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Social status influences responses to unfamiliar conspecifics in a cooperatively breeding fish

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Abstract

In group living animals, individuals may visit other groups. The costs and benefits of such visits for the members of a group will depend on the attributes and intentions of the visitor, and the social status of responding group members. Using wild groups of the cooperatively breeding cichlid fish (*Neolamprologus pulcher*), we compared group member responses to unfamiliar 'visiting' conspecifics in control groups and in experimentally manipulated groups from which a subordinate the same size and sex as the visitor was removed. High-ranking fish were less aggressive towards visitors in removal groups than in control groups; low-ranking subordinates were more aggressive in the removal treatment. High-ranking females and subordinates the same size and sex as the visitor responded most aggressively toward the visitor in control groups. These results suggest that visitors are perceived as potential group joiners, and that such visits impose different costs and benefits on current group members.

Keywords

dominance, group joining decisions, Lake Tanganyika, *Neolamprologus pulcher*, Cichlidae, teleosts.

1. Introduction

Although individuals in social groups often defend their shared territories against conspecifics, such groups may nevertheless receive visits from non-

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group members (Packer et al., 1990; Cockburn, 1998; Bergmüller et al., 2005; Wong & Balshine, 2011a). The reaction to these visitors can be variable across groups and between individuals in the group (Schaffner & French, 1997; Kitchen & Beehner, 2007; Iwata & Manbo, 2013) and this variation in the response to visitors may reflect differences in the goals of visitors, as well as the costs and benefits inflicted by the visitor on different group members. For example, an individual may visit a social group in order to begin the process of joining that group permanently, and the visit may function to facilitate entry into this social unit sometime in the future (Bergmüller et al., 2005). In contrast, individuals may visit a social group to mate or to exploit the group by stealing food, reproduction or by cannibalizing young (Rohwer, 1978; Goodall, 1986; Taborsky, 1994; Hamilton & Dill, 2003). Such behavior will impose costs upon the visited group, but certain members of the group may face higher costs than others, while some members may even benefit from these visits (Schaffner & French, 1997; Kitchen & Beehner, 2007; Lewis, 2008). Thus differences in net costliness of visitation for different group members can lead to differences in the reactions to visitors. In this study, we investigate how group members of a cooperatively breeding cichlid fish respond to simulated visitors, and whether a group member's social status influenced their response to these visitors.

There are multiple ways in which visitors could inflict costs and these costs are likely to differ across individual group members. For example, a dominant reproductive male in the group could lose parentage to a male visitor who manages to spawn with his mated partner, but would not lose parentage to a female visitor and may even gain additional reproductive success if he can mate with her during the visit (Taborsky, 1994; Goymann & Wingfield, 2004). Therefore, we expect males to defend more against male visitors and less against female visitors (Desjardins et al., 2008). If visitors exploit the productivity of groups in other ways such as stealing food (Hamilton & Dill, 2003) or cannibalizing vulnerable group members (Rohwer, 1978; Goodall, 1986), then the response to visitors should depend on the value of such lost resources for each group member. For instance, if offspring are consumed, then close relatives (e.g., parents and full siblings) will face greater costs than other, less related group members.

In many group-living animals, individuals will disperse from their natal group and move into a new group to mate (Greenwood, 1980; Taborsky, 1984, 1985; Rood, 1987, 1990; Komdeur, 1992; Girman et al., 1997;

