

NOTE

Out-Group Threat Promotes Within-Group Affiliation in a Cooperative Fish

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ABSTRACT: In social species, conflict with outsiders is predicted to affect within-group interactions and thus influence group dynamics and the evolution and maintenance of sociality. Although empirical evidence exists for a relationship between out-group conflict and intragroup behavior in humans, experimental tests in other animals are rare. In a model fish system, we show that simulated out-group intrusions cause postconflict increases in intragroup affiliation but no changes in postconflict intragroup aggression. Postconflict affiliation was greater following intrusions by neighboring compared with nonneighboring individuals; neighbors represent greater threats to the dominance rank and breeding success of residents, and they are visible in the aftermath of the intrusion. By providing strong evidence of a link between out-group conflict and postconflict intragroup behavior and demonstrating that intragroup affiliation is affected by the nature of the out-group intrusion, our study shows the importance of considering postconflict behavior for our understanding of cooperation and social structure.

Keywords: cooperation, intergroup conflict, postconflict behavior, signaling, sociality, territorial intrusions.

Background

In many social species, stable persistent groups of individuals defend collective territories (McComb et al. 1994; Radford 2003; Kitchen and Beehner 2007) and face a variety of threats from outsiders. Conspecific groups or coalitions may invade in an attempt to annex the territory or acquire critical resources contained within it (Radford and Du Plessis 2004; Ridley 2012), whereas individual intruders might indicate the imminent attack of other groups (Herbinger et al. 2009) or pose a challenge to particular group members in terms of their position or reproductive success (Kleiber et al. 2007; Mares et al. 2012). Studies on a wide range of taxa have considered the immediate defensive responses to such out-group threats and the factors determining the outcome of

interactions with outsiders (Kitchen and Beehner 2007; Kleiber et al. 2007; Desjardins et al. 2008). However, there has been far less investigation of the impact of out-group conflicts after intrusions and associated defense have ceased, despite the likely influence on group dynamics, individual fitness, and social evolution (van Schaik 1989; Radford 2008a; Bowles 2009; Radford and Fawcett 2014).

Theoretical work has long predicted that conflict with outsiders should affect subsequent behavior among group-mates (Hamilton 1975; Alexander and Borgia 1978). For instance, an increased out-group threat should favor higher levels of cooperation, especially if cohesion between group members is important for success (Reeve and Hoelldobler 2007); greater within-group affiliation or redirected aggression may result if conflict with out-group rivals generates tension or stress between groupmates (Von Holst 1998). Considerable human research using economic games has shown that cooperation between subjects and punishment of noncooperators increase when current payoffs are directly affected by competition from other groups (Erev et al. 1993; West et al. 2006; Gneezy and Fessler 2012). However, to understand more fully the evolutionary roots of sociality, experiments investigating postconflict behavior are required in other species, because species-specific differences in sociality and cooperation could affect intragroup behavior (Radford 2008b; Polizzi di Sorrentino et al. 2012), and out-group conflict is expected to be a major selective force through its potential impacts on both survival and reproduction (Wilson and Wrangham 2003; Mares et al. 2012; Polizzi di Sorrentino et al. 2012). To our knowledge, there have been only two experimental studies on nonhuman animals examining the impact of simulated threats from out-group rivals on postconflict within-group behavior. Radford (2008b) found that playback of vocal choruses from rival groups led to an increase in within-group affiliative behavior in a wild population of green woodhoopoes (*Phoeniculus purpureus*), a cooperatively breeding bird. Polizzi di Sorrentino et al. (2012) found no change in within-group affiliation but increased

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within-group aggression in a single captive group of tufted capuchin monkeys (*Cebus apella*) when aggressive visual interactions with a rival group were allowed.

The extensive literature on conflict between members of the same group (intragroup conflict) suggests that subsequent behavior is affected not just by the occurrence of the interaction but also by the characteristics of the conflict, the identity of those involved, and the relationship between them (Schino et al. 1998; Aureli et al. 2002). Different out-group rivals can represent different levels of threat to the group or to particular group members (Radford 2005; Mueller and Manser 2007), conflicts with outsiders can vary greatly in their duration and intensity (Radford and Du Plessis 2004; Wich and Sterck 2007), and individuals of different dominance status, sex, and age may not contribute equally to interactions with intruders (Heinsohn and Packer 1995; Bruintjes and Taborsky 2008). Yet little is known about the importance of these differences in out-group conflict characteristics and threat levels for postconflict behavior; Radford (2008a) provides the only experimental test, finding a greater increase in postconflict within-group affiliation in green woodhoopoes after playback of stranger groups compared with neighbors.

