

Sex and social status affect territorial defence in a cooperatively breeding cichlid fish, *Neolamprologus savoryi*

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Abstract Members of social groups must defend their shared territory against both predators and competitors. However, individuals differ widely in their contributions to territorial defence. Assessing the variation in response to territorial intrusions provides insight into both the benefits and costs of group living for different group members. In this study, we assessed the response of wild *Neolamprologus savoryi* to experimentally staged territorial intrusions. *Neolamprologus savoryi* is an understudied cooperatively breeding cichlid fish endemic to Lake Tanganyika, East Africa. We found that dominant male and dominant female *N. savoryi* were both highly aggressive towards heterospecific

predators and towards same-sex conspecific rivals. Both dominant males and females were less aggressive towards opposite-sex conspecific opponents, with the relative reduction in aggression being most pronounced in males. Subordinates provided low levels of defence against all intruder types, which suggests that subordinate *N. savoryi* rely on larger group members for protection. Collectively, our results provide insight into the structure and function of *N. savoryi* social groups, and highlights key costs and benefits of cooperation for individual social group members.

Keywords Aggression · Defence · Cooperation · Lake Tanganyika · *Neolamprologus pulcher*

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Introduction

Cooperative breeding systems, where one or more non-breeding subordinate helpers provide alloparental care to the offspring of dominant breeding individuals (Arnold & Owens, 1998; Taborsky, 2001; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2012), represent an interesting evolutionary puzzle (Bernasconi & Strassmann, 1999; Queller et al., 2000; Kokko et al., 2001, 2002; Dugatkin, 2002). Why would an individual ever forego the direct fitness benefits of reproduction and instead provide care for the offspring of sometimes-unrelated group members? The enigma of cooperative breeding has been studied for decades across a wide range of taxa (for theoretical and multi-taxa reviews, see Hamilton, 1964a, b; Kokko et al., 2001, 2002; Bergmüller et al., 2007; for reviews in birds and mammals, see Clutton-Brock, 2002, 2009; in birds, see Gaston, 1978; Brown, 1987; Stacey & Koenig, 1990; Emlen et al., 1991; Zahavi, 1995; Hatchwell & Komdeur, 2000; Koenig & Dickinson, 2004; and in fish, see Wong & Balshine, 2011), and remains one of the enduring questions in behavioural biology.

One often cited benefit of group living is the effectiveness of collective defence of a shared territory (Hamilton, 1964a, b; Gaston, 1978; Krause & Ruxton, 2002). This can include defence against larger predators that require several individuals to deter (Rasa, 1987, 1989; Clutton-Brock et al., 1999), or defence against conspecific intruders that represent competition for resources (Duffy et al., 2002; Schradin, 2004). Within a cooperatively breeding social group, different individuals will gain varying benefits from defence against intruders. Dominant individuals will gain direct fitness benefits when they defend their own offspring from predators, or when they defend their dominant reproductive position from a conspecific intruder (Griffin & West, 2003; Komdeur, 2006). Subordinates can also benefit from defending their group's territory. They may benefit directly if territorial defence reduces their individual predation risk, or functions as a signal of individual quality where performing the behaviour might increase the chances of moving up in the social hierarchy (Zahavi & Zahavi, 1997; Maklakov, 2002; Barclay, 2010; Barclay & Reeve, 2012), joining a new social group (Hellmann & Hamilton, 2014), or lead to inheritance of a reproductive position (Balshine-Earn et al., 1998;

Magrath, 2001; Griffin & West, 2003; Komdeur, 2006; Heg et al., 2009). Subordinates may also benefit indirectly if the offspring protected in the territory are closely related (Queller & Strassmann, 1998; Clutton-Brock, 2002; Griffin & West, 2003).

