comprise a male's harem. Experimental groups selected for this study were all located at least 5 m apart and at 8.5–12 m in water depth. Each group's territory centre was marked with a uniquely labelled rock brought down from the surface. Prior to any experimental manipulations, each group was monitored one to three times (for an average of 15 min) to assess group size, group composition, and individual body size and dominance status. A combination of underwater size estimates (with an underwater ruler), artificial paint marks and unique facial markings were used to reliably identify individuals across repeated visits (Balshine et al. 2001; Stiver et al. 2005). *Neolamprologus pulcher* are extremely site-faithful and individuals vary considerably in both size and black marks on their operculum/gills covers (Taborsky 1984; Stiver et al. 2004).

Intruder (stimulus) fish were collected using fence nets and hand nets. Each intruder fish was kept individually in a mesh holding cage (30 × 30 × 30 cm) until it was used in an experimental manipulation. No stimulus fish was kept in a holding cage for longer than 2 h and all were

released at the original collection site within 1 h. Intruder fish were collected at least 25 m away from any experimental group and conspecific intruders were never collected from the same subpopulation as the experimental groups. The experiments (experiment 1, where the intruders were presented singly, and experiment 2, when they were presented in pairs, see below) were conducted only in the afternoons (to control for diurnal variation in behaviour, Werner et al. 2003). Each group was presented with a new intruder (experiment 1) or set of intruders (experiment 2) once every 4 days. There was a period of 2 weeks between the two experiments when experimental groups were not exposed to any experimental intruders.

Intruders were presented to the social groups singly (experiment 1) and in pairs (experiment 2). In the trials of experiment 1, the intruder was placed in a 1-litre glass jar set in the centre of each study group's territory. The predator of adults was *Lepidiolamprologus elongatus* (mean standard length = 7.8 cm, range 6.7–9.4 cm), a large piscivorous cichlid that could injure or kill all fish in the social group (Taborsky 1984; Balshine et al. 2001; Heg et al. 2005). In the field, breeder turnover is rapid (Stiver et al. 2004) and can be a result of predation events by *L. elongatus* (Taborsky 1984; Balshine et al. 2001; Heg et al. 2005). The predator of young was *Gnathochromis pfefferi* (mean standard length = 6.2 cm, range 5.6–6.6 cm), a medium-sized cichlid whose diet consists of shrimp found in the substrate and of the eggs and young of other fish species (Taborsky 1984; Yuma 1994; Balshine et al. 2001). Experimental groups were also exposed to two conspecific fish; an unfamiliar breeder-sized male (mean = 5.9 cm, range 5.4–6.3 cm), that would threaten the breeding position of the adult male in the group, and an unfamiliar breeder-sized female (mean = 5.3 cm, range 5.1–5.7 cm), to threaten the breeding position of the adult female in the group (Stiver et al. 2006). Breeder-sized conspecifics are able and ready to take over breeding positions as soon as a breeding position becomes available (Balshine-Earn et al. 1998; Stiver et al. 2006; Fitzpatrick et al., unpublished data). Control trials were also conducted in each social group by placing an empty glass jar in the centre of the territory. The order in which the different intruder and the control stimuli were presented was randomized.

Each trial lasted for 10 min and the recorded observations began when at least one of the focal individuals began attacking the intruder within the glass jar; this typically occurred rapidly but always within 1 min of the intruder in the jar being placed in the territory. During these trials, most fish within the group (both focal and nonfocal fish) responded to the intruder by exploring and either attacking the intruder or hiding under a nearby rock. If the breeding male was not currently in the focal territory, he always returned within 1 min of the intruder being placed in the territory. Typically, only the largest fish within the group (and the ones included in this study) continued to respond aggressively towards the intruders throughout the 10-min trials. During each trial, all aggressive behaviour patterns displayed towards the intruder fish or the empty glass jar (controls) by the four focal fish (breeder male and