Here we investigate how interactions with out-group rivals affect postconflict intragroup behavior in the cooperatively breeding cichlid fish *Neolamprologus pulcher*. Groups of this species are territorial, and all group members, including the dominant breeding pair and subordinates of both sexes, contribute to defense against conspecifics (Taborsky and Limberger 1981; Bruintjes and Taborsky 2008; Desjardins et al. 2008). Intrusions by out-group individuals can represent a threat to the position of existing, similarly sized group members (Balshine-Earn et al. 1998). Discrimination of conspecifics is possible from visual cues alone (Hert 1985; Balshine-Earn and Lotem 1998). Clear and easily quantifiable behavioral acts (e.g., affiliation and aggression) are common between groupmates (Taborsky 1984; Mileva et al. 2009; Reddon et al. 2012). Small experimental groups of unrelated individuals are representative of natural situations where there is high predation pressure and rapid turnover rates of breeders (Heg et al. 2004; Dierkes et al. 2005). Numerous previous studies have used captive populations to answer a range of evolutionary, developmental, and behavioral questions (Taborsky 1984; Zöttl et al. 2013; Bruintjes and Radford 2014).

We conducted experimental territorial intrusions to answer two main questions. First, how does conflict with out-group individuals affect subsequent intragroup behavior? We predicted that intragroup affiliation would increase during the postconflict period (see Radford 2008b). Postconflict intragroup aggression might be expected to decrease if group members are enhancing group cohesion (Cords 2002) or to increase if there is redirected aggression (Polizzi di Sorrentino et al. 2012). Second, does the nature of the

out-group conflict influence subsequent intragroup behavior? We compared two biologically relevant scenarios: (1) intrusions by nonneighboring individuals (who were not visible before or after the intrusion) and (2) intrusions by neighboring individuals (who were visible in their own neighboring territory before and after the intrusion). In *N. pulcher*, resident group members show strong defensive responses to intrusions by unfamiliar individuals (Desjardins et al. 2008), but neighbors potentially represent the greater overall threat to the position in the group and breeding success of individual residents (Stiver et al. 2004; Dierkes et al. 2005; Bruintjes et al. 2011). Thus, if postconflict behavior is related to aggression levels against intruders, we predicted greater changes in intragroup behavior following intrusions by nonneighboring individuals, whereas if postconflict behavior relates to out-group threat level, we predicted stronger intragroup behavior following neighbor intrusions.

Methods

Study Species and Husbandry

Neolamprologus pulcher is found in Lake Tanganyika in groups consisting of a dominant pair and 0–16 subordinate helpers (Taborsky and Limberger 1981; Balshine et al. 2001). All group members defend the territory against conspecific and heterospecific intruders (Taborsky and Limberger 1981; Bruintjes and Taborsky 2011). Groups typically consist of unrelated and related individuals with a low overall relatedness (Stiver et al. 2005), and subordinates trade cooperative behavior to be allowed to stay in the territory (Bergmüller et al. 2005b; Fischer et al. 2014). See appendix, available online, for details of study population and husbandry as well as full methodological details.

Experimental Setup

Two experiments were conducted, the first during July–August 2012 and the second during June–July 2013. For each experiment, 14 new groups of three fish comprising a dominant male, a dominant female, and a female subordinate were formed in 80-L transparent aquaria following standard methods (Bruintjes and Taborsky 2008). Female subordinates were used, because they do not impose reproductive costs compared with subordinate males (Heg et al. 2008). Dominant males were >5 mm larger than dominant females, which were >5 mm larger than subordinates. Each aquarium had two clay flowerpot halves in the middle for hiding and breeding.

Pairs of aquaria were placed with their short sides approximately 3 mm apart to form neighboring groups (fig. A1; figs A1–A3 in appendix, available online). Neighboring groups were arranged so that they were not visible to fish

in other aquaria, and neighboring individuals were carefully matched according to size. Stable groups (those where all individuals were free to move throughout the territory without being harassed by fellow group members; cf. Brintjes and Radford 2013) were given >7 days to become accustomed to their neighbors before an experiment. In experiment 1, we were unable to stabilize two groups, and therefore no data were collected from these (resulting in $n = 12$ groups); all groups were available for data collection in experiment 2 ($n = 14$).