Individuals of different status or sex within a cooperatively breeding social group will also face differential costs of defending against territorial intruders. For example, subordinate group members are often smaller, have fewer energy reserves and may be more vulnerable to injury during aggressive encounters than larger and more dominant group members (Mathis, 1991; Johnsson et al., 1999). Subordinate group members may therefore face higher costs from aggressively defending against an intruder and may defend less effectively than a dominant group member. As another example, males and females may incur different costs when reproductive opportunities are lost to territorial intruders (Clutton-Brock & Huchard, 2013), which may lead to sex differences in defence against conspecific intruders. The variation among group members in both the costs and benefits of defence can lead to differences in how much each individual contributes to communal territorial defence. Quantifying the behavioural response of different group members to territorial intrusions therefore provides a window into both the potential costs and benefits of cooperation (Queller & Strassmann, 1998; Clutton-Brock, 2002; Griffin & West, 2003; Desjardins et al., 2008; Heg & Taborsky, 2010; Mares et al., 2012).

In this study, we used territorial defence behaviour to gain insight into the costs and benefits of cooperation in a Lamprologine cichlid fish species, *Neolamprologus savoryi*. Teleost fish are by far the most diverse group of extant vertebrates (Nelson, 2006), and exhibit an incredible diversity of reproductive and social systems (Taborsky, 1987; Godin, 1997; Goodwin et al., 1998; Wisenden, 1999; Taborsky, 2001). In particular, the Lamprologine cichlid fishes, endemic to Lake Tanganyika, East Africa, display an impressive range of reproductive and social systems (Taborsky, 1994, 2001; Rossiter, 1995; Yamagishi & Kohda, 1996; Kawanabe et al., 1997; Mboko & Kohda, 1999; Katoh et al., 2005; Ota & Kohda, 2006; Ota et al., 2012). This is the only group of fishes where cooperative breeding has been widely documented (Taborsky, 1994, 2001; Heg & Bachar, 2006). Of the cooperative species, by far the most research attention

to date has focused on *Neolamprologus pulcher*, which has emerged as a model system for understanding the evolution of cooperative breeding (see review by Wong & Balshine, 2011). However, cooperative breeding occurs throughout the Lamprologine phylogeny (Heg & Bachar, 2006), and cooperative breeding has so far been described in approximately 20 of 90 species of Lamprologine cichlids (Rossiter, 1995; Taborsky, 1994; Sato & Gashagaza, 1997; Schradin & Lamprecht, 2002; Heg & Bachar, 2006). As a tribe, Lamprologine cichlids display traits that are thought to be pre-requisites for cooperative breeding in fishes, such as strong territoriality combined with substrate breeding, and extended parental care (Choe & Crespi, 1997; Emlen, 1997; Heg & Bachar, 2006). However, the specific route taken from these pre-adaptations to a cooperatively breeding social system likely varied among species (Heg & Bachar, 2006). Thus, studying aspects of cooperative breeding and social living across a variety of Lamprologine species provides a valuable opportunity to understand the evolution of cooperative breeding.

Here, we quantified the response of various group members to a suite of experimentally staged territorial intrusions in the cooperatively breeding Lamprologine cichlid, *N. savoryi*, following protocols established for *N. pulcher* (Desjardins et al., 2008). *Neolamprologus savoryi* provides a useful comparison to existing research on *N. pulcher* for a variety of reasons. *Neolamprologus savoryi* is similar in size and appearance to *N. pulcher* (Brichard, 1989; Konings, 1998, 2005; Heg et al., 2005a), and shares a similar ecological niche, with both species being planktivores (Kondo, 1986; Brichard, 1989) that maintain permanent territories in the rocky littoral zone (Brichard, 1989; Kawanabe et al., 1997; Konings, 1998, 2005). These two species live in the same areas, often interspersed within mixed-species colonies (Heg et al., 2005a, 2008), and are exposed to the same predators (Brichard, 1989; Balshine et al., 2001; Heg et al., 2005a, b). Indeed, the two species are so similar in appearance that until 1952 they were thought to be the same species (Trewavas & Poll, 1952). However, recent phylogenies built from mitochondrial DNA (Day et al., 2007; Sturmbauer et al., 2010) and nuclear DNA (Sturmbauer et al., 2010) confirm that the two are separate species. From a comparative perspective, the species are interesting because *N. pulcher* and *N. savoryi* differ in their mating systems. While *N. pulcher* and *N. savoryi* have similar