Balshine-Earn et al., 1998; Stiver et al., 2006; Zöttl et al., 2013a). Visits to prospective groups can precede this dispersal event (Bergmüller et al., 2005). If visitation precedes joining the group, then the response of resident group members to visitors will depend on both the current costs and benefits of the visit, and the future fitness effects of joining. When a new individual joins, the group will increase in size, which may carry both benefits and costs for current group members (Krause & Ruxton, 2002; Lewis, 2008). For example, being part of a larger group may offer greater protection from predation through dilution, predator confusion, defensive efficiency, or increased vigilance (Alexander, 1974; Taborsky, 1984; Sherman, 1985; Krause & Ruxton, 2002; Vucetich et al., 2004; Zöttl et al., 2013b). However, increases in group size may also carry costs such as greater conspicuousness to predators, intensified competition for resources and reproduction, or increased transmission of disease (Alexander, 1974; Côté & Poulin, 1995). If a social hierarchy exists within the group, then higher ranked individuals may stand to gain from potential joiners, while a joiner might push lower ranked individuals further down the social ladder (Rimmer & Power, 1978; Lima & Dill, 1990; Magurran & Seghers, 1991; Martel & Dill, 1995; Brouwer et al., 2005). Therefore, the behavioural response to a potential joiner is expected to depend on both the size of the current group and on each individual's risk of being usurped from its current social position by a joiner.

Using wild groups of the cooperatively breeding cichlid fish *Neolamprologus pulcher*, we examined how group members of different social and reproductive status responded to staged visitation events. *Neolamprologus pulcher* is a useful system to examine how group members perceive visiting individuals because extra-pair and extra-group reproduction, egg and fry cannibalism, and inter-group dispersal all occur (Taborsky, 1984, 1985; von Siemens, 1990; Stiver et al., 2006, 2009, Zöttl et al., 2013a). In *N. pulcher* groups, a dominant breeding pair performs the majority of reproduction (Stiver et al., 2009) while subordinate group members largely forego reproduction and provide alloparental care to the offspring of the dominant pair while queueing for dominant status (Taborsky, 1984; Wong & Balshine, 2011a). Reproduction occurs regularly (monthly) in this species (Desjardins et al., 2011) and either eggs or juveniles are present in most groups (pers. obs.). Dominance is strongly size-based in this species (Reddon et al., 2011a; Dey et al., 2013, 2015), so that the expected rank of a fish can be determined based on its size relative to other group members.

In this study, we presented an unfamiliar conspecific (hereafter 'stimulus fish') of the same sex and similar size to the largest subordinate in the group and recorded the rates of aggression that this stimulus fish received from each group member. Approximately half of these subordinates were female, the other half were male. Further, in half of the social groups, we temporarily removed the largest subordinate group member (hereafter 'removal treatment') and in so doing reduced the group size before presenting the stimulus fish. The remaining groups maintained their full membership and served as controls.

If the stimulus fish were perceived as individuals who would attempt to parasitize reproduction and quickly abandon the group after a short visit, we predicted that dominant males (who father the majority of offspring in the group; Stiver et al., 2009) would guard their paternity and be more aggressive towards male visiting stimulus fish than towards female stimulus fish. As visitors attempting to parasitize reproduction impose similar costs on dominants regardless of whether or not a large subordinate was removed, we predicted no differences in aggression between the removal and control treatments for dominant breeders.

If instead stimulus fish were perceived as predators of eggs or young, then we predicted that dominant individuals (both males and females, who stand to lose direct fitness from such behaviour) would behave most aggressively towards the stimulus fish. In this species, subordinates are typically less related to offspring than are the dominants and the degree of relatedness declines with the age of the subordinate (Stiver et al., 2007). Under this hypothesis, we predicted that neither dominant nor subordinate group members would differ in aggression towards stimulus fish depending on whether a removal had occurred. Previous work has shown that *N. pulcher* do not compensate for lost subordinates (Brouwer et al., 2005).

Finally, we predicted that if stimulus fish were perceived as potential future joiners, then group members at risk of rank usurpation would respond the most vigorously and aggressively towards the stimulus fish (Griesser et al., 2008; Wong & Balshine, 2011b; Iwata & Manbo, 2013). Moreover, after the removal of a high-ranking subordinate, we predicted that dominant fish would reduce their rates of aggression towards stimulus fish because dominant fish stand to gain from replacing the removed group member (Brouwer et al., 2005). In contrast, we predicted that the remaining subordinates who are of lower rank would increase their rate of aggression towards the stimulus fish in defence of their recent increase in rank.