Both experiments involved controlled intrusions into resident territories. To standardize those intrusions, we used three clear Plexiglas presentation cylinders that were either empty (control) or contained one conspecific fish each. Conspecific fish were either the three neighboring individuals or size- and sex-matched individuals from a nonneighboring group. The presentation cylinders were placed 5 cm apart, approximately 5 cm from the entrance of the breeding shelters, for 10 min per intrusion.

In experiment 1, the 12 resident groups received two treatments: (1) presentation of empty cylinders (control), with neighbors visible before, during, and after the presentation; and (2) territorial intrusions by neighboring individuals, who were visible in the adjacent tank before and directly after the intrusion. In experiment 2, 14 different resident groups also received two treatments: (1) territorial intrusions by neighboring individuals, who were again visible in the adjacent tank before and after the conflict; and (2) territorial intrusions by nonneighboring individuals (from an aquarium that was not visible to the residents before or after the intrusion), with neighbors present in the adjacent tank before, during, and after the intrusion. Resident groups received one intrusion per day, with the two treatments separated by 1–4 days but conducted within the same 2-h window; treatment order was counterbalanced in both experiments.

Data Collection and Analysis

All behavioral definitions followed previous work on the study species. During each experimental intrusion, we recorded frequencies of overt attacks (ramming, biting, and tail beats) and aggressive displays (fast frontal approach, fin and opercula spreading, head-down display, and S-shaped bending) directed by each of the three resident group members toward the presentation cylinders (Brintjes et al. 2010); individuals were identified by size. In experiment 2, we also recorded activity levels of the intruders on a scale ranging from 0 (no movement) to 5 (very active; Brintjes and Taborsky 2011).

To examine the influence of out-group intrusions on post-conflict behavior, we recorded frequencies of two types of intragroup behavior during the 10 min before and the 10 min

immediately after an intrusion (i.e., when the cylinders were removed from the focal tank): (i) affiliation (soft touches [also called “bumps”], parallel swimming, and following; Mileva et al. 2009; Reddon et al. 2012) and (ii) aggression (overt attacks and aggressive displays; see above). For the two types of behavior, we recorded both which individual displayed or initiated the act and which group member it was directed toward.

Paired-sample *t*-tests and Wilcoxon matched-pairs signed-rank tests were used to compare total occurrences of a given behavior exhibited by all group members in the two treatments in a given experiment. We then used linear mixed-effects models (LMMs) to explore whether group member types (dominant male, dominant female, and subordinate) were differentially involved in the different behaviors per treatment. Separate paired-sample *t*-tests or Wilcoxon tests were performed to test treatment differences per group member type. For aggression (directed at out-group intruders and between members of the same group), separate tests were conducted on the frequency of overt attacks and aggressive displays and on the combined total. When considering intragroup behavior, separate analyses were conducted for the initiation/donation of an act and for its receipt. If a particular type of group member never initiated or received a particular behavior in any of the groups, it was excluded from that analysis. In all mixed models, the random-effect individual was included to correct for the repeated-measures design. For all intragroup behaviors, we analyzed the differences between the pre- and postintrusion periods. All behavioral data are deposited in the Dryad digital depository: <http://dx.doi.org/10.5061/dryad.3r3v3> (Brintjes et al. 2015).

Results

Experiment 1: Effect of Out-Group Intrusions

Simulated intrusions into a neighboring territory had the expected effect on the immediate defensive behavior of residents. Significantly more total acts of direct aggression (overt attacks and aggressive displays combined) were performed toward cylinders containing out-group individuals than toward empty cylinders (control condition; treatment: $F_{1,33} = 110.66$, $P < .001$ for LMM). However, the treatment-based difference was significantly affected by group member type (treatment \times group member: $F_{2,33} = 27.90$, $P < .001$; group member: $F_{2,33} = 31.21$, $P < .001$; fig. 1A). Although all three group member types attacked out-group individuals more than they attacked empty cylinders (dominant males: $t_{11} = 7.60$, $P < .001$ by paired *t*-tests on treatment differences; dominant females: $t_{11} = 7.21$, $P < .001$; subordinates: $t_{11} = 2.24$, $P = .046$), dominant males exhibited a greater increase in defense than both dominant females ($t_{22} = 2.16$, $P = .042$ by independent-

