Sex differences in group-joining decisions in social fish

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In social animals, decisions about which group to join can have important fitness consequences and may be particularly critical when groups have a strict dominance hierarchy that relates to reproductive success. Choosing a large group may maximize safety, but choosing to join a small group can minimize the delay until a dominant reproductive position can be reached. We explored this trade-off between safety and rank using *Neolamprologus pulcher*, a cichlid fish in which individuals conform to a rigid within-group dominance hierarchy. In this species, females typically inherit dominant positions by ascending in rank, while males commonly take over a dominant breeding position by dispersing into a new group. Because females have fewer opportunities to switch groups, we predicted that females would place higher value on social rank within their group than would males. To test this, we examined male and female *N. pulcher*'s preferences for joining large groups at a low rank versus joining small groups at a high rank. Males showed clear preferences for larger (presumably safer) groups, while females showed no such preferences. In a second experiment, we held joining rank constant, and found that both males and females showed a strong preference for large groups. Our results suggest that when joining a group, females consider both rank and safety whereas males are primarily concerned with safety. Our results help to elucidate the factors underlying social decision making in a cooperative breeder.

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Group membership decisions are of critical importance to social animals (Krause & Ruxton 2002). Membership in a larger group may provide more effective and efficient vigilance (Elgar 1989; Roberts 1996; Uetz et al. 2002), dilute predation risk (Hamilton 1971; Wrona & Dixon 1991), augment mating opportunities (Westneat et al. 2000) and increase foraging success (Drent & Swierstra 1977; Brown 1986; Creel & Creel 1995). However, living in a larger group may also impose certain costs, including increased conspicuousness to predators (Lindström 1989; Cresswell 1994), more competition for food or mates (Janson & Goldsmith 1995) and increased transmission of disease (Hoogland 1979; Brown & Brown 1986). The trade-off between these costs and benefits poses a major life history decision for group-living animals (Krause & Ruxton 2002). Decisions about what size of group to join or whether to allow new members into the group are of particular importance in groups with pronounced dominance hierarchies (Krause & Ruxton 2002; Ang & Manica 2010; Jordan et al. 2010a, b), especially when the social hierarchy represents a queue to breed (Buston & Cant 2006; Wong et al. 2008; Wong 2010; Wong & Balshine 2011a). Larger groups may provide greater safety, but also present a longer

and more difficult path to dominant breeder status (Kokko & Ekman 2002; Ang & Manica 2010). To date, most of the empirical studies examining group size preferences have been conducted in species without long-term dominance hierarchies (see Krause & Ruxton 2002 for a comprehensive review) and hence the potential trade-off between rank and safety has not received much attention.

Neolamprologus pulcher are a highly social, cooperatively breeding cichlid fish endemic to rocky littoral habitats in Lake Tanganyika, Africa (Taborsky & Limberger 1981; Taborsky 1984, 1985; Balshine-Earn et al. 1998; Balshine et al. 2001). *Neolamprologus pulcher* live and breed in stable social groups consisting of a single dominant breeding pair and between 1 and 20 subordinate helpers (Balshine et al. 2001; Heg et al. 2005). Subordinate group members assist the breeding pair by maintaining the territory (removing sand, debris and snails), defending the brood chamber and participating in direct care of the brood (Taborsky & Limberger 1981; Balshine et al. 2001). Individuals in *N. pulcher* groups form a strict linear size-based dominance hierarchy (Balshine-Earn et al. 1998; Fitzpatrick et al. 2008; Wong & Balshine 2011b). The largest male and largest female in each group form a breeding pair and all other group members are reproductively suppressed (Fitzpatrick et al. 2006). Social groups appear to serve a predominantly defensive function (Heg et al. 2004), as the predation pressure in *N. pulcher*'s natural habitat is formidable

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(Balshine et al. 2001; Heg et al. 2004; Wong & Balshine 2011a). As a result of *N. pulcher's* small size (<8 cm adult body length) and adaptability to laboratory conditions where they will perform their full suite of natural behaviour, they are amenable to controlled experimentation that is not ethical or feasible in other cooperatively breeding vertebrates (Wong & Balshine 2011a).

