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Network structure is related to social conflict in a cooperatively breeding fish

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The nature of individual social interactions can have a profound influence on group structure and function. Here, we use social network analysis to examine patterns of dominance interactions and spatial associations in 14 captive social groups of the cooperatively breeding cichlid, *Neolamprologus pulcher*. In this cichlid, social groups are composed of a dominant breeding pair and 1–20 nonbreeding subordinate helpers that form size-based queues for breeding positions. In the current study, we performed the first quantitative analysis of *N. pulcher* dominance hierarchies. We found that dominance hierarchies of *N. pulcher* were highly linear and that interactions within dyads were directionally consistent. We also found that dominance interactions were not equally distributed across the network, but instead occurred most frequently at the top of the social hierarchy. Contrary to our predictions, neither body size asymmetry nor sex predicted the observed dominance interactions and patterns of associations. However, breeders were more connected than helpers within the networks, perhaps due to their policing role. This study is one of a small handful to conduct network analysis on replicate social groups, and thus is one of few studies able to make general conclusions on the social structure of its focal species. The patterns uncovered suggest that conflict over breeding position inheritance has a strong impact on relationships among group members in *N. pulcher*.

Many different species live in groups, and the evolution and maintenance of such social structure strongly depends on the nature of the interactions among individuals. Within social groups, behavioural interactions typically occur nonrandomly among group members (Dugatkin & Sih 1995; Krause et al. 2007). Individuals often preferentially interact with particular social partners because variation in individual attributes (e.g. age, resource-holding potential, sex, personality) causes specific social interactions to be costly or beneficial (Krause 1994; Lusseau & Newman 2004; Pike et al. 2008; Schürch et al. 2010). However, even if all group members are functionally similar, nonrandom interactions may be inherently beneficial. For example, in many species, individuals preferentially group with familiar individuals, because associating with known partners leads to lower aggression and higher foraging success (reviewed in: Griffiths 2003; Ward & Hart 2003). Generally, variation in individual social interactions can influence the structure and function of social groups (Flack et al. 2006), which will in turn influence individual fitness (e.g. Ryder et al. 2008; Silk et al. 2009; Oh & Badyaev 2010). More specifically, patterns of social interactions dictate many aspects of social living, such as the allocation of reproduction (e.g. Herrera & Macdonald 1992), the evolution of cooperation (e.g. Ohtsuki et al. 2006; Voelkl & Kasper 2009), and the transmission of information or disease (Krause et al. 2007; Wey et al. 2008; Godfrey et al. 2009).

Social network analysis provides a quantitative framework for analysing patterns of interactions among individuals (Croft et al. 2004). In its basic form, a social network is composed of individuals (represented by nodes) that are connected by their interactions (represented by edges; Whitehead 2008). In addition to these relational data, attributes of individuals can also be laid onto the network (Croft et al. 2008). Therefore, the network approach allows for analysis of behaviour in the context of an individual's social environment, facilitates exploration of the emergence of behavioural phenotypes at the group or population level (Croft et al. 2008), and is a promising tool for understanding the link between individual traits and group- or population-level phenomena.

While social network analysis has been increasingly employed in behavioural biology (reviewed in: Krause et al. 2007; Wey et al. 2008; Sih et al. 2009), few studies have analysed the network structure of multiple independent social groups of a given species. Indeed, Croft et al. (2008, page 146) noted that such replication is 'conspicuously absent in many network studies'. This trend is beginning to change (e.g. see recent studies by Croft et al. 2005;

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Thomas et al. 2008; McCowan et al. 2008; Madden et al. 2009; Schürch et al. 2010). However, more studies that compare network structure among replicate social groups are clearly warranted if we wish to reach general conclusions about the causes and consequences of the structure of animal societies. For animals that readily perform natural behaviour in captivity, analysing the network structure of captive groups provides a feasible means of gathering data on multiple replicate groups under controlled conditions. While studying the social networks of captive animals may have some drawbacks (e.g. these captive social groups may not precisely mimic the composition of natural groups), there are also advantages in that researchers can more easily manipulate or control factors predicted to affect network structure, and can therefore reach robust conclusions.