breeder female, and a large and a small helper) were recorded. All observations were recorded on PVC slates and later were transcribed at the surface into spreadsheets. The aggressive behaviour recorded included ramming, opercular flaring and biting the jar with the intruder. Although the intruders used were confined to the 1-litre glass jar, the jar was placed on its side and the lengthwise distance allowed the intruders to move around in the jar while ensuring that they interacted with surrounding group members. The intruders behaved aggressively towards the surrounding individuals (they oriented towards attackers and flared their gill covers and bit the sides of the jar from the inside). A new intruder fish or a pair of intruder fish was used for every experimental trial to ensure that the intruder fish did not tire or habituate to the presence of surrounding fish.

In experiment 2, intruders were presented in pairs and each group was exposed to two of four intruder types simultaneously. In each trial, two 1-litre jars containing intruders were placed on opposite sides of the brood chamber, the central position of the territory. Each group was exposed to all six possible combinations of two territory intruders, and we carefully recorded the target of each aggressive act. Control trials in this second experiment were conducted immediately prior to the exposures and consisted of recording the number of aggressive attacks displayed by group members towards two empty glass jars presented in the same location as the intruder fish.

Once all of the behavioural observations were complete, we collected all of the focal individuals within each group by placing a tent net directly over the territory. We then injected a small volume (3–7 ml) of quinaldine (2-methylquinoline; $C_6H_4N:C(CH_3)CH:CH$), an anaesthetic into the centre of the territory while the net was in place and collected the temporarily sedated fish. Fish from each group were placed together in individually marked mesh holding cages (20 × 20 × 20 cm) to recover from sedation and were then slowly (~20 min) brought to the surface (see Morley & Balshine 2002; Fitzpatrick et al. 2006 for further collection details). At the surface, individuals were easily identified using the combination of individual size estimates and markings on each fish. Fish were measured for SL to the nearest millimetre and body mass was measured to the nearest 0.001 g. At the end of this experiment, all the focal fish were sacrificed with a lethal dose of benzocaine (ethyl *p*-aminobenzoate, 1.0 µg/ml) and sexed by examination of the gonads. A series of physiological samples were collected from each fish for other studies (tissues taken included blood for plasma hormone studies, fin and muscle tissue for relatedness studies, gonad weight, sperm eggs, liver and brain tissue for a reproductive physiology study; Fitzpatrick et al. 2006; Stiver et al. 2007; Desjardins et al. 2008; Fitzpatrick et al., unpublished data; Stiver et al., unpublished data).

Statistical Analysis

Statistical analyses were performed using the software JMP 5.1.1 (SAS Institute, Inc., 2004, Cary, NC, U.S.A.).

Data conformed to the assumptions of parametric statistical tests, and hence, two-tailed parametric tests were used throughout. To test for the effect of single intruders on individual behaviour, we used one three-way analysis of variance (ANOVA) with the main effects of sex (male, female), social status (breeder, helper) and intruder type (predator of adults, predator of young, conspecific male breeder, conspecific female breeder) on the number of aggressive acts. We then conducted a two-way ANOVA on the helpers to test only for effects of size (small, large) and intruder type (predator of adults, predator of young, conspecific male breeder, conspecific female breeder) on aggressive acts. Post hoc contrast analyses were conducted to determine where differences exist between the rates of aggression of individual defenders and the rates of aggression received by different intruder types (Rosenthal & Rosnow 1985). To test for the effect of body size and the effect of size difference between the defender and the intruder on defence, we conducted linear regression analysis. All tests were two tailed and alpha levels were adjusted using Bonferroni corrections to control for multiple comparisons performed on the same data set.

At the end of experiment 2, where intruders were presented in pairs, intruders were classified as most attacked by focal fish ('high aggression') and less attacked by focal fish ('low aggression'). The sum of all the 'high aggression' and 'low aggression' scores was used to assign a ranking for intruder types for each category of focal fish. A rank of one was assigned to the intruder fish that had received the most aggression. Ranks are presented rather than absolute aggression levels to compare how individuals of different social status prioritize defence. We used a Friedman's test to analyse these data and post hoc comparisons were performed to identify specific differences (Siegel & Castellan 1988).