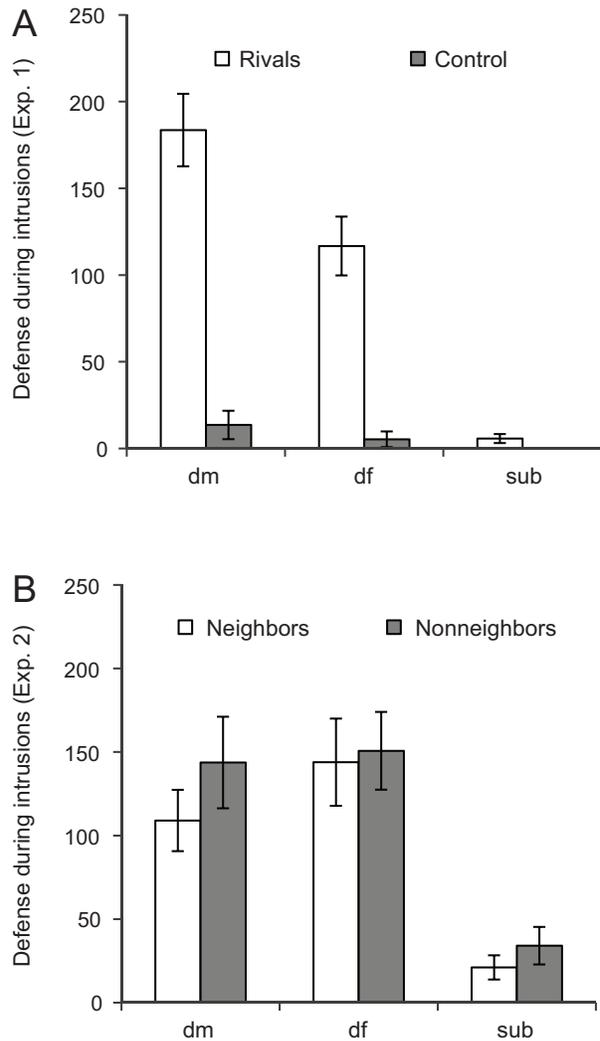


Figure 1: Mean (\pm SE) total out-group aggressive acts (sum of overt attacks and aggressive displays) by dominant males (dm), dominant females (df), and subordinates (sub) toward intrusions of neighbors (Rivals) and empty cylinders (Control; A) and intrusions of neighboring and nonneighboring individuals (B).

samples t -test) and subordinates ($W = 78.0$, $n_1 = n_2 = 12$, $P < .001$ by Mann-Whitney U -test), and dominant females increased their defense more than subordinates ($W = 80.0$, $n_1 = n_2 = 12$, $P < .001$). Qualitatively similar results were found when considering overt attacks and aggressive displays separately (see appendix).

There was a significantly greater increase in total postconflict intragroup affiliation following intrusion of out-group individuals compared with the presentation of empty cylinders ($t_{11} = 5.12$, $P < .001$ by paired t -test; fig. 2A). Affiliation donation increased significantly more following out-group intrusion compared with the control condition (treatment: $F_{1,33} = 17.41$, $P < .001$ by LMM), with all three