Here, we investigate behavioural interactions within social groups in the cooperatively breeding cichlid, *Neolamprologus pulcher*. This species is endemic to Lake Tanganyika, Eastern Africa, and forms permanent socials groups composed of a single dominant breeding pair, and 1–20 male and female subordinate helpers (Taborsky 1984, 1985; Balshine et al. 2001; Heg et al. 2005). The breeding male is always the largest individual, and the breeding female is typically the second-largest individual (Wong & Balshine 2011a), while the nonreproductive helpers form a size-based hierarchy thought to reflect two sex-specific queues for breeding status (Balshine-Earn et al. 1998; Werner et al. 2003; Heg et al. 2004; Hamilton et al. 2005; Fitzpatrick et al. 2008; Mitchell et al. 2009).

To better understand intragroup dynamics in *N. pulcher*, we explored how social conflict influences the structure of social networks. Social conflict may be manifested in aggressive, submissive and/or avoidance behaviours (Balshine-Earn et al. 1998; Aureli & de Waal 2000; Werner et al. 2003; Hamilton et al. 2005; Reddon et al. 2012). Thus, we test five predictions related to social conflict and the structure of dominance and association networks.

(1) There have been widespread claims that *N. pulcher* groups form linear dominance hierarchies (Taborsky & Limberger 1981; Taborsky 1984, 1985; Wong & Balshine 2011a, b; Reddon et al. 2011a, b). However, we are unaware of any specific tests of hierarchy structure in this species. Based on these prior assertions, we predicted that *N. pulcher* dominance hierarchies would be linear, and we performed the first test of this prediction using a quantitative analysis of hierarchy linearity and asymmetry (i.e. directional consistency).

(2) In size-structured groups, conflict is predicted to be highest between individuals of similar size (Enquist et al. 1987; Jennions & Blackwell 1996; Hamilton et al. 2005), either because relative fighting ability is uncertain (Enquist & Leimar 1983) or because subordinates should challenge dominants more frequently if the difference in fighting ability is small (Cant & Johnstone 2000). Therefore, we tested the prediction that dyads with low size asymmetry would be involved in more frequent dominance interactions and would have fewer associations with one another.

(3) Only same-sex individuals are expected to compete for breeding positions. Therefore, we tested the prediction that dominance interactions would occur more frequently and associations would occur less often between same-sex group members.

(4) As the value of a social position rises exponentially with increasing rank, dominance interactions are theoretically expected to most frequently occur towards the top of the dominance hierarchy (Cant et al. 2006). Therefore, we tested this prediction by quantifying the rate of dominance interactions throughout the hierarchy, and explored whether high-ranking group members were involved in more dominance interactions than low-ranking members.

(5) Female *N. pulcher* queue for breeding positions within their natal groups while males more commonly disperse to another group prior to breeding (Stiver et al. 2004, 2006, 2007). We therefore predicted that females would place more value on establishing relationships with group members, and would consequently be more connected within the networks than males. Similarly, we predicted that breeders would be more connected than helpers, because they have a greater interest in the structure of their current group than do the subordinate helpers.

METHODS

Study Animals

Neolamprologus pulcher used in this study were adults from a breeding colony held at McMaster University, Hamilton, ON, Canada. The fish were descendants of breeding pairs caught in Lake Tanganyika, Zambia, and were housed in social groups consisting of a male and female dominant breeding pair with either three or four subordinate helpers of mixed sexes (mean group size $\pm$ SE $= 5.8 \pm 0.1$). This group size and composition is consistent with the structure and size range of wild *N. pulcher* social groups found in Lake Tanganyika (Balshine et al. 2001). The relative size of male and female helpers as well as the ratio of male to female helpers varied among the social groups, but there was always at least one male and one female helper, and there were always both high-ranking and low-ranking helpers within the groups. Each social group inhabited a 189-litre ($92 \times 41 \times 50$ cm) freshwater aquarium outfitted with a heater, thermometer, two filters, about 3 cm of crushed coral sand substrate, and two inverted terracotta flowerpot halves for use as shelters and spawning sites. Social groups were formed approximately 1 month prior to the start of behavioural observations (see below) and each social group had successfully reproduced at least once prior to the start of the study. Fish were fed ad libitum 6 days per week with commercial cichlid flake food.