Ethical Note

Although individuals in the manipulated social groups would have experienced some level of stress from having been exposed to unknown conspecific intruders and heterospecific predators, this level of threat and stress is a normal occurrence and frequent event for wild *N. pulcher* groups. Predators, space competitors and conspecifics attack or intrude on *N. pulcher* territories on a regular basis and such intruders can be observed many times per hour in unmanipulated field situations (Balshine et al. 2001; Heg et al. 2005; Desjardins et al. 2008). No fish disappeared as a consequence of our experimental treatments. The fish were collected across a 4-month period and extreme care was taken not to collect fish from small subpopulations (<10 groups). Neighbouring groups were always left intact to minimize the impact of collection, and neighbouring fish quickly recolonized emptied positions and territories usually within the next couple of days. All research described conformed to protocols approved by the Animal Research Ethics Board of McMaster University and adhere to the Canadian Council for Animal Care guidelines. Also, this research was conducted with the permission and cooperation of the Zambian Department of Fisheries.

RESULTS

Experiment 1: Overall Effects

Overall, there was a relationship between the number of defensive acts and sex, status of the focal individual and the intruder type ($F_{15,184} = 2.439$, $P = 0.003$; Fig. 1). The number of defensive/aggressive acts displayed depended on both the sex and the status of the focal individual (sex*status interaction: $F_{1,184} = 5.178$, $P = 0.02$) but not on intruder type ($F_{1,184} = 2.047$, $P = 0.11$). Breeders displayed more aggressive acts than helpers ($F_{1,184} = 6.822$, $P = 0.009$) and females were more aggressive than males ($F_{1,184} = 3.822$, $P = 0.05$).

Experiment 1: Costs and Benefits of Defence

Breeders defended more against both predators (predator of adults and of young) than helpers ($F_{1,184} = 5.317$,

$P = 0.02$; Fig. 1a). Additional post hoc tests revealed that female breeders displayed more aggression than any other individual within the group ($F_{1,184} = 15.659$, $P < 0.0001$). Female breeders defended more against the predators than did male breeders ($F_{1,184} = 6.241$, $P = 0.01$). There was no detectable difference between male and female breeders in the number of aggressive displays performed towards same-sex conspecifics ($F_{1,184} = 0.042$, $P = 0.84$).

When we examined defence in relation to the type of intruder, all individuals within the group defended against the predator of adults ($F_{3,36} = 1.246$, $P = 0.30$; Fig. 1b). Male breeders defended against the predator of young less than all other individuals ($F_{3,36} = 3.704$, $P = 0.05$). Both male and female breeders defended against the conspecific male intruders more than did the helpers ($F_{3,36} = 5.232$, $P = 0.02$). Female breeders defended against the conspecific female intruders more than did all other individuals in the social group ($F_{3,36} = 4.55$, $P = 0.008$).