Subordinate *N. pulcher* have three possible routes to breeder status (Jordan et al. 2010a; Wong & Balshine 2011a): (1) they can remain in their current group as a subordinate helper in a queue to breed (Kokko & Johnstone 1999), (2) they can disperse and join another group in order to take over the dominant breeding position (Kokko & Ekman 2002) or (3) they can disperse and join another group as a subordinate helper thereby entering another breeding queue (Bergmüller et al. 2005). By leaving its current group and joining another group with a shorter queue (i.e. one with fewer larger same-sex individuals), a subordinate may expedite its ascent to breeding position (Kokko & Ekman 2002; Stiver et al. 2004). However, by joining a group with fewer members or fewer larger group members, a subordinate may sacrifice the inherent safety of a large group (Balshine et al. 2001; Heg et al. 2004). Jordan et al. (2010a) found that when faced with a choice between groups of the same size, *N. pulcher* subordinates prefer to join a group containing larger, more dominant fish, despite the fact that they were subject to higher levels of social aggression in these groups. These results suggest that *N. pulcher* may favour safety over high social rank. If *N. pulcher* always value safety over rank, then we would expect individuals to prefer to join a larger group in a lower rank position than to join a smaller group at a higher rank.

Differences in the route to dominant breeding status between males and female may generate sex differences in group-joining rules (Krause & Ruxton 2002). *Neolamprologus pulcher* represent a 'mammalian type' cooperative breeder (Russell & Lummaa 2009) in that females typically remain in a matrilineal queue and inherit breeder status in their natal group, whereas males often must disperse into a new group before attaining the breeder rank (Stiver et al. 2004, 2006). Males may be more attuned to group demographics (i.e. group composition and/or group size), as they are more likely to face a decision between joining different groups that vary in these parameters (Stiver et al. 2004, 2006, 2007). Alternatively, because females lack the option to disperse, they may place greater emphasis on their rank within the group, while males, because they can disperse, may place a higher value on safety. Female subordinates tend to be more active helpers within the group (Stiver et al. 2005; Desjardins et al. 2008a, b), which may suggest that females highly value their social position within the group.

In our first experiment, we examined the preference for small versus large groups of larger, same-sex conspecifics in subordinate adult *N. pulcher*. We assumed that larger groups would maximize safety while smaller groups would maximize the joiner's rank and would minimize the time until dominance ascension. We conducted preference trials for both males and females and explored sex differences in group size preference. Differences between males and females in their preference for large groups could mean that the sexes vary in the importance they place on safety versus rank or alternatively, in their sensitivity to cues of group size. To differentiate between these possible explanations, we conducted a second experiment in which we examined group size preferences when the joiner's rank was held constant regardless of which group it joined.

METHODS

Experimental Animals and Housing Conditions

All fish used in this experiment were laboratory-reared descendants of animals collected from Lake Tanganyika, Africa.

Focal fish were 64 *N. pulcher* subordinate adults (standard length >4 cm, 32 males and 32 females) selected from 26 different social groups. Each social group from which these focal fish were taken consisted of a single dominant breeding pair and between 2 and 10 subordinate helpers of varying size (1–7 cm) housed in a 189-litre (92 × 41 × 50 cm) aquarium with two filters, two shelters and 3 cm of coral sand as substrate. Stimulus fish were selected from a large communal tank (183 × 48 × 60 cm; 527-litre), which contained approximately 80 adult *N. pulcher*. Water temperature in all aquaria was held constant at $25 \pm 2\,°C$ within chemical parameters that simulated the natural habitat of this species. All fish were fed ad libitum once a day, 6 days a week with dried or frozen prepared cichlid foods.

Testing Apparatus

The preference testing apparatus consisted of a large glass aquarium (90 × 44 × 38 cm; 150-litre), filled with 20 cm of conditioned water. Two smaller glass aquaria (40 × 20 25 cm; 20-litre), also filled with 20 cm of water, were placed inside and pushed against opposite ends of the larger aquarium. These smaller aquaria served as group stimulus chambers and ensured that no chemical cues were transferred between the focal fish and the stimulus fish. Opaque plastic barriers visually isolated the stimulus chambers from one another but allowed the focal fish to freely move between choice zones and inspect both stimulus groups. A 10 cm area (corresponding to approximately two body lengths of the average focal fish) in front of each of the stimulus chambers was clearly marked and formed the choice zone for each stimulus group.