Study Protocol

In total, 14 social groups were used in this experiment. All fish were captured, weighed, measured, sexed by external examination of their genital papillae, and given a unique fin clip 48 h prior to the first observation, so that each fish could be individually identified. Groups were observed for 15 min twice a week for 2 consecutive weeks, for a total of four observation periods and 60 min of observation per group. During each observation period, a pair of observers simultaneously watched each group from a distance of approximately 1.5 m. Fish were given 5 min to acclimate to the presence of observers prior to the onset of recording, and the fish did not appear disturbed by the presence of human observers. One observer scored associations among individuals, recording the individuals within a single body length of each other at the beginning of each minute. A single body length was chosen since this is the spatial distance that social interactions occur in *N. pulcher* and is a widely used spatial metric in fish behavioural studies. The second observer continuously recorded all dominance-related behaviours among all group members, based on a recent ethogram for this species (Sopinka et al. 2009). Specifically, this observer recorded all aggressive displays and behaviours (aggressive postures, puffed throats, head shakes, rams, chases and bites) and all submissive behaviours (submissive postures and submissive displays) that were both produced and received by each fish in the group.

Social Networks

Using this data, we built two social networks, one was based on dominance interactions, and the other was based on associations, for the individuals in each social group. In each network, the weight of connecting edges was determined by summing the number of interactions or associations for each dyad across the four observation periods (see above). Note that *N. pulcher* social networks were stable over the study time period, as networks built from the first two observation periods were highly positively correlated to networks built from the second two observation periods (Mantel tests followed by Fisher's omnibus test (Louv & Littell 1986; Haccou & Meelis 1992): dominance networks: mean $r_S = 0.55$, $f_{28} = 100.4$, $P < 0.0001$; association networks: mean $r_S = 0.46$, $f_{28} = 75.9$, $P < 0.0001$). The network of dominance interactions was created by combining the sociomatrix of aggressive interactions (a matrix in which columns and rows represent individuals, thus each cell in the matrix represents a dyad) with the transposed sociomatrix of submissive interactions (i.e. the actor and receiver are reversed), for each group. Dominance networks had no maximum edge weight, and could be either directed (when exploring dominance relationships as per prediction 1) or undirected (when we used the total number of dominance interactions as a measure of social conflict; as per predictions 2–4), depending on the analysis employed. The association network was undirected, and each dyad had a maximum edge weight of 60 (i.e. if the dyad was associated during every scan across the four observation periods). Four of the 56 subordinate helpers died during the study period and these individuals were removed from all networks. There were no self-loops in any networks (i.e. the diagonal in all sociomatrices was set to 0) and this feature was conserved during all randomization tests.

Network Analysis

Network analysis was performed in R version 2.14.1 (R Development Core Team 2012) and UCINET version 6 (Borgatti et al. 2006). During randomization tests, we held the total number of interactions or associations constant within each social group. When appropriate, we used Fisher's omnibus test (Louv & Littell 1986; Haccou & Meelis 1992) to combine *P* values obtained from each social group into a single value. We determined the direction of the strongest relationship among groups, and subtracted the contribution of groups with the opposite relationship from the combined test statistic, and the resultant overall *P* value (see also Croft et al. 2006). Networks in Figures 1a, b were created using the 'igraph' package in R (Csárdi & Nepusz 2006).

Dominance hierarchy structure

To test prediction 1, we examined the structure of dominance hierarchies using the triangle transitivity method recently developed by Shizuka & McDonald (2012). This measure of dominance hierarchy structure is equivalent to linearity (sensu Landau 1951; de Vries 1995) when all pairwise dominance relationships are known. However, it is advantageous in that it does not become biased when pairs of individuals have not interacted (see Klass & Cords 2011), and/or when group size varies (Shizuka & McDonald 2012). The directed dominance matrix was reduced to a binary dominant/subordinate matrix ($1 = \text{dominant}$, $0 = \text{subordinate}$) based on which individual in each dyad had a larger value in the dominance matrix (i.e. which individual had 'won' more dominance interactions). If a dyad had not interacted, both members were given a 0. Next, the proportion of transitive triangle motifs (t_{tri}) was determined for this binary network, using the 'statnet' package in R (Handcock et al. 2003). The statistical significance of t_{tri} was determined by comparing the empirical value of t_{tri} with values obtained from 2000 permutations of the dominant/subordinate matrix (see Shizuka & McDonald 2012 for details). We also calculated the global asymmetry in dominance interactions across all dyads in each network. In addition to the structural organization of the dominance hierarchy (i.e. linearity or transitivity), the degree to which dominant individuals are likely to win a contest over subordinate individuals is an important characteristic of dominance relationships (van Hooff & Wensing 1987; de Vries et al. 2006; Whitehead 2008). So, for each dyad, we determined the dominant and subordinate individual (as above). Then, we divided the number of interactions in which the dominant individual behaved as such (i.e. they gave aggression or received submission) by the total number of dominance interactions in the network. The resultant statistic ranges from 0.5 to 1, and describes the global likelihood that a dominant individual would be correctly identified given an observation of a single interaction. To test whether dominance interactions among *N. pulcher* were significantly more asymmetrical than random, we performed 2000 permutations (per social group) of the raw dominance interactions. Then, we compared the dominance asymmetry score for networks built from the randomized data with our empirical values.