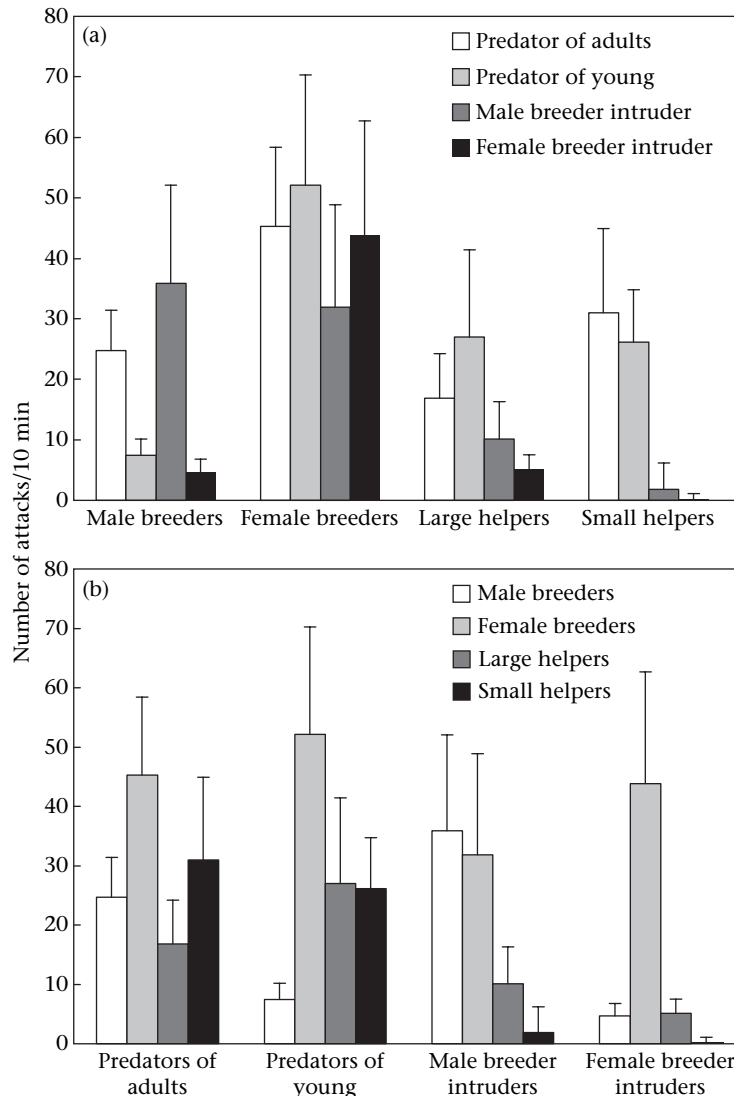


Figure 1. Mean number of aggressive acts (per 10-min trial + SE) directed towards the intruders. Means have been grouped by (a) type of *N. pulcher* defender and by (b) intruder type. All sample sizes equal 10 individuals.

To determine whether helper body size influenced defence response, a two-way ANOVA on helper aggression frequency was conducted with the main effects of helper size (small, large) and intruder type (predator of adults, predator of young, male breeder, female breeder). Overall, the model was significant ($F_{7,92} = 2.147$, $P = 0.046$; Fig. 1a), however, this was driven only by the strong main effect of intruder type ($F_{3,92} = 4.425$, $P = 0.006$). There was no detectable difference between large and small helpers in their response to all intruders ($F_{1,92} = 0.0022$, $P = 0.96$). Both large and small helpers displayed more aggressive acts towards predators (both types, hetero-specific predators of adults and of young) than towards the conspecific intruders (males and females; post hoc linear contrast: $F_{1,92} = 11.904$, $P = 0.0008$). This was even more dramatic in small helpers, who virtually ignored conspecifics (see Fig. 1a).

We tested whether the degree of size difference between the intruder and the focal defending fish influenced the amount of aggressive defence displayed. When all social status categories were combined, no relationships were detected ($r^2 = 0.00034$, $n = 160$, $P = 0.93$). Similarly, within each social status category, no relationship was found (male breeders: $r^2 = 0.03$, $N = 40$, $P = 0.23$; female breeders: $r^2 = 0.011$, $N = 40$, $P = 0.46$; large helpers: $r^2 = 0.01$, $N = 40$, $P = 0.49$; small helpers: $r^2 = 0.037$, $N = 40$, $P = 0.18$).