overall group sizes (Heg et al., 2005a), *N. savoryi* is more strongly polygynous than *N. pulcher* (Kawanabe et al., 1997), and each dominant *N. savoryi* male guards a single territory containing multiple females as well as subordinates (Heg et al., 2005a). However, *N. pulcher* can be monogamous, where each *N. pulcher* dominant male has a single territory containing a single female and subordinates. When polygynous, an individual *N. pulcher* dominant male will guard two or more geographically separate territories, each containing a single dominant female and subordinates (Desjardins et al., 2008; Wong et al., 2012).

In this field-based study, we compared the response of dominant males, dominant females, and large and small subordinate *N. savoryi* to: (1) *Lepidiolamprologus elongatus*, a heterospecific predator of both adults and juveniles; (2) a dominant male conspecific intruder and (3) a dominant female conspecific intruder. Through this series of staged intrusions, we aimed to understand the extent of defence provided by subordinate *N. savoryi*, to understand whether male and female dominant fish provide equal rates of defence, and to determine how the different *N. savoryi* group members respond to predatory versus conspecific challenges. Our end goal was to provide a better understanding of the costs and benefits of cooperation in this highly social fish.

Methods

Study site and study animals

This study was conducted in March and April 2013, at a site located in Kasakalawe Bay, on the southern shores of Lake Tanganyika (8°46'52"S, 31°5'18"E). The study site is characterised by a mix of sand and cobble substrate, and has a gentle descent to depth (for detailed descriptions of the study site, see Balshine-Earn et al., 1998; Balshine et al., 2001; Bergmüller et al., 2005; Dierkes et al., 2005; Heg et al., 2005a, b; Stiver et al. 2005; Wong et al. 2012). *Neolamprologus savoryi* can be found at this site in mixed-species colonies with *N. pulcher* (Heg et al. 2005a, 2008). We located *N. savoryi* at depths between 11 and 14 m using SCUBA. When a target social group was located, the group territory was marked with a numbered rock. The dominant male, the largest dominant female, and a large and small subordinate within that female's sub-territory were identified using individually distinct

markings, and their behaviour was monitored during a 10–15 min baseline behavioural observation. Territories were defined as the area defended by the dominant male and dominant females within each social group. These areas were usually easy to determine, since *N. savoryi* social groups typically guard a small rocky area on sand substrate, often with patches of sand dividing groups. Once defined, territory length and width was measured to the nearest centimetre using a measuring tape. The dominant male and female, as well as a large and a small subordinate, were then captured using fence nets and hand nets, fin-clipped for individual identification, and sex was confirmed by external examination of the genital papillae. Small subordinates that could not be reliably sexed by external examination were classified as juveniles. The groups ($n = 12$) used for this study had a group size of 9 ± 4 individuals (mean \pm standard error of the mean, SEM), and a mean territory of 64 ± 14 cm by 103 ± 19 cm (mean \pm SEM), consistent with previous observations of *N. savoryi* groups at the same site (Heg et al., 2005a).

Staged intrusions

Each social group ($n = 12$ social groups) was given 24–48 h to recover from capture and fin-clipping, and was then exposed to three-staged intrusions and an empty-container control over a 4-day period. Each group experienced a male conspecific intruder, a female conspecific intruder, a heterospecific predator (*L. elongatus*, a common predator of both juvenile and adult *N. savoryi*; Konings, 1998, 2005), and an empty presentation chamber (a transparent plastic container measuring $10 \times 18 \times 30$ cm) as a control in randomized order. The conspecific stimulus fish were adult dominant individuals from other social groups (Table 1), and therefore represented a potential threat to the dominance status of the dominant pair in our focal groups. All intruders were captured from separate colonies at least 20 m away from the focal social groups, to ensure that the group members were unfamiliar with the intruders (Heg et al., 2008). All of the fish used as intruders were measured, and the sex of conspecific intruders was confirmed by visual examination of the genital papillae. We used *L. elongatus* heterospecific predators that were large enough to consume adult *N. savoryi* (Table 1, Taborsky, 1984; Balshine et al., 2001; Heg et al., 2005b). All stimulus fish were captured with fence nets and hand nets, placed