Network-level analysis

We tested our predictions about patterns of social conflict (predictions 2–4) using undirected dominance networks and networks of association described above. We first determined whether there was nonrandom structure in our networks (i.e. if individuals preferentially interacted or associated with particular group members). Using R, we performed 2000 permutations (per social group) of the raw dominance interaction data and compared the standard deviations in the weights of all possible edges between our observed networks and networks built from our randomized data. A high standard deviation in edge weight in our empirical networks (relative to the randomized networks) would indicate that individuals preferentially interact or associate with certain partners. Next, we used the multiple regression quadratic assignment procedure (MRQAP) in UCINET (Krackhardt 1988; Borgatti et al. 2006; see also Wey & Blumstein 2010 for a similar analysis) to regress multiple independent matrices on an observed dependent matrix. In this analysis we used three independent matrices.

(1) To test whether patterns of conflict were related to size asymmetry, we created a sociomatrix for each social group in which each element (i.e. cell) was the standard length of the larger individual divided by the standard length of smaller individual. In this size asymmetry sociomatrix, larger values indicate dyads with large differences in body size.

(2) To test whether patterns of conflict were related to sex, we created a sex-similarity sociomatrix in which a dyad was given a 1 if both individuals were the same sex, or a 0 if they were of different sex.

(3) To determine whether conflict was related to social rank, we created a sociomatrix in which each cell was the sum of the size ranks of the dyad. In *N. pulcher*, body size is highly correlated with social rank (Taborsky 1984, 1985), and size hierarchies are maintained by strategic regulation of growth (Heg et al. 2004). Thus, body size is often used to infer rank in this species (e.g. Hamilton et al. 2005). In our analysis, the value for the cell connecting the largest to the second-largest individual would be 3 (size rank 1 + size rank 2), while the value connecting the fifth-largest to the sixth-largest individual would be 11 (size rank 5 + size rank 6). Thus, a negative effect size for this matrix would indicate that dominance interactions or associations occur most often between high-ranked individuals.

We performed separate analyses for each dominance matrix for each social group, using the double Dekker semipartialling method (Dekker et al. 2007) with 2000 permutations per analysis. We performed a similar MRQAP analysis on networks of associations, except in this case we used only two independent matrices; the size asymmetry matrix and the binary sex similarity matrix described above.

Nodal measures

To investigate differences among individuals in their role in social networks (prediction 5) we compared average nodal strength and eigenvector centrality between males and females, and between breeders and helpers. Node strength measures the total weight of all edges connected to a node (Whitehead 2008), while eigenvector centrality measures how well connected an individual is by considering both the direct connections to the focal node and also the connectedness of the focal node's neighbours (Bonacich 1987; Newman 2004). For each network, we calculated an average strength and eigenvector centrality for each class of individuals (i.e. males and females, breeders and helpers). To test whether there was a significant difference between the classes, we performed 2000 permutations of the data and compared the empirical connectivity values with those calculated from networks built using the randomized data.

Ethical Note

Fish were marked with a dorsal fin clip to allow for visual identification. Fin clipping does not adversely affect behaviour (Stiver et al. 2004) and the fish recovered from this procedure immediately. The methods for animal housing, handling and experimental protocols were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol Number 10-11-71) and adhere to the guidelines of the Canadian Council for Animal Care and the ABS/ASAB.

RESULTS

Neolamprologus pulcher *Groups Form Linear Dominance Hierarchies (Prediction 1)*

The dominance hierarchies were highly linear (permutation test: mean $t_{\mathrm{tri}} = 0.80$, $f_{28} = 50.68$, $P = 0.005$). Of 133 closed triangle motifs across all 14 social groups, 128 were transitive. We also found that dominance relationships in this species were highly asymmetrical (mean dominance asymmetry = 0.90, $f_{28} = 188.44$, $P < 0.001$).

Conflict Is Highest between Group Members of Similar Size (Prediction 2)

Both dominance interactions and associations occurred nonrandomly throughout *N. pulcher* social groups (permutation test: $f_{28} = 189.02$, $P < 0.001$ and $f_{28} = 183.26$, $P < 0.001$, respectively; Fig. 1). However, we found no significant effect of size asymmetry on patterns of dominance interactions or associations (MRQAP: $f_{28} = 1.82$, $P > 0.99$ and $f_{28} = 7.28$, $P > 0.99$, respectively).

