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*.

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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;

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