2. Methods

2.1. Study species

Neolamprologus pulcher is endemic to Lake Tanganyika in East Africa, where it forms social groups that typically consist of a single dominant breeding pair and on average 7–9 subordinates of both sexes (range 1–20, Balshine et al., 2001; Heg et al., 2005). Dominance in *N. pulcher* is strongly associated with body size (Reddon et al., 2011a); the dominant male is the largest group member, while the second largest is typically the dominant female (Wong & Balshine, 2011a). Subordinate group members form a size-based dominance hierarchy (Balshine-Earn et al., 1998; Dey et al., 2013). Subordinates maintain and defend the group territory and may provide alloparental care (Taborsky, 1984; Wong & Balshine, 2011b). The presence of subordinates has a net positive effect on the reproductive success of dominants (Brouwer et al., 2005). Groups with more subordinates raise more young, and larger groups of *N. pulcher* hold higher quality territories (Balshine et al., 2001). Territories (the physical area used and protected by a group of conspecifics) containing large groups are more likely to continue to support social groups across years while territories with small groups were more likely to fade out (Heg et al., 2005), suggesting a positive effect of group size on group persistence over time.

2.2. Experimental protocol

This experiment was conducted in the spring of 2013. Using SCUBA we located *N. pulcher* social groups ($N = 43$) between 11 and 14 m in depth offshore of Kasakalawe Point (8°46′S, 31°4′E) on the southern shore of Lake Tanganyika, near Mplungu, Zambia. In each social group we identified and captured the largest subordinate (hereafter the focal subordinate) by using a combination of a handheld dip net and a fence net. There were 22 groups where the largest subordinate was male (mean standard length (SL) $\pm$ SE $=$ 41.8 ± 3.2 mm) and 21 groups where the largest subordinate was female (mean SL $\pm$ SE $= 44.0 \pm 2.1$ mm). Sex was determined by examination of the genital papilla (Balshine-Earn et al., 1998; Konings, 2005). For each of these focal large subordinate fish, we measured standard length from the tip of the snout to the end of the caudal peduncle (Trewavas, 1983).

We randomly assigned half of the social groups in our study ($N = 21$) to the removal treatment. In the removal treatment, the focal subordinate fish was placed inside a mesh bag within a closed minnow bucket and moved at least 3 m away from the focal social group's territory. This distance and opaque bucket ensured that group members would not interact with the removed subordinate, as *N. pulcher* rarely move far from their territory boundaries (Werner et al., 2003). In the remaining control groups ($N = 22$), we immediately released the captured focal subordinate back into its group following measurement and sexing. In both treatments, we then caught a stimulus fish that was sex and size matched to the focal subordinate (within 2 mm SL) from a territory at least 15 m away. This stimulus fish was placed in a transparent perforated plastic 2.75-l container (approx. 14 × 14 × 14 cm) that had eight small holes to allow water flow, thus providing group members with both visual and chemical cues from the stimulus fish.

Within ten minutes of capturing the focal subordinate, the container containing the stimulus fish was placed within the groups' territory approx. 20 cm from the centre of the territory. We gave the group and stimulus fish one minute to habituate to the disturbance of placing the container in their territory and then began a 10-min observation on all group members. We recorded counts of aggressive displays and overt aggressive attacks directed towards stimulus fish by the dominant pair, by the focal subordinate fish (in control groups only), and by any other smaller subordinates in each social group. Aggressive displays consisted of head down postures, fin raises, and puffed throats, and did not involve the aggressor physically touching the presentation container. Overt aggressive attacks consisted of chases, rams, and bites in which the individual made physical contact with the presentation container. These behaviours are clearly defined and have been described in a number of ethograms developed for this species (Coeckelberghs, 1975; Kalas, 1975; Buchner et al., 2004; Sopinka et al., 2009; Hick et al., 2014; Reddon et al., 2015). 'Fish in a jar' protocols have previously been used in many fish behavioural studies (Itzkowitz, 1990; Haley & Müller, 2002; Garvy et al., 2015), including in studies on *N. pulcher* (Hert, 1985; Taborsky, 1985; Taborsky et al., 1986; Bergmüller & Taborsky, 2005, 2007; Desjardins et al., 2008; Fischer et al., 2014; Hellmann & Hamilton, 2014), and elicit naturalistic responses from the animals exposed to this stimulus. After the 10-min observation period, the stimulus fish was returned to its capture site and the focal subordinate fish from the removal treatment groups were returned to their groups. All presentations occurred between 10:00 and 17:00.

