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Intragroup social dynamics vary with the presence of neighbors in a cooperatively breeding fish

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Abstract

Conflict is an inherent part of social life in group-living species. Group members may mediate conflict through submissive and affiliative behaviors, which can reduce aggression, stabilize dominance hierarchies, and foster group cohesion. The frequency and resolution of within-group conflict may vary with the presence of neighboring groups. Neighbors can threaten the territory or resources of the whole group, promoting behaviors that foster within-group cohesion. However, neighbors may also foster conflict of interests among group members: opportunities for subordinate dispersal may alter conflict among dominants and subordinates while opportunities for extra-pair reproduction may increase conflict between mates. To understand how neighbors mediate within-group conflict in the cooperatively breeding fish *Neolamprologus pulcher*, we measured behavioral dynamics and social network structure in isolated groups, groups recently exposed to neighbors, and groups with established neighbors. Aggression and submission between the dominant male and female pair were high in isolated groups, but dominant aggression was directly primarily at subordinates when groups had neighbors. This suggests that neighbors attenuate conflict between mates and foster conflict between dominants and subordinates. Further, aggression and submission between similarly sized group members were most frequent when groups had neighbors, suggesting that neighbors induce rank-related conflict. We found relatively little change in within-group affiliative networks across treatments, suggesting that the presence of neighbors does not alter behaviors associated with promoting group cohesion. Collectively, these results provide some of the first empirical insights into the extent to which intragroup behavioral networks are mediated by intergroup interactions and the broader social context.

Key words: affiliation, colony, conflict, exponential random graph model, *Neolamprologus pulcher*, network.

Conflict, which often manifests as aggression between group members, is an inherent part of social life in group-living species and can reduce the benefits of group living by increasing social stress, reducing group productivity and leading to group dissolution if left unresolved (Aureli et al. 2002). In many group-living species, subordinate individuals make use of both submissive and affiliative displays to mitigate aggression from dominant group members and increase their likelihood of being tolerated within the group (Huntingford and Turner 1987; Bergmüller and Taborsky 2005; Bruintjes and Taborsky 2008). Submissive behavior can facilitate

group stability by enforcing dominance hierarchies and settling conflict among individuals within a social group (Huntingford and Turner 1987; Hick et al. 2014), whereas affiliative behavior (e.g., grooming in primates) can reinforce friendships, encourage reconciliation, and promote intragroup cooperation (Radford et al. 2016).

The frequency of aggressive, submissive, and affiliative behaviors exchanged among group members often varies across groups (Kutsukake and Clutton-Brock 2008; Madden et al. 2009; Kutsukake and Clutton-Brock 2010), as well as across time within the same social group (Cantor et al. 2012; Godfrey et al. 2013; Bierbach et al. 2014). Given that social stability and the nature of social interactions within a group influence individual fitness (Silk et al. 2003; Barocas et al. 2011; Archie et al. 2014), there have been efforts to first quantify social structure within groups and then to understand factors that modulate social dynamics within and across groups. Mounting evidence demonstrates that social interactions within a group are correlated with group-level attributes, such as group size (Fischer et al. 2014), the relative size of group members (Hamilton et al. 2005), and the sex of group members (Kutsukake and Clutton-Brock 2008). However, much less is known about how the social environment beyond the level of the group, specifically the presence of other conspecific groups, influences social dynamics among group members.

There are at least 3 ways in which neighboring groups can alter within-group dynamics by either reducing or promoting conflict among a given subset of group members. First, neighboring groups can threaten the territory or resources of an established group and may incentivize group members to quickly resolve or reduce conflict within their own group in order to facilitate cooperation in between-group conflict (Radford 2008a; Radford and Fawcett 2014; Bruintjes et al. 2016). Studies examining territorial intrusions and conflict have found that affiliation between dominant and subordinate group members is greater when intergroup conflict is higher (Radford 2008a; Bruintjes et al. 2016). In these cases, affiliative behavior could be exchanged for continued subordinate participation in out-group conflicts (Seyfarth and Cheney 1984; Radford 2011). Second, neighboring groups can offer opportunities for egg dumping (Arnold and Owens 2002) or extra-pair fertilizations (Griffith et al. 2002; Hellmann et al. 2015a). This may result in increased aggression between mates, as the presence of neighboring males and females may provide fitness benefits to one mate by increasing the number of offspring sired, but may be costly to the other mate who may care for offspring that are not their own. Finally, neighboring groups offer opportunities for partner choice by allowing subordinates to potentially move between groups. If neighbors provide an opportunity for subordinates to negotiate based on outside options offered by neighboring groups, dominants should be more tolerant (less aggressive and demand less help) of current subordinates (Bergmüller et al. 2005b; Grinsted and Field 2017; Hellmann and Hamilton forthcoming). Conversely, if neighbors provide dominants with an opportunity to replace current subordinates, neighbors may allow dominants to demand more help and be more aggressive to subordinates when neighbors are present (Bruintjes and Taborsky 2008; Hellmann and Hamilton 2014; Hellmann et al. 2015b). Consequently, the way in which partner choice impacts behavioral dynamics between dominants and subordinates should depend on who is "choosing" partners in this system (Noë and Hammerstein 1995; Cant and Johnstone 2009).

We compared within-group interactions before neighboring groups were visible and while neighboring groups were visible to