Table 1 Sample sizes and standard lengths of the stimulus fish used to determine the aggressive response of *Neolamprologus savoryi* to different territorial intrusions

Intruder type	Sample size	Standard length (mm)
Female conspecific	5	43.4 ± 0.7
Male conspecific	3	57.0 ± 2.5
Heterospecific predator (<i>Lepidiolamprologus elongatus</i>)	5	76.2 ± 4.9

Standard lengths are presented as mean \pm standard error of the mean

Table 2 Aggressive territorial defence behaviours observed and recorded during staged territorial intrusions in the cooperatively breeding cichlid, *Neolamprologus savoryi*

Context	Behaviour	Description
Displays	Aggressive posture	Focal fish lowers its head and raises its tail in front of its opponent
	Frontal display	Also called a puffed throat or an opercular flare. Focal fish extends out its opercula and lower jaw. Often associated with a posture where the head is pointed downwards
	Head shake	Focal fish thrashes its head from left to right repeatedly
	Tail beat	Focal fish thrashes its tail directing water in the direction of its opponent
	S-bend	Focal fish curves its body into an 'S' shape. This behaviour was only directed towards conspecifics
Overt aggression	Charge	Focal fish quickly darts towards another fish
	Ram	Focal fish makes contact with another fish using the head or mouth region, but no obvious bite is taken and jaws remain closed
	Bite	Focal fish bites another fish

in a transparent plastic presentation chamber ($10 \times 18 \times 30$ cm), and were used as an intruder for 2–4 different *N. savoryi* social groups. Stimulus fish were held for no more than 60 min, and all stimulus fish were released unharmed back to their site of original capture following the experimental trials. The behaviour of the stimulus fish was monitored throughout the trials to

ensure that the fish were not unduly stressed, and continued to behave normally and provide a consistent stimulus (i.e., that the stimulus fish continued to move around normally within the presentation chamber and continued to respond to focal fish). Stimulus fish were identified with fin clips prior to release, and we captured stimulus fish from unique locations each day to ensure that the same stimulus fish was not accidentally recaptured. For each simulated intrusion, the presentation chamber was placed on the perimeter of the focal *N. savoryi* group's territory, and the territorial responses of four focal individuals in the group (the dominant male, dominant female and the largest and one small subordinate within that sub-group) were quantified during a 10-min observation period. Behaviours were classified according to an ethogram modified from previous published ethograms for other related Lamprologine cichlid species (Sopinka et al., 2009; Hick et al., 2014). Briefly, the aggressive behaviours scored were aggressive displays (aggressive postures, frontal displays, head shakes, tail beats and s-bends), as well as overt physical aggression (charges, rams and bites) (Table 2).

Statistical analyses

All aggressive behaviours were summed for each individual. A generalised linear mixed model with a negative binomial error distribution and log-link function, appropriate for over-dispersed count data (Bolker, 2008; Zuur et al., 2013), was then used to assess the influence of responder type (i.e., group member type; dominant male, dominant female, large subordinate, small subordinate), intruder type (male conspecific, female conspecific or heterospecific predator), and the interaction effect on the number of aggressive behaviours performed by each individual. To account for repeated measures and group effects, individual nested within group were included as random effects. To account for potential differences in stimulus fish behaviour, stimulus fish individual identity was also included as a random effect. Over-dispersion of count data was assessed visually and then confirmed using the package 'AER' (Kleiber & Zeileis, 2008). Generalised linear mixed models were performed using the 'lme4' (Bates et al., 2013) and 'MASS' (Ripley et al., 2014) statistical packages. Post-hoc comparisons of significant interactions were performed using the 'phia' statistical package (De Rosario-Martinez, 2013). All analyses were