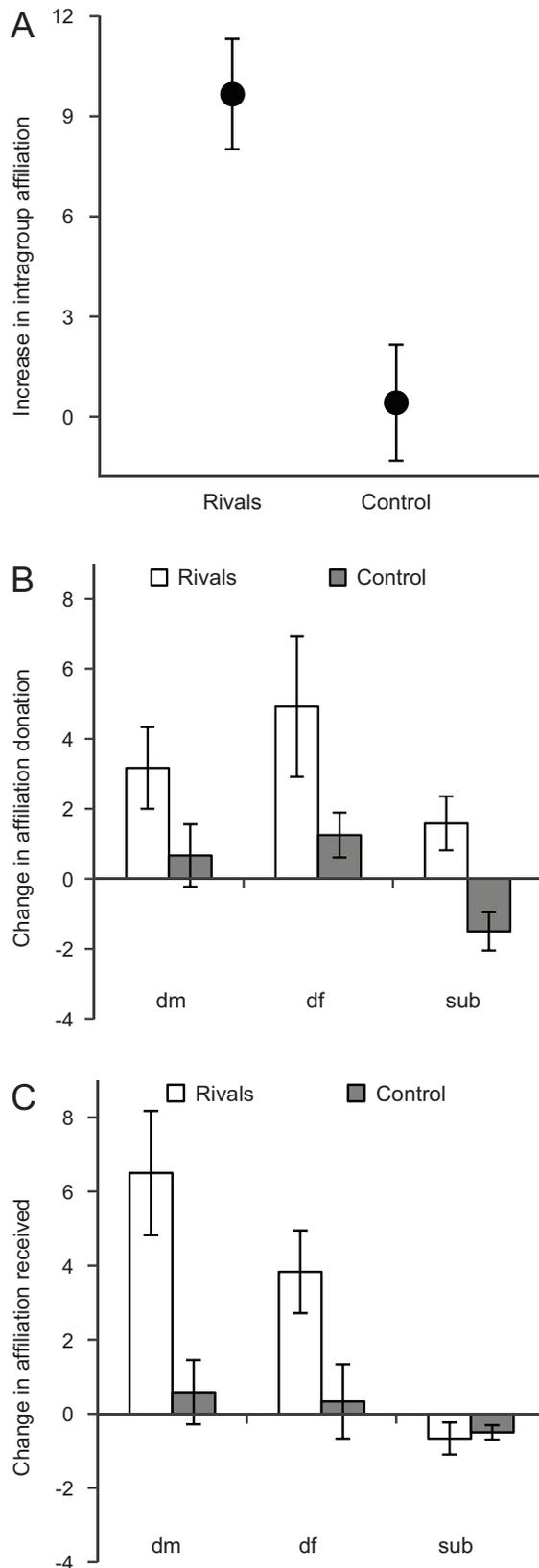
group member types showing a similar treatment-based difference (no significant treatment \times group member interaction: $F_{2,33} = 0.21$, $P = .813$; group member: $F_{2,33} = 2.82$, $P = .074$; fig. 2B). Received affiliation also increased significantly more following intrusions of out-group individuals compared with the control condition (treatment: $F_{1,33} = 21.74$, $P < .001$). However, the treatment-based difference was significantly affected by group member type (treatment \times group member: $F_{2,33} = 7.15$, $P = .003$; group member: $F_{2,33} = 6.46$, $P = .004$; fig. 2C). Dominant males (paired t -test: $t_{11} = 3.45$, $P = .005$) and dominant females ($t_{11} = 3.89$, $P = .003$) received more affiliation following intrusions of out-group individuals compared with the control condition, but subordinates received similar levels of affiliation in both treatments (Wilcoxon test: $Z = -0.11$, $n = 12$, $P = .914$).

No significant differences in postconflict intragroup aggression were detected between treatments (out-group intruders vs. empty cylinders) when considering either overall responses (overt attacks: $Z = -0.36$, $n = 12$, $P = .720$ by Wilcoxon test; aggressive displays: $Z = -0.15$, $n = 12$, $P = .878$; all aggressive acts combined: $Z = -0.24$, $n = 12$, $P = .812$) or those at an individual level (appendix).

Experiment 2: Effect of Intrusions by Neighboring versus Nonneighboring Individuals

Simulated intrusions of nonneighboring individuals led to higher total levels of defense behavior by residents than intrusions from neighbors (LMM: treatment: $F_{1,39} = 4.39$, $P = .043$). Although group member types differed significantly in their overall contributions to defense (group member: $F_{2,39} = 11.42$, $P < .001$), with subordinates contributing significantly less than both dominant males (independent-sample t -test: $t_{26} = 4.41$, $P < .001$) and females ($t_{26} = 26$, $P < .001$), who did not differ significantly ($t_{26} = 0.66$, $P = .515$), all three types showed qualitatively the same greater defensive response to nonneighbor intrusion (no significant treatment \times group member interaction: $F_{2,39} = 0.95$, $P = .397$; fig. 1B). Qualitatively similar results (higher levels of defense against nonneighbors by all group member types) were found when considering only overt attacks, whereas there was no significant difference in the frequency of aggressive displays between treatments (see appendix). The greater levels of aggression exhibited toward nonneighbors compared with neighboring individuals was not a consequence of any significant difference in the activity levels of the two intruder types ($Z = -1.65$, $n = 28$, $P = .100$ by Mann-Whitney U -test).