The number of subordinates (individuals greater than 1.5 cm SL) varied between social groups (range: 1–13). However, the number of subordinates per group did not differ between treatments (independent samples t-test: $t = 0.104$, df $= 41.9$, $p = 0.92$). Nonetheless, to account for any variation among social groups related to group size, we included the number of subordinates in the group as a factor in subsequent statistical models (see below). We did not track each subordinate fish smaller than the stimulus fish individually, so the counts of aggressive behaviours performed by all non-focal subordinates within a group were pooled. Anecdotally we observed that attacks and displays were primarily performed by the largest of these smaller subordinates. Desjardins et al. (2011) found that *N. pulcher* vary in their activity through the course of the day. Because our observations occurred in both the morning and afternoon, we controlled for this variation by including this information as a binomial effect in our statistical analyses (see below).

The frequency of aggression produced by each group member towards the stimulus fish could be interpreted as the amount of defence against an intruder (Desjardins et al., 2008; Hellmann & Hamilton, 2014), or as the inverse of the willingness of that group member to accept the stimulus fish into the group (Jordan et al., 2010). We first tested whether the sex or status of individuals in the control groups was related to their aggressive responses towards stimulus fish using generalized linear mixed models with the overt attack and display counts by individual group members (and a pooled value for the non-focal subordinates) as the dependent variables. This model included individual status, stimulus fish sex, their interaction, group size, and time of day as fixed effects. Group identity was treated as a random effect. Counts of aggressive acts were overdispersed so a negative binomial distribution with a log-link function was used.

Second, we investigated whether the removal of a high-ranking subordinate influenced the status-specific response of dominant males, dominant females, and smaller subordinates. We included individual counts of aggressive attacks and displays (respectively) towards stimulus fish as the dependent variable in each of these generalized linear models. Treatment (removal versus control groups), the sex of the stimulus fish, their interaction, as well as the time of day were included as fixed factors, and as in the previous model, the number of subordinates in the group was included as a covariate. As before, these models used a negative binomial distribution with a log link-function. All statistical analyses were performed using SPSS 22.0.

3. Results

3.1. Does a group member's status influence its responses to the stimulus fish?

Dominant males performed significantly fewer aggressive displays than any of the other group members ($F_{3,78} = 6.56$, $p = 0.001$; Figure 1a). Dominant females and the sex- and size-matched subordinates performed aggressive overt attacks towards the stimulus fish more frequently than did dominant males or smaller subordinates in control groups ($F_{3,78} = 6.62$, $p < 0.001$; Figure 1b). Male stimulus fish in control groups received more aggressive displays than female stimulus fish overall ($F_{1,78} = 4.298$, $p = 0.04$), but the interaction of individual status and stimulus fish sex was not significant ($F_{3,78} = 0.11$, $p = 0.95$). There was no relationship between the number of overt attacks stimulus fish received and its sex in the control groups ($F_{1,78} = 0.08$, $p = 0.78$).