Experiment 2: Defence Priorities

When the intruders were presented as pairs to the same groups used in experiment 1, we were able to generate priority ranks for defence based on the number of attacks displayed by focal fish in each paired intruder trial (Table 1). The priority that fish placed on attacking each type of

Table 1. The mean rank of aggression received for each intruder type was based on the number of aggressive displays observed across all double exposure trials

Intruder	Focal fish			
	Male breeders	Female breeders	Large helpers	Small helpers
Predator of adults	2.1±0.35	2.2±0.34	2.0±0.34	2.8±0.35
Predator of young	2.9±0.32	2.3±0.37	2.1±0.34	1.7±0.35
<i>Neolamprologus pulcher</i> breeder male	1.8±0.32	3.5±0.17	3.0±0.34	3.0±0.35
<i>N. pulcher</i> breeder female	3.2±0.32	2.0±0.29	2.9±0.34	2.5±0.35

A high rank (e.g. 1) corresponds to high levels of aggression received across all trials, while a low rank (4) corresponds to low levels of aggression received across all trials. The responses of four focal fish in each social group towards four types of intruder were used to generate these ranks. In all cases $N = 10$. Ranks are presented rather than absolute aggression levels to compare how individuals of different social status prioritize defence.

intruder varied and depended on the social status of the focal fish ($\chi^2 = 7.888$, $P = 0.05$). For male breeders, the predators of adults and the male conspecific intruders had the highest and equal aggression/priority ranks, the predators of young received an intermediate rate of defence and the female conspecifics had the lowest rate and rank of aggressive defence ($\chi^2 = 11.195$, $P = 0.01$). For female breeders, the predator of adults, the predators of young and the female conspecific intruders all had similar defence ranks, while the male conspecific intruders received the least aggression and therefore had the lowest rank ($\chi^2 = 9.515$, $P = 0.02$). Large helpers showed an equal response to the four intruder types ($\chi^2 = 2.161$, $P = 0.53$). Finally, small helpers directed most of their aggression towards the predators of young and directed the least amount of aggression towards the adult breeding male conspecifics ($\chi^2 = 9.36$, $P = 0.02$).

DISCUSSION

Why did Male Breeders Defend Less than Female Breeders?

The sex differences observed in defence may be influenced by differences in perceived paternity/maternal certainty and alternative reproductive opportunities. In a wide variety of species, uncertainty in paternity decreases the amount of paternal care provided (birds: Møller & Birkhead 1993; Sheldon & Ellegren 1998; Westneat & Stewart 2003; mammals: Busse 1985; Buchan et al. 2003; Wolff & Macdonald 2004; Adrian et al. 2005; fishes: Neff & Gross 2001; Neff 2003; Rios Cardenas & Webster 2005). A previous field study reported that 41.7% of *N. pulcher* breeding males did not father all young in their groups; 8 of 35 young could be attributed to extrapair fathers (Hensel 2005). In contrast, breeding females were identified as mothers of young in the group 92% of the time (Hensel 2005). In addition, as argued above, by holding multiple territories (up to six; Desjardins et al. 2008), *N. pulcher* male breeders have a greater variety of breeding options relative to breeding females (Limberger 1983; Desjardins et al. 2008). Hence, when a predator of young enters a territory and preys upon young, this is unlikely to represent a breeding male's only reproductive option (Emlen & Oring 1977), and the female breeders have more to gain by defending the current brood against predation (Perrone & Zaret 1979).

Why did Helpers Defend More against Predators than against Conspecifics?

Predators may have represented a greater threat to helper survival and to the continued existence of a social group compared with conspecific intruders. Since helpers are not typically closely related to the breeders or the current brood of young (Dierkes et al. 2005; Stiver et al. 2005), it is unlikely that helpers perform defensive behaviours to secure indirect fitness benefits via kin selection (Hamilton 1964). Unrelated helpers may, however,