understand how the presence of neighboring groups was associated with changes in within-group social dynamics. To do this, we experimentally created laboratory groups of *Neolamprologus pulcher*, a cooperatively breeding cichlid fish native to Lake Tanganyika in East Africa. These fish form colonies of 2–200 permanent territorial groups (Stiver et al. 2007). Each group is composed of a dominant male and female pair, with 0–20 subordinates that provide help in the form of territory defense, territory maintenance, and alloparental care (Wong and Balshine 2011a). Dominance is strictly size-based, such that the dominant male and female are the largest individuals and subordinates form sex-specific, size-based dominance hierarchies (Wong and Balshine 2011a). Male group members maintain consistent differences in size, which likely reduces conflict that would otherwise arise among similarly sized individuals (Heg et al. 2004; Hamilton et al. 2005; Hamilton and Heg 2008). Submission is an effective behavior that reduces aggression in *N. pulcher* (Bergmüller and Taborsky 2005; Bruintjes and Taborsky 2008), while affiliative behavior is used to reinforce participation in territory defense (Bruintjes et al. 2016) and is associated with reduced cortisol levels (Ligocki et al. 2015b). Neighboring groups are not direct competitors for food: individuals in this species feed in the water column and territories are used as protection from predators and breeding substrate (Gashagaza 1988; Wong and Balshine 2011a). Further, whole-group takeovers of neighboring territories are relatively rare in this species; instead, outside threats traditionally come from single individuals seeking out reproductive opportunities, as male and female dominants lose reproduction to subordinates within their group as well as to individuals in neighboring groups (Dierkes et al. 1999; Stiver et al. 2009; Hellmann et al. 2015a). Further, outside individuals may threaten the stability of group composition. Subordinates disperse between groups (Bergmüller et al. 2005a; Jungwirth et al. 2015) and while dominants generally do not move between territories, dominant males are polygynous and are at least capable of usurping a neighboring male's territory (O'Connor et al. 2015). Consequently, these outside individuals may only threaten a subset of group members, while having neutral or even beneficial effects on other group members.

After isolated groups stabilized following group formation, we exposed groups to neighbors and observed behavioral interactions within and between groups when groups were isolated, immediately after groups were introduced to neighbors, and 30 days after the introduction of neighbors. Because changes in 1 individual's behavior are not independent of those of other group members, we used exponential random graph models (ERGMs), in addition to traditional regression models, to evaluate changes in social dynamics (Wasserman and Pattison 1996). ERGMs control for the interdependency of behavioral relationships within a group and evaluate the extent to which social dynamics among group members are influenced by individual attributes (e.g., sex and size) and structural dependency in social ties (e.g., reciprocity). By using these models, we can test hypotheses related to understanding how social structure varies across different contexts and how emergent properties of the social system may contribute to these changes (Wasserman and Pattison 1996; Robins et al. 2007; Lusher et al. 2013; Silk and Fisher 2017).

We had 3 separate predictions regarding the impact of neighboring groups on within-group social dynamics. If within-group dynamics change in response to the threat that neighboring groups pose to the focal group, then we predicted that affiliative behavior would be higher when groups had neighbors compared with when groups were isolated, as affiliative behavior can be used to promote

cooperation among current group members when the potential for intergroup conflict is high (Radford 2008a, 2011). If within-group dynamics change in response to the reproductive opportunities offered by neighboring groups, then we predicted that aggression between the dominant male and female pair would be higher when neighbors were present compared with when they were absent, as reproductive conflict between mates is expected to be higher when there are additional opportunities for extra-pair fertilizations (Eggert and Sakaluk 1995; Valera et al. 2003; Goetz et al. 2008). If within-group dynamics change in response to opportunities for subordinates to move between groups, then we predicted that aggression and submission between dominants and subordinates would be altered when neighbors were present compared with when neighbors were absent.

Materials and Methods

Study organism and housing conditions

All experimental fish were wild caught or F1 offspring of wild-caught fish from the Kambwimba region of Lake Tanganyika (8°32′ S, 31°9′ E). All wild-caught fish had been in captivity in our lab for at least 3 months prior to the beginning of the experiment. We used a total of $n = 106$ individual fish for this experiment. Prior to the experiment, all fish were marked uniquely with elastomer dye and given a dorsal fin clip to indicate sex. Fish recover from this procedure rapidly and receiving these markers has no apparent effect on subsequent behavior (Stiver et al. 2004; Dey et al. 2015). On the day that groups were formed, all group members were weighed to the nearest 0.001 g (Ohaus Adventurer Pro AV213C) and measured for standard length (SL) to the nearest 0.01 mm (Fisher Scientific Traceable calipers). To mirror natural conditions, a 12:12 h light:dark schedule was maintained for the duration of the experiment and water temperatures were kept constant at 27 ±1°C. Fish were fed daily and *ad libitum* with either TetraMin flakes (5 days a week) or frozen *Daphnia* or *Artemia* (twice per week).

Experimental setup

During the experiment, 2 groups were placed on opposite sides of a barrier in a 208-L (122 cm long × 32 cm wide × 53 cm high) aquaria lined with 3 cm of black sand substrate. Each group had 2 inverted terracotta flowerpot halves that served as shelter and potential breeding substrate, as well as 2 PVC tubes near the top of the tank that served as hiding spots for subordinate fish. The 2 groups in each aquarium were separated by 2 clear plexiglass barriers that were flush against the walls and floor of the aquarium and extended above the top of the water line. This largely prevented water flow between the 2 groups, although some water flow between the groups was possible and therefore, chemical communication between the groups may have occurred. Consequently, differences in interactions when neighbors were blocked from view versus visible may not be due so much to the complete absence of neighbors or different perceived densities of conspecifics, but rather due to the absence of *interactions* with neighboring groups and differences in how much groups know about their neighbors (e.g., group composition, size of group members).

During the first 40 days after group formation, there was an opaque barrier between the plexiglass barriers that prevented groups from seeing or interacting with each other. After 40 days, the opaque barrier was removed and groups were able to interact across a clear

barrier. *Neolamprologus pulcher* can distinguish familiarity, identity, and sex using only visual cues (Balshine-Earn and Lotem 1998; Frostman and Sherman 2004; Hellmann and Hamilton 2014; Kohda et al. 2015; Sabol et al. 2017), suggesting that chemical cues are not necessary for individuals to accurately identify the sex and familiarity of neighboring group members.

All eggs that were laid during the experiment were removed immediately from the groups to remove any confounding influence of parental care on intragroup and intergroup social interactions, although a previous study in this species found that the structure of interaction networks does not strongly vary with reproductive events (Dey et al. 2015). Nevertheless, any behavioral observations conducted within 24 h of egg-laying and removal were removed from the dataset.