Conflict Is Higher between Same-sex Individuals (Prediction 3)

We found no significant effect of sex on the observed patterns of dominance interactions or associations (MRQAP: $f_{28} = 3.75$, $P > 0.99$ and $f_{28} = 9.50$, $P > 0.99$, respectively).

Conflict Is Higher Near the Top of the Social Hierarchy (Prediction 4)

Dominance interactions were significantly more likely to occur between individuals at the top of the hierarchy (MRQAP, effect of rank: $f_{28} = 65.28$, $P < 0.001$; Fig. 2).

Females Are More Connected Than Males and Breeders Are More Connected Than Helpers (Prediction 5)

In dominance networks, breeders had significantly higher strength (permutation test: $f_{28} = 139.66$, $P < 0.001$) and eigenvector centrality ($f_{28} = 133.04$, $P < 0.001$) than did helpers (prediction 5: Fig. 3). There was no difference in strength or eigenvector centrality ($f_{28} = 14.12$, $P = 0.98$ and $f_{28} = 21.74$, $P = 0.79$, respectively) between males and females (Fig. 3). In association networks, breeders had significantly higher strength ($f_{28} = 121.12$, $P < 0.001$) and eigenvector centrality ($f_{28} = 97.21$, $P < 0.001$) than helpers (prediction 5: Fig. 3). Finally, there was no difference in strength or eigenvector centrality ($f_{28} = 6.63$, $P > 0.99$ and $f_{28} = 27.21$, $P = 0.51$, respectively), between males and females in association networks (Fig. 3).

DISCUSSION

In this study, we used social network theory to explore interaction patterns within groups of the cooperatively breeding cichlid, *N. pulcher*. Consistent with our predictions, *N. pulcher* hierarchies were highly linear, with highly asymmetrical and directionally consistent interactions between dyads. While neither dominance interactions nor patterns of associations were directly related to body size asymmetry or sex, we found that dominance interactions were not equally distributed across the network, but instead occurred most frequently at the top of the social hierarchy. Finally, breeders were more connected than helpers within the networks.

We found that *N. pulcher* social groups form highly transitive (and therefore linear) dominance hierarchies with large asymmetries in dyadic dominance interactions (i.e. dominance interactions were strongly directional within dyads). Such a pattern is expected when there is large variation in resource-holding potential among individuals, and dominance ranks should therefore be predetermined by differences in individual attributes (Chase & Seitz 2011). In *N. pulcher*, as in most fishes, resource-holding potential is strongly correlated with body size (Reddon et al. 2011b) and *N. pulcher* social groups are stratified according to body size (Taborsky 1984, 1985). Therefore, there should rarely be multiple individuals with similar resource-holding potential, and as observed, dominance hierarchies should be linear and highly asymmetrical.

Within *N. pulcher* social groups, certain pairs of individuals experienced greater social conflict relative to other dyads. In agreement with our prediction, social conflict was highest towards the top of the size hierarchy. When social groups take the form of reproductive queues, there should be conflict over social status because higher-ranking individuals are more likely to inherit a breeding position. While it is beneficial for all individuals to increase their social rank, the consequences of rank change are greatest for high-ranking individuals (Cant et al. 2006). Thus, high-ranking individuals ought to invest more heavily in deterrent displays towards subordinates and in aggressive tests of dominants compared with lower-ranked individuals. In support of this idea, the aggression levels of several species of social insects (e.g. *Ropalidia marginata*, Chandrashekara & Gadagkar 1992; *Dinoponera quadriceps*, Monnin & Peeters 1999; *Polistes dominulus*, Cant et al. 2006) have been experimentally shown to be influenced by rank, rather than vice versa. Furthermore, aggression rates increase with social rank in several social vertebrates (e.g. *Equus caballus*, Araba & Crowell-Davis 1994; *Pan troglodytes*, Muller & Wrangham 2004), although such tests rarely consider confounding variables such as sex or body size. In the current study, we provide strong support for the influence of social rank on intragroup conflict in *N. pulcher*, by showing a strong correlation between dyad rank and rates of