Table 3 Results of a generalised linear mixed model with a negative binomial error distribution and a log-link function, exploring the influence of responder type (breeder male, breeder female, top-ranked subordinate and second-ranked subordinate), intruder type (male conspecific, female conspecific and a heterospecific predator of young and adults), and the interaction effect on the number of aggressive defence behaviours produced during a territorial intrusion in the cooperatively breeding cichlid fish *Neolamprologus savoryi*

Model term	DF	Residual DF	F value	P value
Responder type	3	130	44.2	<0.001
Intruder type	2	133	4.1	0.03
Interaction effect	6	124	6.3	0.01

Individual nested within group were included as random effects to control for repeated measures and group effects. Intruder identity was included as a random effect to control for potential differences in stimulus fish behaviour. See Fig. 1 for statistical differences among groups. See 'Methods' section for full statistical information

performed in R version 3.0.2 (R Core Team, 2008). The level of significance was assessed at $\alpha = 0.05$.

Results

None of the *N. savoryi* showed any aggressive response towards the empty presentation chamber, and we were able to conclude that the fish were reacting specifically to the stimulus fish within the container. Both male and female dominant *N. savoryi* defended vigorously against *L. elongatus* predators, and against same-sex conspecific intruders (Table 3, Fig. 1). There was a significant interaction effect between responder and intruder type (Table 3), where dominant fish did not respond as strongly to an opposite-sex conspecific as they did to a predator or same-sex conspecific rival (Fig. 1). Dominant males especially showed less aggression than dominant females towards opposite-sex conspecific intruders (Fig. 1). Subordinate *N. savoryi* exhibited low levels of defence against the predator and against conspecific intruders of both sexes (Table 3; Fig. 1).

Discussion

This study quantified territorial defence rates among various group members of the cooperatively breeding Lamprologine cichlid, *N. savoryi*, in order to

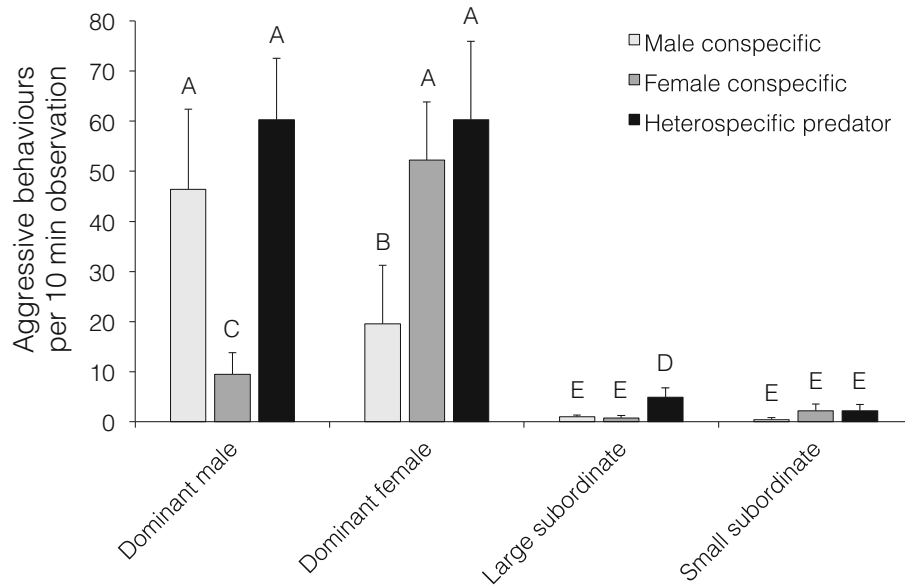


Fig. 1 The aggressive responses of individuals of different social status in the cooperatively breeding cichlid *Neolamprologus savoryi* to three different classes of territorial intrusion: conspecific male, conspecific female and heterospecific predator. Dominant breeding fish responded more strongly to a heterospecific predator and to a same-sex conspecific rival than to an opposite-sex conspecific intruder. Large subordinates

responded with low levels of aggression towards a predator, but overall, subordinate fish had a lower response to all intruder types relative to dominant fish. Mean response \pm standard error of the mean is presented. Different letters indicate statistically significant differences among groups ($\alpha = 0.05$). See Table 3 and ‘Methods’ section for full statistical information

understand relative costs and benefits of social living for different social group members. We found that both large and small subordinate fish provided low levels of defence against all intruder types. Both dominant males and females provided higher levels of defence against predators and same-sex conspecific intruders than against opposite-sex conspecific intruders. In particular, dominant males had reduced aggression towards opposite-sex intruders relative to dominant females.