Group formation and behavioral observations

From October 2014 to November 2015, we formed 31 social groups of unrelated *N. pulcher*, each composed of a dominant male and female breeding pair and 2–3 subordinates with at least 1 subordinate male and 1 subordinate female per group ($n = 27$ groups with 3 subordinates, $n = 4$ groups with 2 subordinates). All individuals were likely to be reproductively mature (SL > 35 mm: Taborsky 1985) and sexed by examination of external genital papillae. In these groups, the dominant male was the largest (and therefore, most dominant) fish in the group and the dominant female was the second largest fish in the group. All subordinates were at least 5 mm shorter in SL than the dominant male and female. We assembled up to 8 groups at a time; we formed new groups by reshuffling former group members or using new individuals. Some individuals were therefore members of 2 social groups throughout the course of the 13-month experiment. We controlled for pseudoreplication in 2 ways. First, in our regression models, we used random effects of individual and group identity to control for variation in behavior due to individual identity. Although we used $n = 106$ total fish in this experiment, we had a total of $n = 76$ unique fish that were still present in the groups by day 30 (see below). Second, we ran our network analysis (see below for "Materials and Methods") removing the minimum number of groups necessary to produce a network in which each individual was a member of only 1 social group.

All subordinates were unrelated to the dominants within their group, and all group members had never interacted prior to group formation. Groups were given 30 days after group formation to stabilize, as aggression can be high while dominance hierarchies are being established. In the initial days after group formation, some subordinates received high levels of aggression from the dominants and were subsequently removed from the group to prevent further injury. These subordinates were not replaced; instead, we controlled for changes in group composition throughout the experiment (due to death or removal of group members) by only analyzing changes in network structure using groups that did not change in composition across time periods.

At 30 days post-group formation, we had 11 social units that were composed only of a male and female pair (i.e., social mates) and 20 social units that were composed of a dominant male and female pair with subordinates ($n = 5$ groups with 1 subordinate, $n = 9$ groups with 2 subordinates, and $n = 6$ groups with 3 subordinates). At 30-days post-formation, each pair or group was observed for 30 min daily for 10 days (days 30–39). After 10 days, the opaque barrier isolating the groups was removed, such that groups were now visible to their neighbor on the other side of the tank. Groups were observed for 30 min daily for the first 10 days after removal of

the opaque barrier to understand the impact of novel neighbors on intragroup dynamics (days 40–49). Thirty days after the removal of the opaque barrier, we observed groups again for 30 min daily for 10 days (days 70–79).

All behavioral observations were recorded and videos were scored by the same observer (J.K.H.) using species-specific ethograms (Ligocki et al. 2015a; Reddon et al. 2015; Sopinka et al. 2009). Behaviors were categorized as overt aggressive attacks (ram, bite, mouth fight), restrained aggressive displays (fin raise, fast approach, operculum spread, head jerk, head down display), submissive displays (tail quivers, hook, submissive posture), and affiliative behaviors (parallel swim, bump, join). Because aggression toward neighboring groups was across a barrier, we scored any behaviors as overt aggression when the actor made contact with the barrier (e.g., rammed the barrier in an attempt to ram a neighboring fish). Within-group overt aggression was relatively rare, so we combined counts of overt and restrained aggression when analyzing within-group dynamics.

Statistical and network analysis

To test how affiliative, submissive, and aggressive interactions between the dominant male and female pair (i.e., between social mates) changed with the presence of neighbors, we used generalized linear mixed models [GLMMs; R packages lmerTest (Kuznetsova et al. 2017) and glmmADMB (Fournier et al. 2012; Skaug et al. 2016)] with a negative binomial distribution because count data were overdispersed. Dependent variables for each model were the sum of all affiliative, submissive, or aggressive behaviors, respectively, observed across the 10 observations. In each model, we included fixed effects of period (pre-exposure to neighbors, days 30–39; immediate post-exposure to neighbors, days 40–49; delayed post-exposure to neighbors, days 70–79) and the presence of subordinate males or females in the group (binomial) to control for variation in behavioral interactions between dominant males and females due to group composition. For models of aggression and submission, we also included a fixed effect of the amount of aggression received from their social mate, to account for variation in dominant male or female behavior due to their social mate's activity. For models examining affiliative behavior, we included the fixed effect of the amount of affiliation received from their social mate. We used Tukey's honest significant difference tests (R package multcomp) as a post hoc analysis to control for multiple comparisons and analyze where the differences lie among the treatment groups. We also included random factors of individual ID (nested within group identity) in all models, because many individuals were a member of 2 social groups. Dominant death occurred in 2 groups; therefore, $n = 29$ social pairs/groups were used to evaluate social dynamics between the dominant male and female pair.

We analyzed social network structure in the groups with a dominant pair and subordinates [R version packages: statnet (Handcock et al. 2008), ergm (Hunter et al. 2008), and ergm.count (Krivitsky 2013)]. We built weighted, directed networks of aggression, submission, and affiliation for the isolated time period. The weight of the edges in these networks was determined by the total number of interactions directed from 1 individual to another across the 10 observations in the time period. Then, to quantify how within-group social dynamics changed between pre-exposure (days 30–39) and immediate post-exposure (days 40–49) periods and between immediate and delayed post-exposure (days 70–79) periods, we assembled difference networks. In the difference network, each edge weight

was the difference in the number of interactions between 2 time periods. Because all edges must be positive values, we added the absolute value of the minimum edge weight to all within-group edge weights to make all values positive. Therefore, higher values denote that behaviors were more common in the later period than the earlier period.