3.2. How does subordinate removal influence aggression towards the stimulus fish?

Dominant females in the removal treatment groups performed fewer overt attacks towards the stimulus fish relative to dominant females in control groups (Treatment: $\chi^2 = 15.18$, $p < 0.001$; Figure 2a). Dominant females also tended to perform fewer aggressive threat displays towards stimulus fish in the removal treatment but this pattern did not reach significance (Treatment: $\chi^2 = 3.18$, $p = 0.07$; Figure 2b). In both treatments, dominant females performed fewer overt attacks towards male stimulus fish than towards female stimulus fish (Stimulus fish sex: $\chi^2 = 4.66$, $p = 0.03$; Figure 2a). The interaction between stimulus fish sex and treatment did not explain variation in the number of overt attacks by dominant females towards the stimulus fish ($\chi^2 = 2.589$, $p = 0.11$). Dominant males very rarely performed overt attacks and these overt acts were performed by only a few individuals; thus overt attacks by dominant males were not considered in subsequent analyses. Overall, dominant males performed fewer threat displays against male stimulus fish in removal treatment groups than they did in the control groups, but dominant males did not differ in their behaviour towards female stimulus fish depending on treatment (Treatment × Stimulus fish sex: $\chi^2 = 3.98$, $p = 0.046$, Figure 2c). In contrast to dominant fish, the smaller non-focal subordinates performed more aggressive displays (Treatment: $\chi^2 = 4.06$, $p = 0.044$; Figure 3a) and more overt aggressive attacks

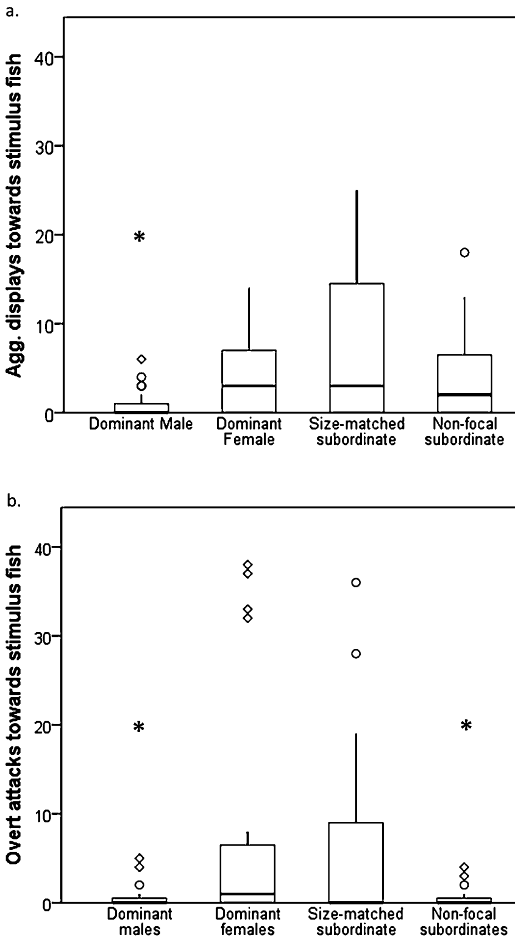

Figure 1. Boxplots of counts of (a) aggressive displays and (b) overt attacks towards the stimulus fish in control groups ($N = 22$). Values for non-focal subordinates represent the sum of all subordinate group members smaller than the focal individual. Dominant males performed significantly fewer displays than any other group members (1a; $p = 0.001$), and dominant females and size-matched subordinates performed significantly more attacks than dominant males or non-focal subordinates (1b; $p < 0.001$). Asterisks indicate significantly different values ($\alpha = 0.05$). Data is presented as boxplots and shows the median and quartiles values, as well as minimum and maximum values excluding >1.5 times the interquartile range (marked with circles; diamonds indicate values > 3 times the interquartile range).

(Treatment: $\chi^2 = 8.28$, $p = 0.004$; Figure 3b) towards the stimulus fish in removal groups relative to subordinates in the control groups.