help with codefence to gain direct benefits, as has been observed in other species (Reyer 1984; Whittingham et al. 1997; Queller et al. 2000; Clutton-Brock 2002). Helpers may gain parenting skills (Brown 1987; Komdeur 1996; but see Taborsky 1984), ensure help in return (Trivers 1971; Ligon & Ligon 1978), increase their chances of inheriting a future territory or mate (Reyer 1980; Woolfenden & Fitzpatrick 1984), or be 'paying rent' to protective breeders (Gaston 1978; Balshine-Earn et al. 1998; Bergmüller et al. 2005; Stiver et al. 2005). Helpers may also defend to increase their own survival probability or to ensure and augment their groups continued survival and thus gain protective benefits of group living, active protection by breeders and access to a well-maintained shelter system in the territory (Taborsky 1984; Cockburn 1998; Kokko & Ekman 2002; McGowan et al. 2003). When breeders are experimentally removed, the group can sometimes break down, and this is especially true when female breeders are removed (Stiver et al. 2006). In contrast, a take-over by another conspecific breeder never led to group dissolution, and hence, conspecific intruders may not pose the same degree of threat to helpers as do predators.

Was Defence Modulated According or in Relation to Intruder Size?

Body size asymmetries often dampen the escalation of an aggressive interaction and determine who will win (Parker 1974; Maynard Smith & Parker 1976; Enquist & Leimar 1983; Beaugrand et al. 1996; Petersen & Hardy 1996; Morrell et al. 2005). In our study, defence rates were not correlated with the degree of size difference between defenders and intruders. While large breeders did defend against intruders at a higher rate than the smaller helpers, this was entirely driven by female breeders that were not the largest fish in the group. Generally, large body size is beneficial in fights; larger individuals tend to suffer fewer injuries and win conflicts more often compared with smaller individuals (Beaugrand & Zayan 1985; Beaugrand et al. 1996; Drummond 2006). For example, in the juvenile Atlantic salmon, *Salmo salar*, body size is an important predictor of contest outcome; larger intruders were more likely to displace smaller residents in aggressive encounters (Cutts et al. 1999). Our results suggest that *N. pulcher* modulate defence in response to the type of intruder and not simply the size of the intruder.

Was there Division of Labour in *N. pulcher*?

Breeders attacked intruders more than did helpers, but helpers participated in territory defence and sometimes did so quite vigorously. In other cichlid species, males commonly defend more than females and do so from the periphery of the territory boundaries, while females remain more closely affiliated with the brood performing the majority of the hygienic duties (Barlow 1974; Smith-Grayton & Keenleyside 1978; Dupuis & Keenleyside 1982; Mrowka 1982; Itzkowitz 1985; Barlow 1991; Lavery

& Reeb 1994; Annett et al. 1999). This form of labour division is also observed in many cooperative species (Faulkes et al. 1991; Lacey & Sherman 1991). For example, in the Damalarand mole-rats, *Cryptomys damarensis*, and the naked mole-rats, *Heterocephalus glaber*, smaller individuals form worker groups and participate more in colony maintenance than large individuals and breeders (Faulkes et al. 1991; Lacey & Sherman 1991). In other cooperatively breeding species there is no division of labour; helpers perform the same activities as the breeding individuals (Solomon & French 1997; Langen & Vehrencamp 1999; Koenig & Dickinson 2004). In *N. pulcher*, there is no division of labour or helper-specific behaviours; breeders and helpers defended against all intruder types, using the same suite of aggressive behaviours, but did so at different rates.

Here we have shown sex differences in defensive responses to territory intruders. We suggest that sex differences in parentage uncertainty and in available alternative reproductive options may be responsible for the higher female than male defence rates. Further work is now needed that manipulates reproductive opportunities for both sexes as well as examines the relatedness between breeders and helpers and between breeders and young in the groups. Without this information it is impossible to tease apart whether paternity, relatedness levels or reproductive opportunities influenced defence rates. To examine the influence of sex differences in reproductive opportunities on defence rates, one could replicate this experiment using monogamous groups; males with only one reproductive territory would be expected to defend more. By comparing these two types of mating groups (monogamous versus polygynous) we may be able to determine the extent to which alternative reproductive opportunities influence response to territory intruders. Despite these limitations, our research has added to our knowledge of the costs and benefits associated with territory defence and has shed some light on an understudied class of costly cooperative behaviours (joint defence).

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