We analyzed network structure using ERGMs (Wasserman and Pattison 1996). As in traditional regression models, these models test how independent variables predict the weight of the edges. Because ERGMs control for the interdependency of social ties when evaluating behavioral data, they improve upon traditional statistical methods (Whitehead 2008). ERGMs allow for simultaneous estimations of substructures (e.g., transitivity of relationships) and individual attributes (e.g., size) or pairwise attributes (e.g., sex homophily) that contribute to network data. Similar to Dey et al. (2015), we assembled a supernetwork composed of all social groups and restricted all possible edges to those occurring among group members (Figure 1). To examine factors that contribute significantly to determining network structure, we tested the independent variables of: (1) the "sum" term, which is similar to the intercept term in a regression model, (2) status homophily, which tests whether interactions are more likely to occur between individuals of the same status (dominant or subordinate), (3) sexual homophily, which tests if there is an increased chance of interactions between same-sex dyads, (4) actor effect of sex, which tests if 1 sex is more likely to initiate behavioral interactions, and (5) dyadic differences in size (SL), which tests if interactions are more likely to occur between individuals close in size. Further, we tested for structural dependence between edges by evaluating the tendency for (6) reciprocity, which tests if the weight of an edge from 1 group member to another predicts the weight of the reciprocal edge, and (7) cyclical triads, or the tendency of individuals to form cyclical triads, which are markers of unstable dominance hierarchies. These variables were chosen prior to examining the data based on our predictions outlined in the
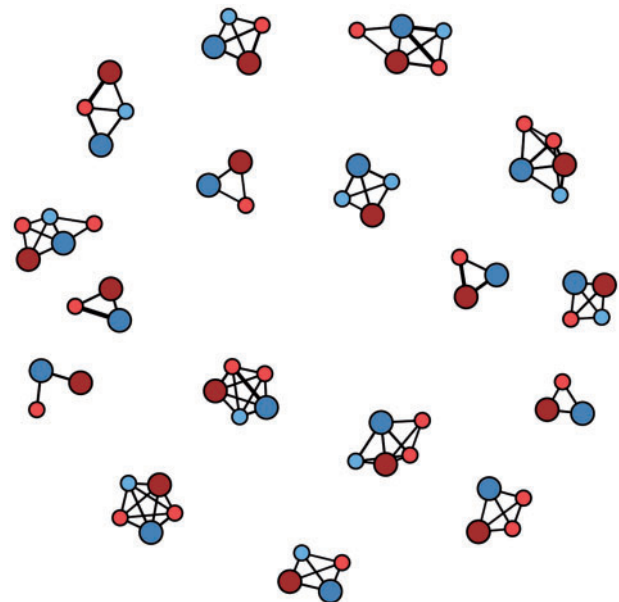

Figure 1. Aggressive supernetwork structure for *N. pulcher* groups prior to exposure to neighbors (days 30–39). Larger nodes represent dominant individuals, red nodes represent females, and blue nodes represent males. Thicker edges indicate that more aggression was exchanged between a given dyad.

introduction and based on characteristics that define sex-specific, size-based dominance hierarchies (Wong and Balshine 2011a; McDonald and Shizuka 2012; Dey et al. 2013, 2015; Dey and Quinn 2014).

ERGMs use a Markov-chain Monte Carlo estimation technique to approximate the maximum likelihood. We specified a sampling interval of 5000 and a burn-in of 50,000 proposals, and used Poisson reference graphs for each model (Dey et al. 2015). Models were checked for degeneracy and goodness of fit using the mcmc.diagnostics function. Examinations of model diagnostics did not indicate a high correlation between status homophily and size difference so we included both terms in our ERGMs; further, the effects of status homophily and size difference did not change when the only 1 or both variables were included in the models (Hellmann JK, Hamilton IM, unpublished data). To eliminate potential issues with pseudoreplication in the ERGM models, which do not allow for random effects of identity, we only used a subset of observed groups such that each individual was only represented in the network once. Therefore, we analyzed a total of 17 groups in the networks examining social dynamics in isolated groups ($n = 5$ groups of 3 individuals, $n = 6$ groups of 4 individuals, $n = 6$ groups of 5 individuals). Because difference networks contained only groups that did not change in composition between time periods, we analyzed 13 groups in the difference network comparing pre-exposure groups and immediate post-exposure groups with neighbors ($n = 5$ groups of 3 individuals, $n = 2$ groups of 4 individuals, $n = 6$ groups of 5 individuals) and 11 groups in the difference network comparing immediate and delayed post-exposure groups ($n = 6$ groups of 3 individuals, $n = 2$ groups of 4 individuals, $n = 3$ groups of 5 individuals).

Because potential changes in group dynamics may be due to changes in time rather than changes in the visibility of neighbors, we analyzed if network structure changed within the first 10 days of observation (days 30–34 vs. days 35–39) and if the magnitude of that change was less than the change in network structure between when groups were isolated (days 35–39) and neighbors were visible (days 40–44). We also evaluated changes within the delayed post-exposure period (days 70–74 vs. days 75–79). If within-group dynamics merely change according to time, then we expected to see changes in social dynamics changing similarly within and across time periods. These methods and results are included in the Supplementary Material.

Finally, we used GLMMs with a negative binomial distribution to test for differences in aggression toward the neighbor group due to status (dominant or subordinate), sex (male or female), treatment period (days 40–49 or days 70–79), and neighbor group size. To understand how group dynamics impacted aggression to neighboring groups, we ran 2 GLMMs. The first had dominant aggression to neighbors as the dependent variable, with fixed effects of dominant male aggression to dominant females, dominant female submission to the dominant male, and the presence of subordinates in the group (binary). The second had subordinate aggression to neighbors as the dependent variable, with fixed effects of aggression and affiliation received from the dominants. For all models, we checked independent variables for collinearity. Individual ID nested within group was included as a random effect for all models.

Results

Are interactions between social pairs influenced by the presence of neighbors?

Dominant males were less aggressive (i.e., had a lower frequency of aggressive acts) to dominant females when neighbors were recently present compared with the pre-exposure period when groups were isolated (GLMM with Tukey's HSD: $Z_{74} = -2.36$, 0.048; Figure 2A); this trend weakened when neighbors were present for 30 days, such that there was no significant difference in dominant male aggression between the pre-exposure period and the delayed post-exposure period ($Z_{74} = -1.87$, $P = 0.14$; Figure 2A). Dominant females were similarly aggressive to dominant males in the pre-exposure period compared with the post-exposure periods (immediate: $Z_{74} = -0.15$, $P = 0.99$; delayed: $Z_{74} = -0.71$, $P = 0.75$), but were significantly
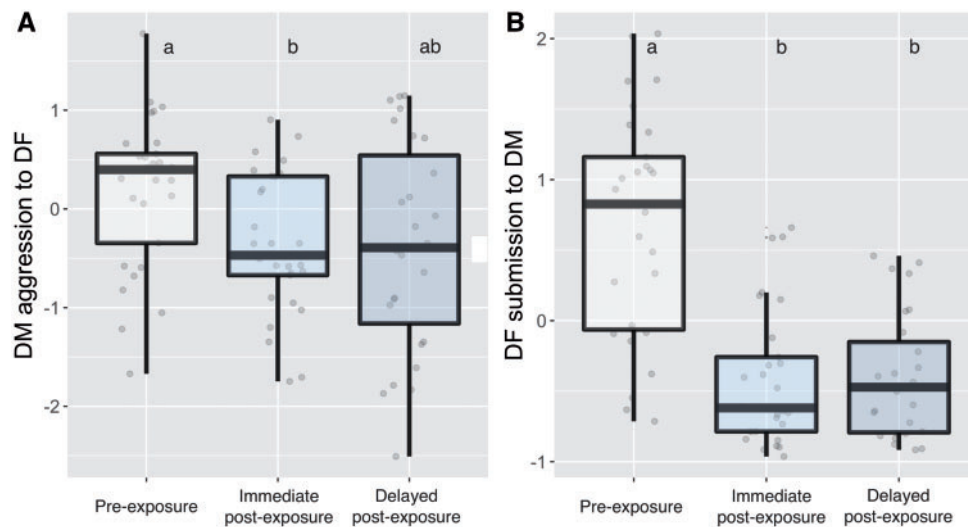