Postconflict intragroup affiliation increased following both treatments but was significantly greater after intrusions of neighbors compared with nonneighboring fish ($t_{13} = 2.58$, $P = .023$ by paired t -test; fig. 3A). Affiliation



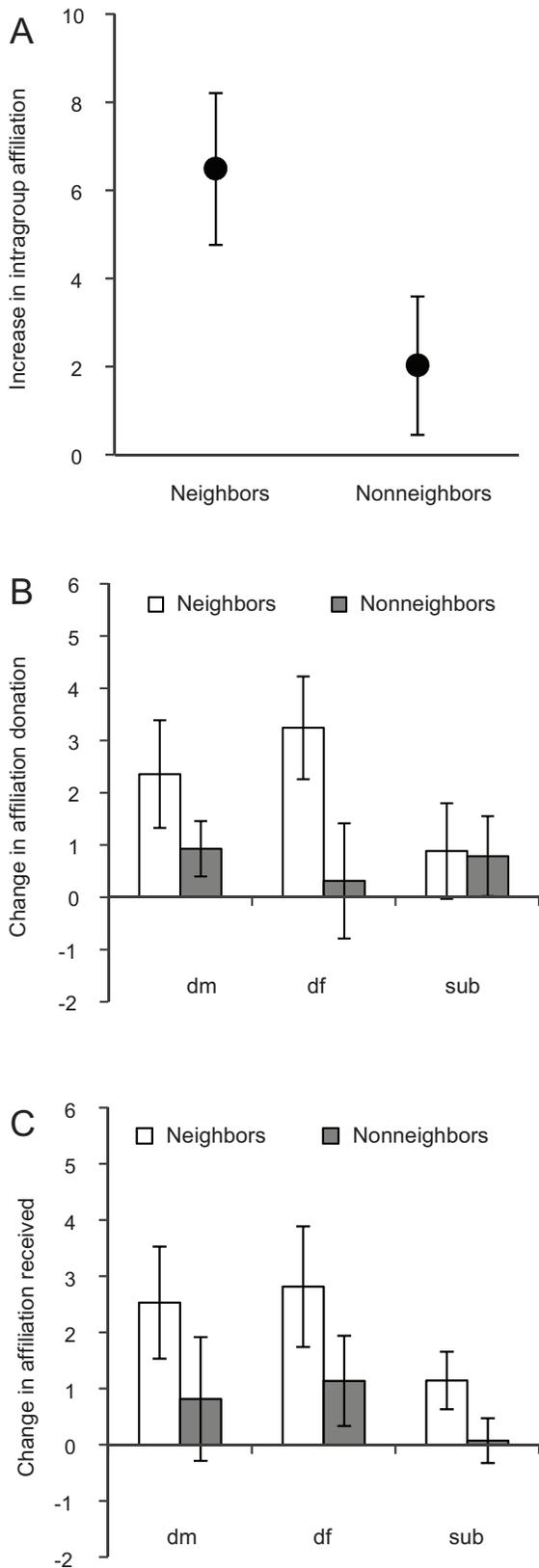
donation increased significantly more following intrusions by neighbors compared with nonneighbors ($F_{1,39} = 4.41$, $P = .042$ by LMM), with all three group member types showing a similar treatment-based difference (no significant treatment \times group member interaction term: $F_{2,39} = 1.33$, $P = .276$; group member: $F_{2,39} = 0.58$, $P = .565$; fig. 3B). Similarly, affiliation received increased significantly more following intrusions by neighbors compared with nonneighbors ($F_{1,39} = 6.75$, $P = .013$), with all three group member types showing a similar treatment-based difference (no significant treatment \times group member interaction term: $F_{2,39} = 0.13$, $P = .877$; group member: $F_{2,39} = 1.04$, $P = .362$; fig. 3C).

Overall levels of postconflict intragroup aggression did not differ significantly, depending on whether the intruders were neighboring or nonneighboring individuals (overt attacks: $Z = -0.14$, $n = 14$, $P = .888$ by Wilcoxon test; aggressive displays: $t_{13} = 1.65$, $P = .122$ by paired t -test; all aggressive acts combined: $t_{13} = 1.34$, $P = .205$). At an individual level, there was also no significant effect of intruder treatment on intragroup aggression; there was a nonsignificant trend for dominant females and subordinates to receive more aggressive displays from groupmates following the intrusion of neighbors compared with that of nonneighboring individuals (appendix).

Discussion

Simulated territorial intrusion of out-group individuals, which generated the expected defense behavior (see also Desjardins et al. 2008), resulted in postconflict increases in intragroup affiliation but no significant changes in postconflict intragroup aggressive behavior. Evidence was found that dominant individuals, who defended more than subordinates, subsequently received more affiliation from their groupmates. Moreover, the level of postconflict affiliation was affected by the intrusion scenario: there was greater affiliation in the aftermath of intrusions by neighboring compared with nonneighboring individuals, even though aggression levels were higher against the latter. Our study therefore provides novel empirical support for a direct link between out-group conflict and postconflict intragroup behavior in nonhuman animals and indicates that the nature of the intrusion can influence the amount of postconflict affiliation shown among groupmates.