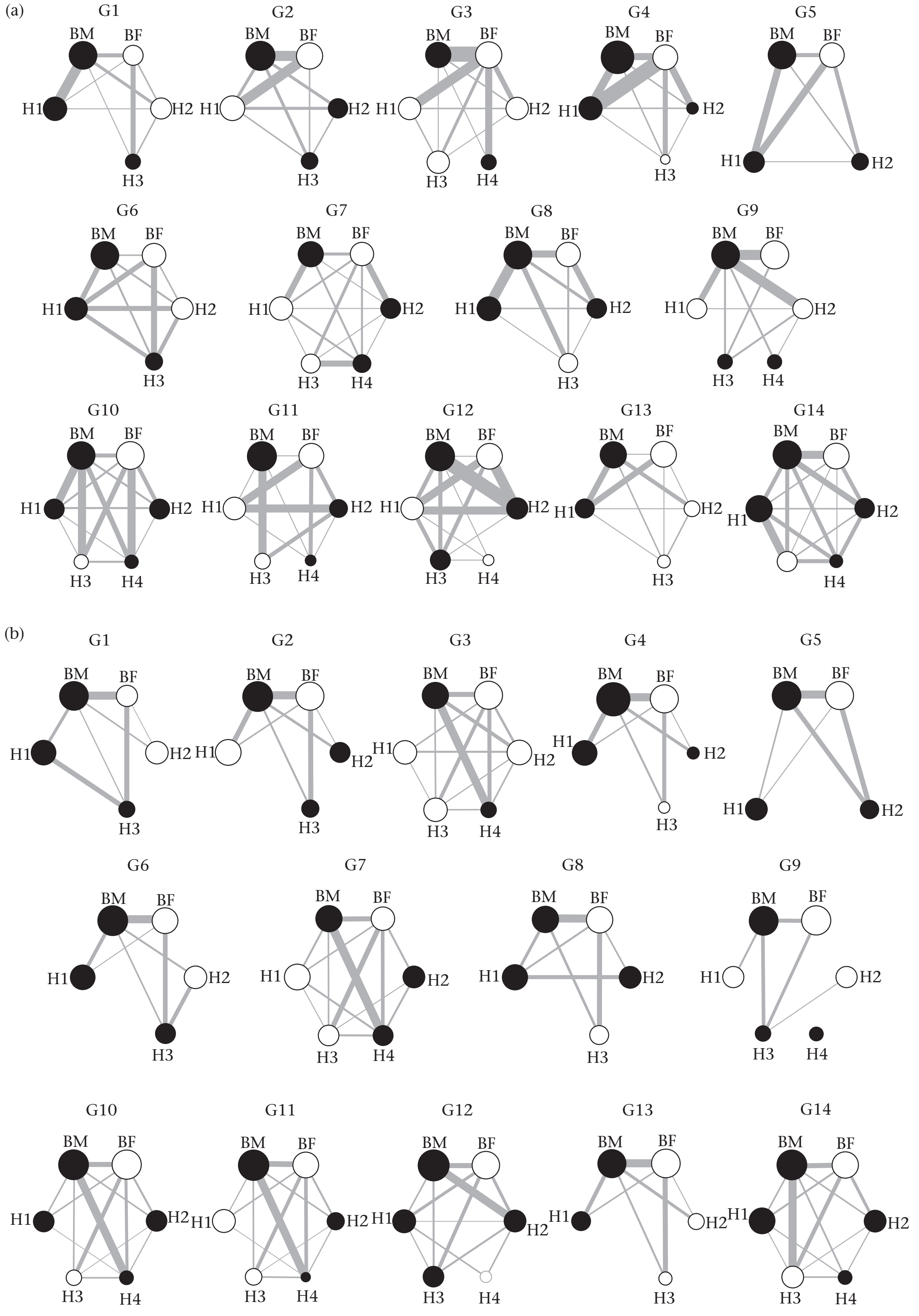

Figure 1. Networks of (a) dominance interactions and (b) associations in *Neolamprologus pulcher*. Nodes (circles) represent individual fish in each of 14 captive social groups; node labels indicate the breeding male (BM), breeding female (BF) and nonbreeding helpers in order of standard length (with H1 being the largest helper); node colour indicates sex (black = male, white = female); node size is scaled to individual body size. The thickness of connecting edges is scaled to the number of dominance interactions and the number of associations that occurred between each dyad across all observation periods and is comparable both within and among groups.