Figure 2. (A) Dominant male aggression toward the dominant female was higher prior to exposure to neighbors (white: days 30–39) compared with the immediate post-exposure period when neighbors were recently visible (light blue: days 40–49), but this trend did not persist into the delayed post-exposure period when neighbors had been present for 30 days (darker blue: days 70–79). (B) Dominant female submission toward the dominant male was higher prior to exposure to neighbors (white: days 30–39) compared with both periods when neighbors were present. Data presented are the residuals of the regression model without the fixed effect of treatment period, plotted against treatment period.
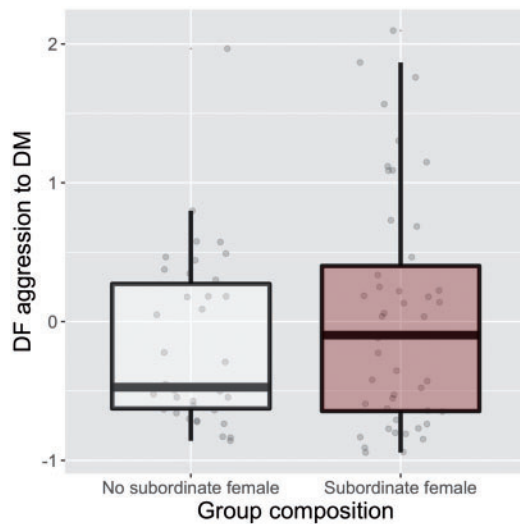
Figure 3. Dominant females were more aggressive to dominant males in their group when there were subordinate females present in their group. Data presented are the residuals of the regression model without the fixed effect of subordinate female presence, plotted against the binomial variable of subordinate female presence in the group.

more submissive to dominant males during the pre-exposure period compared with the post-exposure periods, even after controlling for variation in the amount of aggression received from the dominant male (immediate: $Z_{74} = -7.19$, $P < 0.001$; delayed: $Z_{74} = -6.65$, $P < 0.001$; Figure 2B). Dominant male aggression toward the dominant female and dominant female submission were not significantly altered by the presence of subordinate males (DM: $Z_{74} = -0.43$, $P = 0.67$; DF: $Z_{74} = -1.42$, $P = 0.16$) or subordinate females (DM: $Z_{74} = -0.93$, $P = 0.35$; DF: $Z_{74} = -0.12$, $P = 0.90$) in the group. However, dominant females were significantly more aggressive to dominant males when subordinate females were present in the group ($Z_{74} = 2.81$, $P = 0.005$; Figure 3), although there was no significant impact of subordinate male presence ($Z_{74} = 0.25$, $P = 0.80$).

Dominant male or female affiliative behavior toward their mate was not significantly different in the pre-exposure period compared with the immediate post-exposure (DF: $Z_{74} = -0.63$, $P = 0.80$; DM: $Z_{74} = -1.94$, $P = 0.13$) period or the delayed post-exposure period (DF: $Z_{74} = 0.01$, $P = 1.00$; DM: $Z_{74} = -1.40$, $P = 0.34$). It also did not vary with the presence of subordinate males (DF: $Z_{74} = -1.63$, $P = 0.10$; DM: $Z_{74} = 0.40$, $P = 0.69$) or subordinate females (DF: $Z_{74} = -0.70$, $P = 0.48$; DM: $Z_{74} = -0.25$, $P = 0.80$) in the group.

Are social interactions within a group influenced by the presence of neighbors?

Because some individuals were used across more than 1 group and ERGMs do not allow for random effects of individual identity, we analyzed network structure in a subset of groups to avoid potential issues with pseudoreplication. Across all time periods, males and females initiated similar levels of aggression (non-significant effect of actor sex in all networks: Tables 1 and 2). Females were more submissive to other group members than males (negative effect of actor sex: Table 1), although a significant effect of actor sex in the difference network indicates that this trend was stronger prior to exposure to neighbors compared with the immediate post-exposure period (Table 2). This difference between pre-exposure and post-exposure groups persisted into the delayed post-exposure period where

neighbors had been present for 30 days (non-significant effect in immediate vs. delayed post-exposure difference network; Table 2).

During the pre-exposure period when groups were isolated, there were similar frequencies of aggression between same-sex and opposite sex group members, while submission was more frequently exchanged between opposite-sex group members relative to same-sex group members (sexual homophily: Table 1). Both aggression and submission became significantly more sexually homophilic when groups were initially exposed to neighbors compared with the pre-exposure period (positive effect of sexual homophily in the pre- vs. post-exposure difference network: Table 2); this effect persisted into the delayed post-exposure period for submission (non-significant effect of immediate vs. delayed post-exposure difference network; Table 2), but not for aggressive interactions (negative effect in difference network; Table 2).

