

The effects of familiarity and social hierarchy on group membership decisions in a social fish

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Members of animal groups face a trade-off between the benefits of remaining with a familiar group and the potential benefits of dispersing into a new group. Here, we examined the group membership decisions of *Neolamprologus pulcher*, a group-living cichlid. We found that subordinate helpers showed a preference for joining familiar groups, but when choosing between two unfamiliar groups, helpers did not preferentially join groups that maximized their social rank. Rather, helpers preferred groups containing larger, more dominant individuals, despite receiving significantly more aggression within these groups, possibly owing to increased protection from predation in such groups. These results suggest a complex decision process in *N. pulcher* when choosing among groups, dependent not only on familiarity but also on the social and life-history consequences of joining new groups.

Keywords: group membership; familiarity; social hierarchy; *Neolamprologus pulcher*

1. INTRODUCTION

Social rank within groups influences the costs and benefits of group living, in particular access to food, mates and shelter (Krause & Ruxton 2002). Rather than queuing for an improved social position within an existing group, an individual may accelerate its progress if it can enter a new group at a higher rank. Subordinates in size-based hierarchies therefore have multiple group membership options: (i) to remain in their original group and potentially attain breeding status (Kokko & Johnstone 1999), (ii) to move into another group as a breeder (Kokko & Ekman 2002), or (iii) to move into another group as a subordinate (Bergmüller *et al.* 2005). Moving into another group as a subordinate may expedite attaining a breeding role because of a shorter queue (Kokko & Ekman 2002), or because the joining member achieves a higher rank than in the original group.

Although moving into an alternative group may improve an individual's rank, continued association with familiar individuals may confer even greater benefits, including enhanced stability of dominance

hierarchies, and reduced within and among group aggression (Frostman & Sherman 2004). Although the majority of studies addressing familiarity effects examine species that form temporary groups (Ward & Hart 2003), the continuing associations among members of stable groups may magnify the beneficial effects of familiarity. Moreover, entering an unfamiliar group in search of a more dominant position necessarily requires the re-establishment of social hierarchies, which often entails prohibitive costs (Cristol 1995), further enhancing the relative benefit of associating with familiar individuals.

Animals moving among groups must therefore choose among groups offering benefits of familiarity and groups that may improve their social position. *Neolamprologus pulcher* is a group-living cichlid with helpers-at-nest (Taborsky & Limberger 1981). Dominance hierarchies are size-based, and subordinate helpers can inherit dominant breeding status (Balshine-Earn *et al.* 1998; Stiver *et al.* 2004) but occasionally helpers move among groups (Stiver *et al.* 2004; Bergmüller *et al.* 2005). Here, we examine *N. pulcher* group membership preferences to test the hypothesis that helpers prefer to join familiar groups when possible, but when faced with unfamiliar groups choose based on the likelihood of improving their social position. As group membership reflects a balance between the decisions of insiders and outsiders (Higashi & Yamamura 1993), we also examine the aggressive, submissive and social interactions between focal and resident helpers.

2. MATERIAL AND METHODS

We conducted experiments in November 2008 at Kasakalawe Bay, Lake Tanganyika, Zambia. We collected eight established groups of *N. pulcher* as stimulus groups (table S1 in the electronic supplementary material) and 20 extra helpers from other groups. Fish were acclimatized in holding tanks for 24 h before experimental trials. To measure preference behaviour, we used binary choice procedures in test tanks on the lakeshore (200 × 50 × 80 cm, filled to 25 cm), placing stimulus groups behind mesh screens (5 mm diameter). We constructed two identical territories at each end of the test tank using lake rocks and introduced one stimulus social group into each. We tested the association preference of two focal helpers from each group for a familiar versus unfamiliar group (experiment I, $n = 12$ helpers), or for familiar breeders versus familiar helpers (experiment II, $n = 14$). We also tested the preference of focal individuals for one of two unfamiliar groups that differed in their social composition (experiment III, $n = 14$). Stimulus groups for experiment I were composed of a size-matched breeding pair plus two helpers from either the group originally containing the focal fish (familiar), or from a group collected more than 50 m from the familiar group (unfamiliar Stiver *et al.* 2007). Stimulus groups for experiment II were composed of either the breeding pair, or two large helpers (40–60 mm standard length (SL)) from the focal fish's original group. Stimulus groups for experiment III were composed of size-matched breeding pairs with either two small helpers (20–30 mm SL; 'groups with small helpers'), or two large helpers (40–60 mm SL; 'groups with large helpers'); both were unfamiliar groups. Stimulus groups were acclimated for 30 min, after which a single focal fish of intermediate size (30–40 mm SL) was introduced and allowed to explore the tank for 5 min. After 5 min, we measured the time spent by the focal fish within two body lengths of mesh screens for the first 10 min after introduction. For experiment III, we also removed the screens and measured the time focal helpers spent within each of the stimulus groups (immediately adjacent to or within the rock territory) for the second 10 min after introduction, as well as the aggressive (bites, puffed throats, rams), and submissive interactions (Sopinka *et al.* 2009) between focal and resident fish. In experiment III, we also recorded the group eventually joined 3 h after introduction. To determine whether preferences after 3 h persisted, focal fish were left in the test tank overnight in five trials; in all cases, the group chosen after 3 h was the same the following morning.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0732> or via <http://rsbl.royalsocietypublishing.org>.