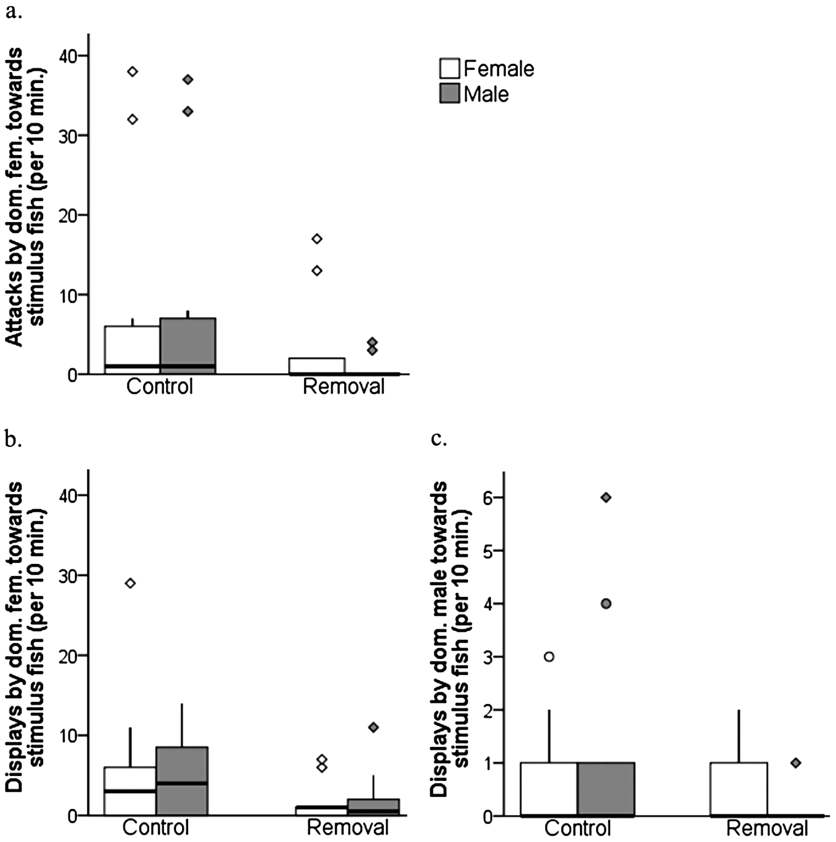

Figure 2. Boxplots of aggressive acts towards the stimulus fish; (a) overt attacks by dominant females, (b) aggressive displays by dominant females and (c) threat displays by dominant males in control groups ($N = 22$) and removal treatments ($N = 21$). Dominant females performed significantly fewer attacks (1a; $p < 0.001$) towards stimulus fish regardless of their sex after a removal, and dominant males performed fewer displays towards male stimulus fish after a removal (1c; $p = 0.046$). Values > 1.5 times the interquartile range are marked with circles, and diamonds indicate values > 3 times the interquartile range.

Group size did not affect the number of aggressive displays performed towards the stimulus fish by the dominant male ($\chi^2 = 0.21$, $p = 0.65$) or the number of overt attacks and aggressive displays by the dominant female (Attacks: $\chi^2 = 0.19$, $p = 0.66$; Displays: $\chi^2 = 0.35$, $p = 0.55$). Neither the sex of the stimulus fish, nor the number of subordinates in the group had a significant effect on the number of overt attacks (Stimulus fish sex: $\chi^2 = 0.03$, $p = 0.87$; number of subordinates: $\chi^2 = 0.03$, $p = 0.85$) or aggressive