In the pre-exposure period, submission and aggression were most commonly exchanged between group members with a large size difference (positive effect of SL difference: Table 1 and Figure 4). However, groups in the immediate post-exposure period had significantly more aggression and submission exchanged between similarly sized individuals compared with isolated groups (negative effect of size difference: Table 2 and Figure 4). When groups were isolated, dominant aggression and submission were more frequently exchanged between the dominant pair rather than directed toward subordinates (dominant status homophily: Table 1 and Figure 4); however, in the immediate post-exposure period, dominant aggression and submission were more frequently exchanged with subordinates than with their social mate (Table 2 and Figure 4). All of these effects persisted into the delayed post-exposure period for aggressive interactions; however, these changes in the submission network were stronger in the immediate post-exposure period compared with the delayed post-exposure period (positive effects for both parameters; Table 2).

Across all time periods, males and females initiated similar levels of affiliative behaviors (no effect of actor sex in any network: Tables 1 and 2). Affiliation was exchanged primarily between males and females rather than between individuals of the same sex in both the pre-exposure period and immediate post-exposure period (negative effect of sexual homophily: Table 1; no effect of either parameter in the difference network: Table 2); however, affiliation was significantly more sexually homophilic when groups had neighbors for 30 days compared with recent neighbors (positive effect of sexual homophily in the difference network: Table 2). In the pre-exposure period when groups were isolated, affiliative behavior was more frequently exchanged between individuals with a large size difference relative to similarly sized individuals (SL, negative effect of size homophily; Table 1), but affiliative behavior between similarly sized individuals was more common in the immediate post-exposure period than the pre-exposure period (negative effect of size differences: Table 2). This effect continued to strengthen in the delayed post-exposure period (Table 2). Across both the pre-exposure and immediate post-exposure time period, there was a higher frequency of affiliation exchanged between individuals of the same rank than between individuals of different ranks (i.e., dominant–dominant affiliation was more common than dominant–subordinate affiliation; positive effect of status homophily, Table 1; no effect of status homophily in difference network, Table 2). However, subordinates exchanged more affiliation with dominants when neighbors were present for 30 days compared with when neighbors were recent (negative effect of subordinate homophily in the difference network: Table 2).

Table 1. Results of ERGM fit for behavioral networks for groups prior to exposure to neighbors (days 30–39)

Pre-exposure period	Aggression			Submission			Affiliation		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Sum	2.15	0.06	**<0.001**	−0.20	0.19	0.30	2.12	0.06	**<0.001**
Difference in SL	0.06	0.003	**<0.001**	0.06	0.007	**<0.001**	0.05	0.003	**<0.001**
Sexual homophily	0.02	0.03	0.52	−0.30	0.09	**0.001**	−0.34	0.05	**<0.001**
Actor sex (male)	0.03	0.03	0.35	−0.14	0.05	**0.005**	0.007	0.02	0.73
Status homophily									
Dominant–dominant	0.16	0.05	**0.001**	1.33	0.10	**<0.001**	2.36	0.05	**<0.001**
Subordinate–subordinate	−1.09	0.07	**<0.001**	−1.04	0.18	**<0.001**	0.42	0.06	**<0.001**
Cyclical triads	−0.73	0.05	**<0.001**	−0.94	0.32	**<0.001**	−0.93	0.04	**<0.001**
Reciprocity	−1.07	0.04	**<0.001**	−1.59	0.15	**<0.001**	−0.37	0.02	**<0.001**

Bold values indicate significance ($P<0.05$).

Notes: we tested the effects of dyadic differences in SL (positive values signify that individuals with bigger size differences interact more frequently), sexual and status homophily (positive values signify that individuals of the same sex/status interact most frequently), actor effects of sex (positive values signify that males initiate behaviors more frequently than females), cyclical triads, and reciprocity.

Table 2. Results of ERGM fit for difference networks comparing network dynamics of pre-exposure groups that were isolated (days 30–39) and post-exposure groups recently exposed to neighbors (days 40–49), as well as comparing post-exposure groups recently exposed to neighbors (days 40–49) to those with neighbors that had been present for 30 days (days 70–79)

Pre- vs. immediate post-exposure period	Aggression			Submission			Affiliation		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Sum	5.88	0.01	**<0.001**	4.39	0.04	**<0.001**	5.38	0.02	**<0.001**
Difference in SL	−0.007	0.001	**<0.001**	−0.004	0.002	**0.04**	−0.003	0.001	**0.02**
Sexual homophily	0.02	0.01	**0.01**	0.09	0.02	**<0.001**	−0.006	0.009	0.52
Actor sex (male)	−0.003	0.007	0.63	0.13	0.03	**<0.001**	−0.008	0.009	0.37
Status homophily									
Dominant–dominant	−0.05	0.02	**0.002**	−0.11	0.04	**0.001**	0.02	0.02	0.17
Subordinate–subordinate	−0.02	0.01	0.14	−0.01	0.03	0.72	−0.03	0.02	0.07
Cyclical triads	−0.004	0.006	0.51	0.07	0.03	**<0.001**	−0.04	0.006	**<0.001**
Reciprocity	−0.03	0.006	**<0.001**	0.10	0.02	**<0.001**	0.001	0.008	0.87

Immediate vs. delayed post-exposure period	Aggression			Submission			Affiliation		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Sum	5.23	0.02	**<0.001**	0.02	0.005	**<0.001**	5.29	0.02	**<0.001**
Difference in SL	−0.001	0.002	0.66	0.02	0.005	**<0.001**	−0.005	0.002	**0.002**
Sexual homophily	−0.03	0.01	**0.03**	−0.05	0.05	0.33	0.06	0.01	**<0.001**
Actor sex (male)	0.006	0.009	0.53	0.01	0.04	0.78	0.005	0.007	0.45
Status homophily									
Dominant–dominant	−0.01	0.02	0.59	0.17	0.06	**0.007**	−0.02	0.02	0.36
Subordinate–subordinate	−0.02	0.02	0.32	0.09	0.06	0.13	−0.05	0.02	**0.02**
Cyclical triads	−0.03	0.008	**0.002**	0.04	0.03	0.21	−0.04	0.008	**<0.001**
Reciprocity	−0.04	0.01	**<0.001**	0.02	0.02	0.47	−0.02	0.01	**0.01**

Bold values indicate significance ($P<0.05$).

Notes: Negative estimates indicate that a given variable had a stronger influence in the earlier time period.