Figure 2: Postconflict intragroup affiliation following intrusions of neighbors (Rivals) and empty cylinders (Control; experiment 1); shown are mean (\pm SE) differences in the number of affiliative behaviors observed, postintrusion minus preintrusion. Total intragroup affiliation levels (A), individual affiliation levels donated (B), and individual affiliation levels (C) received by dominant males (dm), dominant females (df), and subordinates (sub). $N = 12$ groups.



Our finding that out-group intrusions lead to increased intragroup affiliation (more soft touches, follows, and parallel swimming by *Neolamprologus pulcher* group members) matches that from a study of birds (Radford 2008b) but contrasts with experimental work on a single monkey group (Polizzi di Sorrentino et al. 2012). At a proximate level, increases in postconflict affiliation may be the result of greater social stress or tension induced by conflict (Von Holst 1998). Participation in allogrooming (a commonly recorded affiliative behavior) reduces indicators of stress in both mammals and birds (Schino et al. 1988; Aureli and Yates 2010; Radford 2012), and increased time in close proximity is also a recognized means of reducing postconflict tension in primates (e.g., Verbeek and deWaal 1997; Mallavarapu et al. 2006). Whether postconflict affiliative behavior also has this effect in fish has yet to be determined, although it is known that the receipt of tactile stimulation (e.g., soft touches) can lower stress levels (Soares et al. 2011), whereas follows and parallel swimming result in prolonged close proximity of group members. Ultimately, such affiliative behavior might be used to strengthen bonds between group-mates and thus enhance group cohesion (Dunbar 1991).

All three types of group member increased the donation of postconflict affiliative behavior following out-group intrusions, but it was the dominant pair who received the most in experiment 1. Because dominants performed more aggressive acts than subordinates toward out-group intruders, this finding is in line with previous studies showing that green woodhoopoe group members contributing the most to out-group conflict received the most allogrooming, both in the immediate aftermath (Radford 2008b) and in border areas, where such conflicts were most likely (Radford 2011). One theoretical possibility is that affiliative behavior is traded for participation in out-group conflicts (as is true for some birds and mammals; e.g., Seyfarth and Cheney 1984; Barrett et al. 1999; Radford 2008b), but whether this is also the case in fish remains to be tested. More generally, considering links between defense contributions and subsequent intragroup interactions might provide insight into the variation often found in the helping efforts of different group members (Bergmüller and Taborsky 2005; Radford 2008b).

As predicted, the amount of postconflict affiliation shown by *N. pulcher* group members was affected by the intrusion scenario: the greatest increase in affiliative behavior was

Figure 3: Postconflict intragroup affiliation following intrusions of neighboring and nonneighboring individuals (experiment 2); shown are mean (\pm SE) differences in the number of affiliative behaviors observed, postintrusion minus preintrusion. Total intragroup affiliation levels (A), individual affiliation levels donated (B), and individual affiliation levels received (C) by dominant males (dm), dominant females (df), and subordinates (sub). $N = 14$ groups.

seen following neighbor intrusions, to which the residents had exhibited lower levels of aggression than when non-neighboring individuals intruded. Unlike in green woodhoopoes (Radford 2008*b*), higher levels of out-group aggression were therefore not followed by greater levels of intragroup affiliation, and so immediate and subsequent responses to territorial intrusions are not necessarily always tightly coupled. One possibility for the lower level of intragroup affiliation following intrusions of non-neighbors is that the residents are energetically constrained by the greater defense effort, because aggression is costly in *N. pulcher* (Grantner and Taborsky 1998). Alternatively, higher levels of postconflict affiliative behavior could signal social cohesion to neighbors that were still visible in the aftermath in experiments 1 and 2 (see also Cords 2002); non-neighboring intruders were out of sight during the postconflict period. Most plausibly, perhaps, the greater affiliation might be because neighboring individuals represent the bigger threat to individual resident group members (Stiver et al. 2004; Dierkes et al. 2005; Bruintjes et al. 2011), because subordinate group members can sporadically change groups (Bergmüller et al. 2005*a*). Resident individuals might therefore be more stressed, which could lead directly to more affiliative behavior (Von Holst 1998).