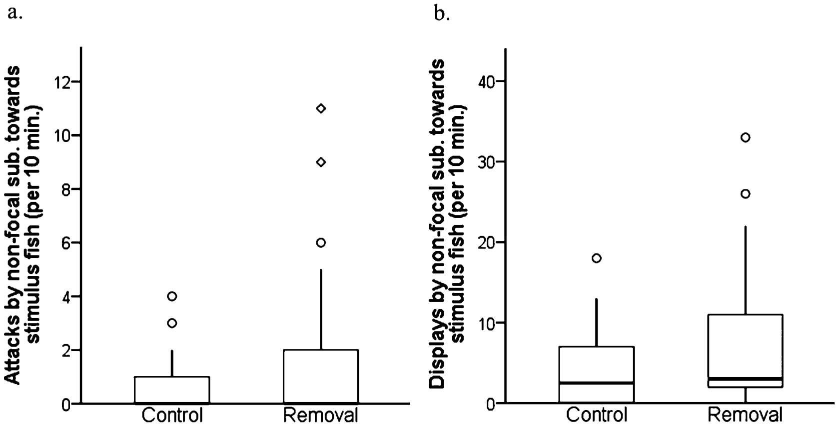

Figure 3. Boxplots of (a) displays and (b) overt attacks towards the stimulus fish by non-focal subordinate group members in the removal treatment ($N = 21$) and control groups ($N = 22$). Non-focal subordinates performed more displays (1a; $p = 0.044$) and attacks (1b; $p = 0.004$) towards stimulus fish after a removal had occurred. Values $>$ 1.5 times the interquartile range are marked with circles, and diamonds indicate values $>$ 3 times the interquartile range.

displays (Stimulus fish sex: $\chi^2 = 0.79$, $p = 0.37$; number of subordinates: $\chi^2 = 0.06$, $p = 0.81$) performed by smaller non-focal subordinate fish.

4. Discussion

Our results were consistent with the hypothesis that stimulus fish were perceived as potential joiners to the group. We predicted that if the stimulus fish was perceived as a potential joiner, then size- and sex-matched subordinates would be most aggressive to the unfamiliar conspecific. Subordinate group members matched in terms of size and sex would be expected to face the greatest conflict over status with the stimulus fish, and several other studies have shown that agonistic interactions in *N. pulcher* are greatest between individuals close in size (Hamilton et al., 2005; Wong & Balshine, 2011b; Reddon et al., 2011a; Dey et al., 2013). We found that both size- and sex-matched subordinates and dominant females from intact groups exhibited more frequent aggressive behaviours than did other group members.

Our results were not consistent with visitors being perceived as egg or fry predators. Although subordinates increased their rates of aggression after a removal, which is consistent with compensation for a lost group member, dominant fish, the most invested in and most closely related to the current offspring, should not have performed fewer aggressive acts after removal if visitors were perceived as predators.

Dominant females face potential reproductive competition from female joiners, and indeed were more aggressive toward female stimulus fish than towards male stimulus fish. Sex-specific aggression towards unfamiliar individuals of the same sex and status has also been described in the group-living false clown anemonefish, *Amphiprion ocellaris* (Iwata & Manbo, 2013). Lewis (2008) observed a similar pattern in female Sifaka (*Propithecus verreauxi verreauxi*), a primate from Madagascar. Females in Lewis' study behaved aggressively towards female non-group members, and encouraged males to reside in the group through affiliative behaviours. Lewis (2008) suggested that female group members facilitate membership depending on the sex of potential joiners. While our dominant males might eventually face reproductive competition with successfully joining males, they did not differ in their defence against male or female stimulus fish in control groups, and after a removal were less aggressive towards male stimulus fish. This finding suggests dominant males do not consider the visiting stimulus fish to be strong reproductive competitors.

Both male and female dominants were less aggressive toward the stimulus fish in groups from which a subordinate had been removed. This result is inconsistent with the hypotheses that stimulus fish were perceived as cuckholders or predators of eggs or fry. We suggest instead that dominants were less aggressive in reduced groups because these dominants benefit from restoring the group to its prior size by replacing the lost subordinate following the experimental removal. Allowing new group members to join, bringing the group back to its previous size and strength, may result in increased frequency and quality of alloparental care (Schaffner & French, 1997; Balshine et al., 2001) or simply dilute predation risk or the work effort needed to maintain the territory (Foster & Treherne, 1981; Hebblewhite & Pletscher, 2002; Zöttl et al., 2013b). Indeed, Schaffner & French (1997) found that dominant female marmosets, *Callithrix kuhli*, from small groups behaved less aggressively towards strangers, and suggested that dominant individuals may facilitate group joining events by being tolerant of unfamiliar individuals. These benefits of increased group size could have also applied in our control groups. However, dominants might benefit less from visitors in control groups for two reasons: (1) they may face diminishing returns of additional subordinates as group size increases beyond the resources/shelters available in that territory and (2) there may be increased conflict amongst subordinates as group size increases (Rannala & Brown, 1994; Balshine-Earn et al., 1998; Granter & Taborsky, 1998; Taborsky & Granter, 1998; Wong & Balshine, 2011b), which could detract from the extra alloparental care and the time dedicated to maintaining and defending the territory (Brouwer et al., 2005). Conflict between subordinates could also attract attention from predators (Rimmer & Power, 1978; Lima & Dill, 1990; Magurran & Seghers, 1991; Martel & Dill, 1995).