Procedure

In each trial, a single stimulus fish was placed in one of the stimulus chambers and three stimulus fish were placed in the other chamber. The chamber that received the large or small stimulus group was randomly assigned by means of a coin flip. Research on other freshwater fish species has shown that fish possess the numerical abilities to make discriminations of this type and magnitude (Agrillo et al. 2007; Dadda et al. 2009). In the first experiment ($N = 40$, 20 males and 20 females), all of the stimulus fish were larger than the focal fish and the focal fish always joined a group at the bottom of the dominance hierarchy (either in rank 2 in the small group or in rank 4 in the large group). In the second experiment ($N = 24$, 12 males and 12 females), stimulus fish were chosen so that the focal fish would be the second-largest individual (rank 2) regardless of whether it chose to associate with the small or the large group. Each focal fish was used only once. The stimulus fish were drawn with replacement from the same population for both experiments. Stimulus fish were changed after each trial, ensuring that focal fish were exposed to different combinations of stimuli. Only same-sex animals were used as stimuli in both experiments to ensure that grouping decisions represented a form of social partner choice (sensu Dugatkin & Sih 1995) and not mate choice. The focal fish were always unfamiliar with the stimulus fish. Outside of those criteria, stimulus fish were selected at random from the fish in the communal tank.

Once the stimulus fish were in place, a focal fish was removed from its social group and introduced into the central choice chamber of the preference apparatus. We allowed the focal fish and the stimulus fish to acclimate to the apparatus for 5 min. During this acclamation period, the focal fish could freely swim about the apparatus and view both stimulus groups. Following the acclimation period, we filmed the apparatus for 10–15 min (15 min in experiment 1; 10 min in experiment 2). After the first observation, we stopped filming for an interobservation interval (40 min in

experiment 1; 30 min in experiment 2) during which the focal fish remained undisturbed and could continue to view the stimulus fish. After the interobservation interval, we resumed filming for an additional 10 min (second observation period). Previous research on this species has shown that short-term preferences in affiliating with one group over the other predict the ultimate decision to join that group (Jordan et al. 2010a). After the second observation period, the focal and stimulus fish were returned to their respective home tanks. All trials took place between 1100 and 1600 hours. One female managed to escape from the central group-preference area during the first observation period in the first experiment, so the data for that observation was excluded.

Behavioural and Statistical Analyses

A trained observer, blind to the sex of the fish and study hypotheses, scored each trial from the video recordings. We divided each observation period into 5 min blocks to explore the consistency of behaviour throughout each trial. During each of the 5 min blocks, we recorded the time (in seconds) that each focal fish spent with the majority of its body inside each of the two choice zones (within approximately two body lengths of each stimulus chamber). We also scored the number of times that each focal fish switched from one choice zone to the other.

During both experiments, we recorded the activity of each stimuli group (scored as the number of movements of greater than one body length made by each stimulus fish), because stimulus activity levels can affect group preferences (Gómez-Laplaza 2006). We also recorded the number of aggressive acts the stimulus fish directed towards the focal choosing fish in experiment 2.

All group preference and stimulus fish activity data were normally distributed and were analysed with two-tailed parametric statistics. We compared the proportions of males and females that preferred the large group using a chi-square test. To compare the time that each focal fish spent in proximity to the large group versus the small group and any sex differences in this relationship, we performed an ANOVA with time spent in each of the two choice zones during each 5 min observation block as the within-subjects factor and sex as a between-subjects factor. The social group from which the focal fish originated had no effect on the time spent in either choice zone (one-way ANOVA with social group as a random effect); hence, subjects were combined across social groups for all analyses. We compared the activity of the small and large stimulus groups using an ANOVA, with group size as a within-subjects factor and sex as a between-subjects factor. Data on aggressive behaviour directed by the stimulus fish towards the focal fish in experiment 2 were not normally distributed and were analysed using a Wilcoxon signed-ranks test.