We found no clear-cut effects of out-group intrusions on postconflict aggression in either experiment. Our results contrast with work performed on a single group of captive tufted capuchin monkeys that showed an increase in intragroup aggression following visual exposure to another group (Polizzi di Sorrentino et al. 2012). Those authors argued that the aggression increase might be caused by the high male sex ratio in the adjacent group, because group composition can influence conflict outcome (e.g., Radford and Du Plessis 2004; Mueller and Manser 2007). The individuals used for our experimental intrusions were carefully size and sex matched to rule out this possibility. In our experiments, all group members contributed to defense against intruders. Because social monitoring of groupmates is common in group-living species, including *N. pulcher* (Hellmann and Hamilton 2014), future work might profitably explore the possibility of punishment if individuals, especially subordinates, fail to contribute when responding to out-group threats (Gneezy and Fessler 2012).

In conclusion, our experimental work has demonstrated that territorial intrusions by out-group individuals can influence subsequent levels of affiliation between *N. pulcher* groupmates, and it thus provides evidence of a link between out-group conflict and postconflict intragroup behavior in a fish. Moreover, we show that different out-group intruder scenarios not only induce differences in aggression levels during the conflict but also affect intragroup behavior in the aftermath; immediate and subsequent responses to intrusions may not, however, be tightly coupled. As it becomes clearer

that the relationship between out-group conflict and intragroup behavior is not uniquely human, future work on tractable study systems such as the model fish species used here will allow a deeper understanding of both the functional and the mechanistic underpinnings of social evolution.

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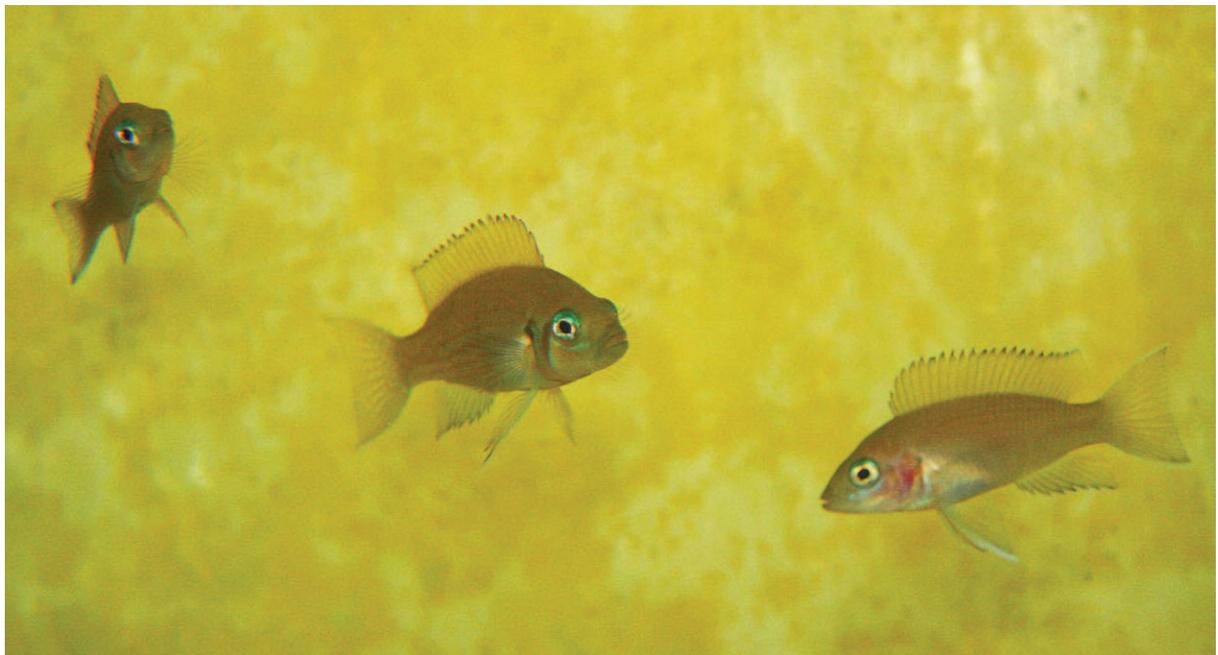
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Three “princesses of Burundi” (*Neolamprologus pulcher*) in the aquarium. Photo credit: Susan Rothenberger.