First, we aimed to understand the extent of defence provided by subordinate *N. savoryi*. A previous observational study of *N. savoryi* documented that subordinate *N. savoryi* will provide some territorial defence against predators (Heg et al., 2005a). However, here we experimentally manipulated the opportunity for defence and quantified the level of subordinate *N. savoryi* defence against either predators or unfamiliar conspecifics. Subordinates performed very little to no defence. The sizes of the heterospecific territorial intruders were not noted in the previous study of *N. savoryi* (Heg et al., 2005a), and it is possible that subordinate *N. savoryi* only defend against smaller, less threatening intruders and avoid confrontations with larger and more

dangerous predators, such as those used as stimulus fish in our study. It is also possible that the predators varied in some other way between the studies. For example, factors such as the reproductive status of heterospecific intruders have also been shown to influence the extent of aggressive territorial defence behaviour in a species of South American cichlid fishes (*Amphilophus zaliosus*; Lehtonen et al., 2010). Nevertheless, the *N. savoryi* subordinates in this study provided much lower levels of defence relative to *N. savoryi* dominant individuals.

Our results are in contrast to studies in the closely related *N. pulcher*, where subordinate individuals provide as much (Desjardins et al., 2008) or more (Balshine et al., 2001) defence against predators as the dominant male. Furthermore, the presence of subordinates significantly increases the survival of offspring within *N. pulcher* groups (Brouwer et al., 2005) and subordinate *N. pulcher* increase rates of defence when predation risk is artificially increased (Desjardins et al., 2008; Heg & Taborsky, 2010), which suggests that subordinates play a critical role in communal defence of the territory in *N. pulcher*. In a previous study of *N. pulcher*, small and large subordinate *N.*

pulcher performed approximately 20–35 aggressive defence behaviours towards *L. elongatus* predators during a 10-min observation period (Desjardins et al., 2008), while in this study, large subordinate *N. savoryi* performed an average of five aggressive defence behaviours in the same period of time towards a predator of the same species. The smaller subordinate *N. savoryi* produced an average of only two aggressive defence behaviours in 10 min. Since the heterospecific intruders used in this study were matched in size to the *L. elongatus* predators used in the previous experiment on *N. pulcher* (mean standard length of 76 mm in this study, and 78 mm in the previous study on *N. pulcher*; Desjardins et al., 2008), the predation threat represented by the stimulus fish should have been similar between the two studies. The difference in subordinate behaviour between the two species suggests that *N. savoryi* subordinates may gain fewer benefits or experience higher costs through contributing to shared territorial defence than do subordinate *N. pulcher*. In particular, it is likely that the benefits of participating in communal defence differ for subordinates of the two species. One factor that may be important is the level of direct reproduction gained by subordinates of each species. In *N. pulcher*, subordinates gain direct reproduction, and more helpful female subordinates are more likely to gain reproductive opportunities (Heg et al., 2009) and more likely to inherit a reproductive position (Balsine & Buston, 2008). Preliminary genetic analysis in *N. savoryi* suggests that both male and female subordinate *N. savoryi* occasionally reproduce within their social groups, but rates of subordinate reproduction are low (Dik Heg, pers. comm.). However, more detailed investigation of subordinate reproduction, as well as investigation of factors such as social group inheritance by subordinates in both *N. pulcher* and *N. savoryi*, as well as in other social cichlids, would shed light onto the benefits of cooperation for these fishes.