Ethical Note

No animals sustained any injuries or showed signs of undue stress during or after the experimental procedure. Methods described for animal housing and handling were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol No. 10-11-71) and adhered to the guidelines of the Canadian Council for Animal Care.

RESULTS

Experiment 1: Join a Large Group at Low Rank or Join a Small Group at High Rank?

In total, 17 of 20 males and 12 of 20 females spent more time with the large group. The proportion of males that preferred the large group tended to be greater than the proportion of females that did so, but this difference was not significant (chi-square test: $\chi_1^2 = 3.14$, $P = 0.08$). Across all fish (males and females combined) there was a strong preference for the large group (ANOVA: $F_{1,36} = 10.88$, $P = 0.002$), suggesting that N. pulcher strategically choose larger groups even though it would mean assuming a lower rank. There was no effect of observation time point ($F_{4,144} = 0.47$, $P = 0.76$), indicating that the fish's preference for affiliating with the large stimulus group over the small one was stable across all the observation blocks. There was no effect of sex ($F_{1,36} = 2.114$, $P = 0.16$) in this analysis, indicating that males and females spent similar amounts of time on average in association with conspecifics. Interestingly, the interaction between sex and group size preference verged on significance ($F_{1,36} = 3.77$, $P = 0.06$), suggesting that male and female N. pulcher may allocate their time differently between the two kinds of groups.

The near-significant interaction between sex and group preference along with our a priori expectations about sex differences led us to analyse the preferences for groups separately for each sex. When analysed separately, males strongly preferred to affiliate with the large group over the small group (ANOVA: $F_{1,18} = 12.416$, $P = 0.002$; Fig. 1a), while females spent similar amounts of time with the large and small groups ($F_{1,18} = 1.03$, $P = 0.32$; Fig. 1b), indicating that the overall strong group preference reported above was driven by males.

Males and females made a similar number of switches between choice zones (mean ± SE: males = 14 ± 2; females = 13 ± 2; Welch's t test: $t_{36.8} = 0.55$, $P = 0.59$). Overall there was more total activity in the large stimulus group (measured as the mean ± SE per-minute rate of movement: large group = 8.7 ± 0.4; small group = 3.6 ± 0.3; ANOVA: $F_{1,38} = 131.39$, $P < 0.001$), but the per-individual activity was significantly higher in the small stimulus group (mean ± SE: large group = 2.9 ± 0.1; small group = 3.6 ± 0.3; $F_{1,38} = 8.63$, $P = 0.006$). There were no sex differences observed in
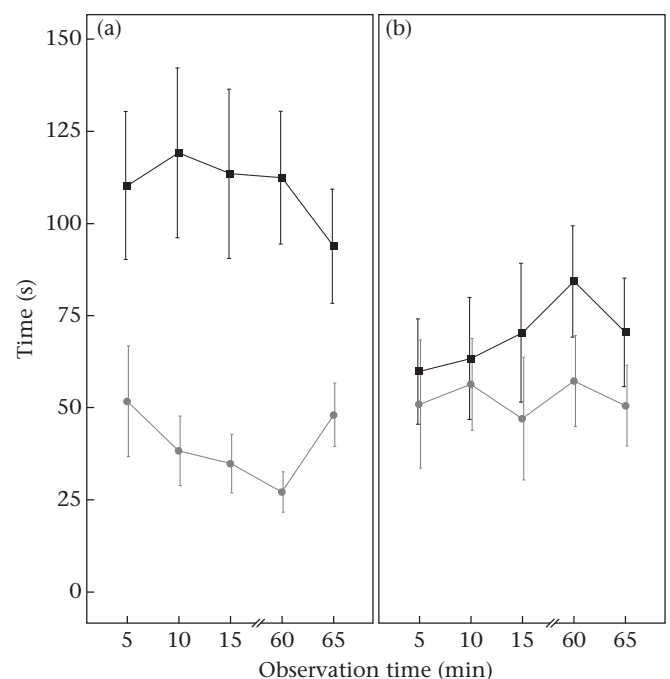

Figure 1. Experiment 1. Mean ± SE time spent (in seconds) in association with the small (circles and grey lines) and large (squares and black lines) stimulus groups in 5 min blocks during the first (0–15 min) and second (60–70 min) observation periods for (a) males and (b) females.

either measure (total activity: $F_{1,38} = 0.05$, $P = 0.83$; activity per fish: $F_{1,38} = 1.29$, $P = 0.26$).