3. RESULTS

Focal helpers preferentially associated with familiar stimulus groups compared with unfamiliar stimulus groups (Wilcoxon signed-rank test $Z = 2.36$, $n = 12$, $p = 0.02$, figure 1). However, focal fish showed no preference for their own dominant breeders over large subordinate helpers from their own groups ($Z = -0.078$, $n = 12$, $p = 0.94$). Focal helpers initially showed no preference for unfamiliar groups containing either large or small helpers in the first 10 min through mesh screens ($Z = -1.398$, $n = 14$, $p = 0.16$), or in the second 10 min with open access ($Z = -0.175$, $n = 14$, $p = 0.86$). However, after 3 h, focal helpers had joined groups with large helpers significantly more often than groups with small helpers (χ^2 -test, $\chi^2_{(1)} = 4.6$, $n = 14$, $p < 0.05$; figure 2).

There were significantly more focal-resident aggressive interactions with large helpers than with small helpers (aggression from resident helpers towards focal helper, t -test, $t = -3.919$, d.f. = 13, $p = 0.002$; aggression from focal helper towards resident helpers, $t = -2.567$, d.f. = 13, $p = 0.02$), and more submissive acts towards resident helpers by the focal helper ($t = -3.044$, d.f. = 13, $p = 0.009$). No submissive displays by resident breeders or focal helpers towards focal helpers were observed. Aggression and submissive acts between breeders and helpers were not significantly different from expected values calculated from time spent in each group (aggressive acts from breeders, $t = 0.527$, d.f. = 13, $p = 0.607$; aggressive acts towards breeders, $t = 0.865$, d.f. = 13, $p = 0.40$; submissive acts, $t = -1.629$, d.f. = 13, $p = 0.13$).

4. DISCUSSION

Group membership decisions of *N. pulcher* reflect the capacity to discriminate and preferentially associate with familiar over unfamiliar conspecifics. Focal helpers preferred to associate with familiar individuals, a preference that may ameliorate aggression between group members, or facilitate advantageous reciprocal behaviours among familiar conspecifics (Croft *et al.* 2005). However, focal helpers showed no preference for breeders or helpers from their original group, suggesting that either cues used to distinguish familiar individuals are shared by helpers and breeders, or helpers have no preference for associating with particular group members.

When choosing among unfamiliar groups, we expected individuals to base group-living decisions on their probability of attaining breeding status (Buston 2004). However, *N. pulcher* helpers did not preferentially join groups in which they would be larger than resident helpers and thereby increase their social position. Although hierarchies in some other social species function as strict queues (Buston 2004), breeding vacancies are not always inherited by existing group members in *N. pulcher*, occasionally being filled by conspecifics outside the group (Balshine-Earn *et al.* 1998; Stiver *et al.* 2007). *Neolamprologus pulcher* subordinates may therefore be under weak selective pressure to join groups based on social rank relative to other social fishes, and instead base grouping decisions on other fitness currencies.