Local network substructures

Aggressive, submissive, and affiliative networks were characterized by a strong, negative effect of reciprocity, which means that individuals who received high levels of aggression, submission, and affiliation were unlikely to reciprocate those behaviors. Similarly, networks were characterized by strong negative effects of cyclical triads (Table 1), which means that cyclical triads were less frequent than expected by chance. Negative effects of both reciprocity and cyclical triads indicate that dominance hierarchies are stable. As the influence of cyclical triads and reciprocity on network structure was significantly different between the beginning (days 30–34) and end (days 35–39) of the isolated period (see Supplementary Material),

we are unsure if changes in cyclical triads and reciprocity across time periods (isolated: days 30–39, new neighbors: days 40–49) are due to time or experimental treatment.

Between-group aggression and neighbor characteristics on within-group interactions

In general, there was a higher frequency of aggression toward neighbors during the initial post-exposure period (days 40–49) compared with the delayed post-exposure period (days 70–79; GLMM: $Z_{167} = -3.03$, $P = 0.003$). Across both time periods, dominants were more aggressive (i.e., showed a higher number of aggressive
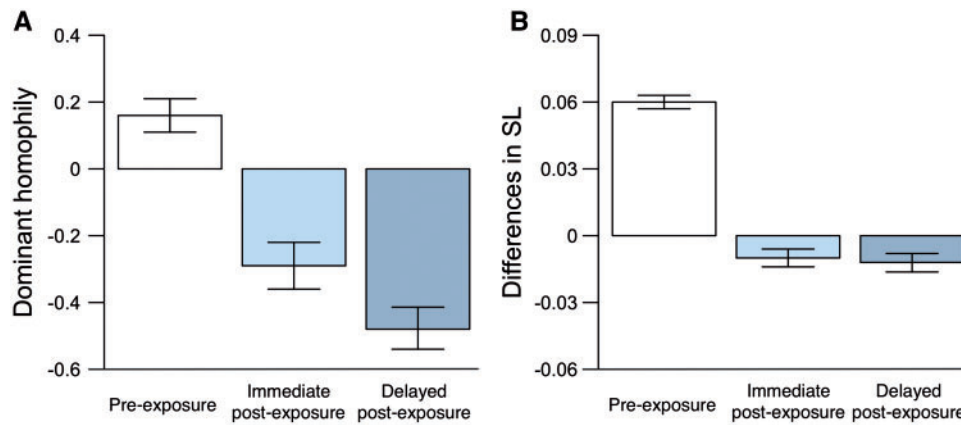
Figure 4. ERGM parameter estimates (with standard error bars) for aggressive social networks due to dominant homophily (**A**) and size differences among group members (**B**) for the pre-exposure (days 30–39), immediate post-exposure (days 40–49), and delayed post-exposure (days 70–79) period. Positive estimates of dominant homophily indicate that dominants are aggressive primarily to their mate, whereas negative estimates of dominant homophily indicate that dominants are aggressive primarily toward subordinates. Positive estimates of size differences indicate that aggressive interactions are exchanged primarily between group members with a large size difference, whereas negative estimates of size differences indicate that aggressive interactions are exchanged primarily between group members with a small size difference.

acts) to neighbors than subordinates ($Z_{167} = -10.36$, $P < 0.001$) and males were more aggressive to neighbors than females ($Z_{167} = 2.39$, $P = 0.02$). Aggression toward neighbors was not significantly altered by neighbor group size ($Z_{167} = -0.08$, $P = 0.93$).

We also found that aggression toward neighbors was impacted by group-level dynamics. Dominant aggression toward neighbors was positively correlated with dominant male aggression toward the dominant female ($Z_{46} = 2.03$, $P = 0.04$), but negatively correlated with dominant female submission to the dominant male ($Z_{46} = -2.98$, $P = 0.003$). Further, dominants tended to be more aggressive to neighbors when there were no subordinates present in their group (i.e., when the social unit was composed of only a dominant male and female pair) compared with when there were subordinates in their social unit ($Z_{46} = -1.87$, $P = 0.06$). We found no evidence that subordinate aggression to neighbors was significantly impacted by affiliation ($Z_{53} = -0.10$, $P = 0.92$) or aggression ($Z_{53} = -0.04$, $P = 0.97$) received from the dominants.

Discussion

Previous studies have found that the presence and density of neighboring groups are correlated with increased subordinate cooperation, increased subordinate eviction, and altered reproductive sharing in *N. pulcher* (Hellmann and Hamilton 2014; Hellmann et al. 2015a, 2015b). However, less was known about how neighbors impact group-level behavioral dynamics. By manipulating the presence of neighbors, we can evaluate how neighbor groups change both the magnitude and target of conflict within a group. This can lend insight into who benefits most from the opportunities offered by neighboring groups, and can better elucidate if groups perceive neighbors as reproductive competitors, future group members, or threats to the territory as a whole.

We found that group-level social dynamics were characterized by strong negative effects of reciprocity and cyclical triads across all time periods, demonstrating that network ties are self-organizing (i.e., the existence of certain ties promotes other ties to come into existence) and that dominance hierarchies are likely stable across all time periods (McDonald and Shizuka 2012). Further, we found that network structure was influenced by the status, sex, and size of the group members, although the ways in which individual attributes

contributed to network structure varied across periods. Specifically, aggression and submission between the dominant male and female were both more frequent when groups were isolated than when groups had recently been exposed to neighbors. In contrast, aggression and submission between similarly sized group members and dominant aggression toward subordinates were relatively more frequent in the immediate post-exposure period compared with the pre-exposure period.