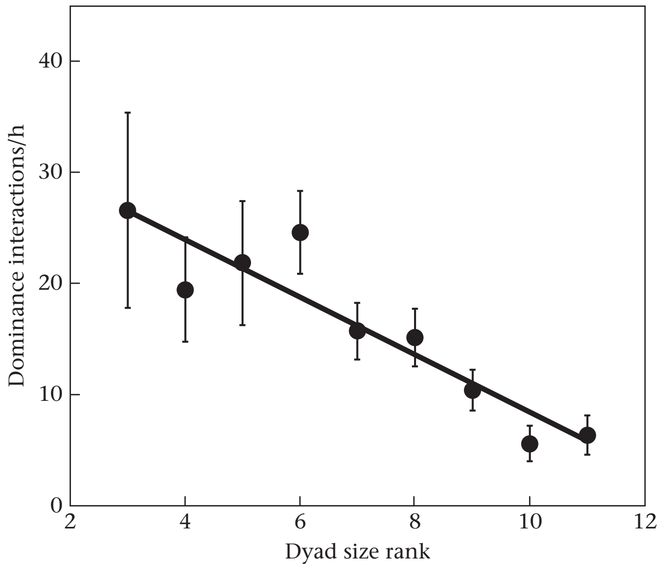

Figure 2. Mean ± SE dyadic dominance interaction rate as a function of the sum of the size rank of the members of the dyad (e.g. size rank 1 + size rank 2 = 3) in *Neolamprologus pulcher* groups. Values are pooled across all 14 social groups. The black line indicates a regression through the average values at each dyad size rank.

dominance interactions while controlling for several alternative hypotheses.

While higher-ranked individuals had more conflict with one another compared with lower-ranked individuals, neither sex nor size asymmetry were related to aggression. We had predicted increased conflict between same-sex and similarly sized individuals, since these individuals should pose the greatest threat to each other within the reproductive queue (Hamilton et al. 2005; Mitchell et al. 2009). When body size asymmetry is low, subordinates ought to challenge dominants more readily because they have a higher chance of being successful (Cant & Johnstone 2000). However, we found no relationship between sex or size asymmetry and the level of conflict. This may be because the relative value of winning a conflict is low for subordinates far down the reproductive queue. Thus, conflicts may be rare among low-ranking individuals, even when those individuals are the same sex and similar in size. As a result there may only be a weak (and in this study, nonsignificant) effect of sex and size asymmetry on the overall patterns of social conflict in a group. It is also likely that individual *N. pulcher* do not always have perfect knowledge of the sex of all other group members, especially among sexually suppressed subordinates, and thus sex-specific dominance hierarchies may simply not form. Finally, note that patterns of aggression are complex, and may be dependent on external ecological factors as well as the characteristics of the individuals involved (Reeve 2000). Furthermore, the current models used to predict patterns of aggression within social groups (i.e. reproductive skew models) consider only direct reproduction as the resource over which individuals compete, which is not appropriate for predicting aggression patterns among nonbreeding subordinates. We argue that models that incorporate future reproductive prospects (e.g. social rank) and resources not directly linked to reproduction (e.g. shelter) may be more appropriate and better predict patterns of conflict in *N. pulcher*.

In the current study, we observed that breeders were more connected than helpers in dominance and association networks. In addition to investing heavily in deterrent signals directed at large helpers to maintain their social status (see above), breeders may also be more connected than helpers if they use dominance interactions to police the behaviours of, and interactions among, helpers. Pay-to-stay models of cooperative breeding predict that breeders will punish helpers who provide insufficient help (Gaston