Another aim of this study was to investigate territorial defence behaviour in dominant male and female *N. savoryi*, and to determine how members of the social group responded to different intruder types. We found that dominant males and females defended at similar rates against the predator. This result is in contrast to many studies in other cichlid species, where levels of defence are often found to be dissimilar between males and females. For example, the male parent will invest more in territorial

Table 4 Standard lengths of male and female dominant *Neolamprologus savoryi* and *Neolamprologus pulcher* at the field site in Kasakalawe Bay (collected by the same authors for this and other studies)

Species	Sex	Sample size	Standard length (mm)
<i>Neolamprologus savoryi</i>	Male	24	55.6 ± 0.9
	Female	14	44.4 ± 0.9
<i>Neolamprologus pulcher</i>	Male	26	57.8 ± 0.8
	Female	15	52.9 ± 0.9

At this field site, *N. savoryi* have greater sexual size dimorphism (relatively smaller dominant females) than *N. pulcher*. Standard lengths are presented as mean ± standard error of the mean

protection than the female in Midas cichlids (*Amphilophus citrinellus*; Rogers, 1988) and in convict cichlids (*Amatitlania nigrofasciata*; Itzkowitz et al., 2001, 2002, 2005). In another South American cichlid (*Amphilophus xiloanensis*), males defend at a higher rate towards conspecific intruders, while females defend more vigorously against predators (McKaye & Murry, 2008). Our result that dominant males and females defend at similar rates is also in contrast to patterns of territorial defence in *N. pulcher*, where dominant females defend at much higher rates than dominant males against predators (Balshine et al., 2001; Desjardins et al., 2008). There are several possible reasons for this difference between the two Lamprologine species. First, in *N. savoryi*, the dominant male is more related to other group members than the dominant female (Dik Heg, pers. comm.). In contrast, *N. pulcher* females are more related to other group members than are males (Stiver et al., 2004, 2005; Dierkes et al., 2005). Therefore, female *N. pulcher*, and particularly dominant female *N. pulcher*, have higher investment in the current social group than do males, which may explain the elevated rates of territorial defence in the dominant female *N. pulcher*. Further, while *N. pulcher* and *N. savoryi* are overall similar in size (Brichard, 1989; Konings, 1998, 2005; Heg et al., 2005a), *N. pulcher* have reduced sexual dimorphism (larger dominant females) relative to *N. savoryi* at our study site (Table 4). The relatively larger dominant female *N. pulcher* may face fewer costs providing territorial defence relative to dominant female *N. savoryi*, and therefore provides higher rates of defence. In another cooperatively breeding Lamprologine cichlid species, *Julidochromis ornatus*, the

smaller parent, regardless of sex, will perform major parental duties, including staying close to offspring, while the larger parent will be more likely to defend the territory against intruders (Awata & Kohda, 2004), supporting the importance of relative size differences in determining patterns of territorial defence behaviour.

We found that dominant male and female *N. savoryi* both defended vigorously against same-sex conspecific rivals, and displayed a muted response to opposite-sex conspecific intruders. This is likely because an intruder of the opposite sex may represent a potential mating opportunity, while a same-sex intruder represents a potential competitor. In another Tanganyikan cichlid, *Eretmodus cyanostictus*, defending mates from competitors can be as important as defending a suitable territory (Morley & Balshine, 2003). We found that while dominant males and females both defended at similar levels against a same-sex intruder, dominant females defended more aggressively than dominant males against an opposite-sex intruder. As a result, conspecific males received slightly more aggression overall than conspecific female intruders. This difference may be related to the polygynous mating system of *N. savoryi*, where each dominant *N. savoryi* male guards a single territory containing multiple females (Kawanabe et al., 1997; Heg et al., 2005a). Adding additional dominant females to a polygynous group may be less costly in terms of disrupting the overall social group structure than a potential male take-over.

Overall, the results of this study highlight that both social structure and the social roles of different group members differ greatly between Lamprologine species. These results emphasise the value in Lamprologine cichlids as a model for understanding the evolution of cooperative breeding. Future research documenting the variation in cooperative breeding systems within this cichlid tribe, and understanding how variation in social systems relate to natural history and the phylogenetic relationships among species, will be highly valuable and lend insight into the evolution of cooperation.

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