The behavior of smaller subordinates was also consistent with the hypothesis that simulated visitors were perceived as potential joiners to the group. Smaller subordinates behaved more aggressively towards the stimulus fish in the removal treatment than in control groups. We suggest that the subordinates in our experiment perceived their increased rank resulting from the removal, and thus increased their aggression towards unfamiliar individuals threatening their newly acquired rank (Wong & Balshine, 2011b). While subordinates in both treatments faced a demotion in rank, individuals higher in the dominance queue are closer to achieving a reproductive rank, and thus may defend their status more vigorously than individuals lower in the queue (Dey et al., 2013). Interestingly, if small subordinates in the reduced groups did indeed perceive a change in their rank, this occurred quite rapidly (<15 min after the removal). Behavioural and physiological indicators of perceived changes in rank have been shown to arise quite rapidly in another cichlid fish, *Astatotilapia burtoni* (Chen & Fernald, 2011). It is also possible that smaller subordinates were compensating for the lost defensive efforts of the missing focal subordinate group member, or that the largest remaining subordinate had taken up more defensive 'duties' in its newly acquired status. However, Brouwer et al. (2005) found no evidence that remaining subordinate group members increased their amount of territory defence after a similar subordinate removal experiment. We also found no evidence that the overall size of the group had an effect on subordinate aggression.

Our results are most congruent with the hypothesis that visitors were perceived as prospective joiners to the group, however we do not suggest visitors would have been accepted into the group on their initial visit. While *N. pulcher* often disperse and subsequently join groups (Stiver et al., 2006, 2007), the process by which joining events occur is not well understood. Joining events have been observed only a handful of times in nature (Bergmüller et al., 2005) and the response to these immigrants was initially aggressive in nature (S. Balshine, pers. obs.). Zöttl et al. (2013a) found that immigrating fish that faced high rates of aggression from a breeding pair were generally rejected from the group. However, many of these groups were visited multiple times each hour, and it appears that successful joiners are highly familiar with their new group by the time they join.

It is unclear why male stimulus fish faced less aggression from dominant females in general, or why dominants of both sexes appear to be more tolerant of male 'visitors' than female fish after a removal. Sex differences in dominant response may simply result from visiting subordinate males being a more common occurrence for *N. pulcher* groups. Stiver et al. (2006) found that removed dominant males were much more likely to be replaced by joining individuals, while vacant dominant female positions were more often claimed by a female already in the group. Also, male *N. pulcher* disperse further (Stiver et al., 2007) and more frequently (Stiver et al., 2006) than do females.

By examining the factors influencing group responses to a visiting conspecific, our study complements previous work on between-group movement in cooperative species (Rood, 1987; Zack & Rabenold, 1989; Bergmüller et al., 2005; Schaffner & French, 2007; Jordan et al., 2010a; Le Vin et al., 2010; Reddon et al., 2011b). Here we present evidence that the behaviour of individual group members differed depending on their status and sex, and our results are consistent with stimulus fish being perceived as potential joiners. Smaller subordinates' responses depended on their relative rank, while dominants' responses depended on whether a subordinate had recently been removed from the group and, for dominant females, on the sex of the stimulus fish. Our results highlight that group joining decisions, and thus emerging group structure, are the product of both joiner preferences and the responses of current group members.

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