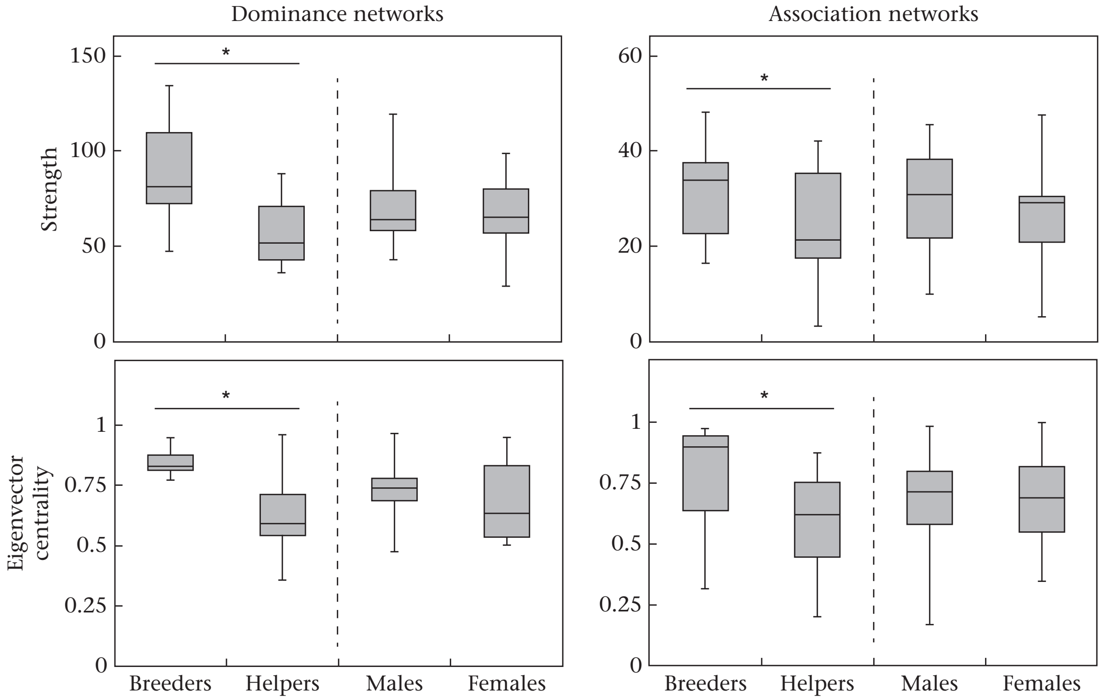

Figure 3. Connectivity in *Neolamprologus pulcher* social networks. Shown are the strength and eigenvector centrality of classes of individuals for networks of dominance interactions and association in 14 captive social groups. Box plots show the 75th percentile, median and 25th percentile, as well as the minimum and maximum values (whiskers). $^*P < 0.05$.

1978; Kokko et al. 2002). The evidence for such dominant policing of subordinate helping in *N. pulcher* is weak (Wong & Balshine 2011a). However, it is possible that breeders do police helpers in terms of their shelter or space use. Furthermore, breeders may be more connected if they police interactions among helpers to increase group stability and/or productivity. Third-party policing is thought to be most common in societies with high interindividual variance in power, because policing by high-ranking individuals will be more effective and less costly in this situation (Flack et al. 2005). Size-structured hierarchies in social fish fit these criteria, and there were several observations of breeders interfering in helper–helper conflicts in this study (C. M. O'Connor & A. R. Reddon, personal observation) and in previous field studies (S. Balshine, personal observation). A further comprehensive study of policing in *N. pulcher* social groups is probably warranted.

Finally, we show that patterns of association between *N. pulcher* group members are nonrandom. These patterns were not explained by sex or size asymmetry of group members. One possible explanation is that both in captivity and in the wild, individual *N. pulcher* establish small subterritories within the larger group territory (Werner et al. 2003). Such segregation of space could lead to nonrandom association patterns, because individuals will predominantly associate with neighbours. Subterritoriality was widely observed in this study, however, it seems that the arrangement of subterritories was not dependent on the sex or body size of the individuals in neighbouring subterritories. While captivity will always constrain animals in their ability to move throughout their environment (Estévez & Christman 2006), the aquaria used in this study were a similar size to the median territory size reported for wild *N. pulcher* (Balshine et al. 2001). Thus, the patterns of association observed in this study are unlikely to have been generated by the captive environment alone and may be similar to those in wild populations.

In conclusion, this study is one of only a few to examine network structure in multiple replicate social groups of a given species. This approach facilitates making general conclusions about the social structure in this cooperatively breeding cichlid. We provide the first explicit analysis of dominance hierarchy structure in *N. pulcher*, and confirm the assumption that hierarchies are strongly linear and dominance interactions are directionally consistent. Furthermore, we provide evidence that while dominance interactions and associations occur nonrandomly, they are not related to body size asymmetry or sex. Thus, there is little support for sex-specific dominance hierarchies in *N. pulcher*. Our results do show, however, that there is increased social conflict at the top of the size hierarchy, which is consistent with theoretical predictions based on intensified conflict as the probability of inheriting a breeding position increases. Finally, we demonstrate that breeders are more connected than helpers, which suggests interesting avenues for future research on policing in this species. Taken together our results provide valuable information on the structure of social groups in a model cooperative breeding species. Future research examining how network structure influences reproductive success, growth, survival as well other aspects of group function (e.g. predator defence) will be valuable in gaining a more complete understanding of sociality in this intriguing fish.

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