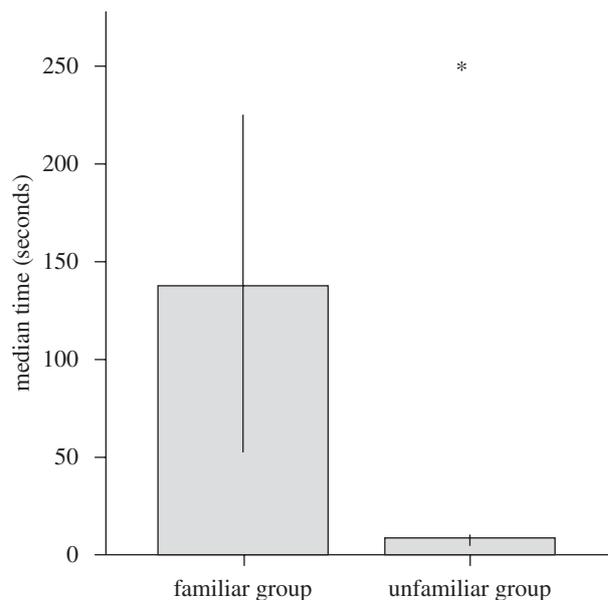


Figure 1. Median time (seconds \pm interquartile range) spent with stimulus groups of familiar fish or unfamiliar fish; asterisk denotes significant difference at $\alpha = 0.05$.

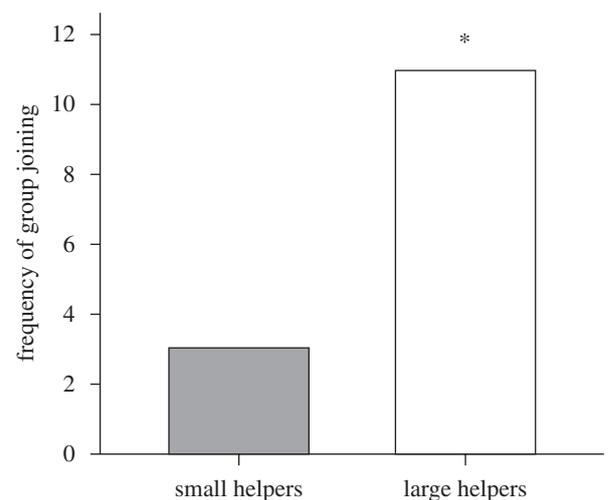


Figure 2. Frequency of joining groups containing breeders and small helpers or breeders and large helpers; asterisk denotes significant difference at $\alpha = 0.05$.

Neolamprologus pulcher subordinates showed a preference for joining groups containing larger, dominant helpers, despite initially increased aggressive interactions with these individuals. A preference for groups with larger helpers may indicate that factors besides the improvement of rank, such as relative predation risk in different groups (Heg *et al.* 2004), may be of greater importance in group joining decisions in high predation environments such as Lake Tanganyika (Taborsky & Limberger 1981). Although a preference for joining groups with large helpers resulted in focal helpers receiving more aggression within groups, the protection from predation offered by associating with larger group members (Heg *et al.* 2004) may be sufficient to offset the increased aggression and lower social position within these groups. We did not detect a preference for groups of small or large helpers in the first 20 min after introduction, but

observed a preference for groups with large helpers 3 h after introduction. This suggests that helpers may need more time to assess group characteristics and distinguish between demographically different groups (Doligez *et al.* 2002), and is consistent with previous studies showing that helpers visit the same groups many times before finally joining them (Bergmüller *et al.* 2005).

The pattern of aggression shown by existing group members provides insight into the internal mechanisms of group formation. Large helpers were significantly more aggressive to joining focal fish than were breeders or small helpers, suggesting that aggressive behaviours were not simply a territorial response shared equally among all group members. Rather, the observed pattern of aggression indicates that different group members have divergent interests concerning group augmentation and intra-group competition. For the breeders, acceptance of smaller subordinate helpers is likely to confer benefits associated with increased helping (Taborsky 1984). For small helpers, acceptance of larger group members may increase survival prospects by providing better territory defence against predators (Heg *et al.* 2004) or simply reflect an inability to prevent joining by larger conspecifics. In contrast, large resident helpers presumably will not immediately share the benefits of additional brood care provided by additional helpers, and may perceive medium-sized helpers only as competitors. These divergent reactions suggest that members of *N. pulcher* groups in different social positions use contrasting currencies when evaluating membership options, and suggest that conflict between group members is an important factor shaping the structure and dynamics of animal groups.

We demonstrate that benefits of familiarity and association with large individuals influence group-living decisions in *N. pulcher*. Because members of *N. pulcher* groups are often related (Stiver *et al.* 2005), familiarity and kinship may be interlinked, and recognition of familiar individuals may provide a mechanism for the evolution of kin-selected behaviours. Hence, the combination of kin- and familiarity-associated benefits may outweigh the benefits of grouping decisions based solely on the social rank. Further research into the interaction between direct and indirect benefits of grouping behaviour will clarify the relationships between familiarity, kinship and social evolution.

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