An increase in aggression between dominant and subordinate individuals when neighbors were present is consistent with the hypothesis that within-group dynamics are altered by the outside options offered by neighboring groups. These findings are also consistent with the results of several previous studies in this species that suggest that subordinates "pay" more (in terms of an increase in received aggression and more help provided) to remain on the territory when there are neighbors present (Bruintjes and Taborsky 2008; Hellmann and Hamilton 2014; Hellmann et al. 2015b). However, these results are in contrast to the results of a theoretical model (Hellmann and Hamilton forthcoming) and empirical studies in cichlid fish (Bergmüller et al. 2005b) and paper wasps (Tibbetts and Reeve 2008; Grinsted and Field 2017) which show that subordinate help decreases as outside options increase. Biological market theory predicts that outside options should benefit the partner that "chooses" (Noë and Hammerstein 1995; Bshary and Grutter 2002; Bshary and Noë 2003), suggesting that the presence of neighbors increased partner choice for dominants in this study. However, it is likely that the "choosy" partner may vary among species as well as within the same species depending on the relative leverage that an individual has in a given social situation (Lewis 2002). For example, subordinates may have more leverage to negotiate based on outside options in situations in which dominants gain large fitness benefits from subordinate help, relative to situations in which subordinate help is less needed (Taborsky 1985; Zöttl et al. 2013). Further, outside options may be relatively unimportant in informing social dynamics in systems without pay-to-stay cooperation (Hellmann and Hamilton forthcoming) or in groups where dominants and subordinates are related (Cant and Johnstone 2009; Quinones et al. 2016). Consequently, greater exploration into how neighboring groups influence cooperation and the stability of current social relationships would be highly beneficial to understanding when and to what

extent group members can negotiate to improve their current social situations based on outside options.

An increase in conflict among similarly sized individuals (i.e., rank-related conflict) when neighbors were present is also consistent with the hypothesis that the presence of neighbors alters within-group conflict by introducing the potential for group composition to change. In species with size-based dominance hierarchies such as *N. pulcher*, conflict tends to be greatest between similarly sized group members (Wong et al. 2007; Hamilton and Heg 2008; Heg and Hamilton 2008; Ang and Manica 2010) because relative fighting ability is less certain between group members close in size (Reddon et al. 2011). When neighbors are present, current group members may be in conflict over the joining of a new subordinate, which could benefit high-ranking group members who would gain benefits from the additional help and protection associated with a greater number of subordinates, but would be costly to low-ranking subordinates who would descend in the dominance hierarchy if a larger subordinate joined the group (Heg et al. 2005; Ligocki et al. 2015a). Conversely, the potential for subordinates to leave the group may also disrupt the dominance hierarchy, as subordinate removal from the group induces temporary aggression between group members of adjacent rank as group members re-establish their rank position (Wong and Balshine 2011b). Collectively, these results suggest that providing opportunities for group composition to change may reduce the stability of dominance hierarchies.

We predicted that if neighbors represent reproductive opportunities, aggression between the dominant male and female pair would be higher in groups with neighbors compared with isolated groups. Instead, we found that the presence of neighbors was associated with reduced conflict between the dominant male and female pair, lending little support to the hypothesis that neighbors promote reproductive conflict between social mates. Similarly, we observed little change in the frequency and target of affiliation before and after exposure to neighbors, providing little support for the hypothesis that out-group threats increase affiliation among group members by threatening the group as a whole. This is in contrast to Bruintjes et al. (2016) and Radford (2008a), who found that post-conflict affiliation increased following experimental territorial intrusions by neighboring and non-neighboring conspecifics. However, territorial intrusions are a more intense form of out-group conflict than the constant nearby presence of neighboring groups where territory boundaries were never crossed. Consequently, the intergroup conflict present in our study may have never presented a great enough threat to the focal group to promote higher within-group affiliation. Consistent with this hypothesis, Polizzi di Sorrentino et al. (2012) found that visual exposure to neighbors in tufted capuchins was not sufficient to produce changes in within-group affiliation. Further, in green woodhoopoes, changes in within-group affiliative behavior were only seen when groups faced more intense and longer out-group threats (Radford 2008b). Consequently, further work is needed to understand how within-group affiliation varies with the type and severity of out-group threat.

Changes among experimental periods could be due to time or the presence of neighbors, as observations during the pre-exposure period occurred sooner to group formation than observations during the post-exposure periods. Our results are largely inconsistent with what would be expected under the time hypothesis; our supplementary analysis demonstrates that the influence of individual attributes (sex, status, size) on network structure had stabilized by day 40. Changes in the effect of these parameters on networks were greater between time periods than within time periods. Further, changes in

aggression and submission networks between pre-exposure groups (days 30–39) and immediate post-exposure groups (days 40–49) were greater than changes between days 40–49 and days 70–79 (delayed post-exposure groups), despite greater differences in time between the latter 2 time periods. Finally, the changes in our network structure are consistent with what we predicted given that previous studies found that the presence of neighbors increases conflict between dominants and subordinates (Hellmann and Hamilton 2014; Hellmann et al. 2015b). Nevertheless, further research comparing network structure in groups that form in the presence of neighbors versus those that form while isolated and are later exposed to neighbors would help distinguish which, if any, of the reported patterns are due to time rather than the presence of neighbors.

In conclusion, for our network analysis, we used ERGMs to evaluate social dynamics within groups (Wasserman and Pattison 1996). These models control for the dependency among social relationships, allowing us to not only ask questions about how individual attributes (e.g., actor sex) affect social dynamics, but to expand the scope of our analysis to assess how structural dependency among social ties (e.g., status homophily) and emergent group level characteristics of the social network itself (e.g., reciprocity: Silk and Fisher 2017) influence group-level social dynamics. Here, we demonstrate that the target of within-group conflict shifts in the presence of neighbors: isolated groups are characterized by higher conflict between the dominant breeding pair while groups with neighbors are characterized by rank-related conflict and conflict between dominants and subordinates. This suggests that, rather than promote group cohesion or reproductive conflict, neighbors may foster conflict by introducing opportunities for group composition to change. However, further studies independently manipulating the availability of outside opportunities for dominants and subordinates would elucidate when and to what extent partner choice impacts the structure and stability of dominance interactions in animal societies. Further, measuring changes in hormone levels (e.g., cortisol) and gene expression in these manipulative experiments may help us understand the ways in which subsets of group members are impacted by the presence of these outside options.

Ethics Statement

All methods were approved by The Ohio State University IACUC (protocol ID 2008A0095). As stated above, efforts were made to minimize injuries resulting from high levels of aggression by monitoring groups daily and removing subordinate group members that received high levels of aggression.

Author Contributions

J.K.H. and I.M.H. conceived the study. J.K.H. conducted the experiment, scored all behavior, performed the statistical analyses, and wrote the initial manuscript. Both J.K.H. and I.M.H. revised the manuscript.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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