Experiment 2: Join a Small or a Large Group When Rank is Held Constant?

In total, 11 of 12 males and 9 of 12 females preferred the large group (the proportion of males versus females that preferred the large group was similar, Fisher's exact test: $P = 0.59$). Across all individuals, there was a strong preference for the large group (ANOVA: $F_{1,22} = 19.14$, $P < 0.001$; Fig. 2) and this preference was stable over time ($F_{3,66} = 1.54$, $P = 0.21$). The effect of sex was not significant, indicating that males and females spent similar amounts of time associating with the social groups ($F_{1,22} = 0.61$, $P = 0.44$). The sex by group-preference interaction was not significant, indicating that males and females did not differ in their preference for the large group ($F_{1,22} = 1.18$, $P = 0.29$). Their strong preference for large groups was maintained when each sex was examined separately (males: $F_{1,11} = 14.62$; $P = 0.003$, Fig. 2a; females: $F_{1,11} = 5.52$, $P = 0.04$, Fig. 2b).

Males and females did not differ in the number of switches between the choice zones (mean ± SE: males = 8.3 ± 1.8; females = 10.0 ± 1.3; Welch's t test: $t_{20.5} = -0.76$, $P = 0.45$). As in the first experiment, the large stimulus group was more active overall (ANOVA: $F_{1,22} = 20.62$, $P < 0.001$) and the per-individual activity was greater in the small group ($F_{1,22} = 4.52$, $P = 0.045$). Among the stimulus fish, there were no sex differences in activity (total activity: $F_{1,22} = 0.04$, $P = 0.85$; activity per individual fish: $F_{1,22} = 0.743$, $P = 0.40$). There was no difference between the small and large groups in the number of aggressive acts directed towards the focal fish (Wilcoxon signed-ranks test: $Z = 0.00$, $N = 24$, $P = 1.00$) and the overall rates of aggressive behaviour were extremely low (mean ± SE = 0.05 ± 0.01 aggressive acts/min).
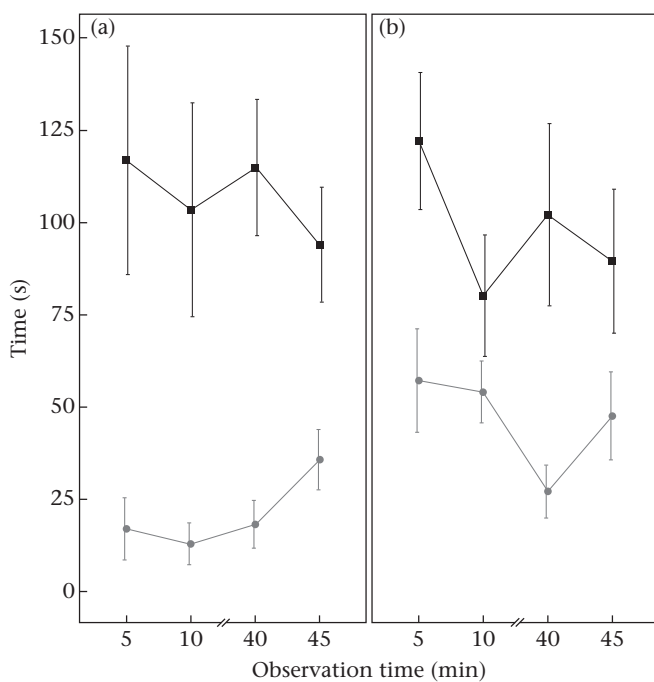

Figure 2. Experiment 2. Mean ± SE time spent in association with the small (circles and grey lines) and large (squares and black lines) stimulus groups in 5 min blocks during the first (0–10 min) and second (40–50 min) observation periods for (a) males and (b) females.

DISCUSSION

Male *N. pulcher* showed a strong and consistent preference for associating with a large group regardless of the rank they would assume when joining that group. Females by contrast, preferred large groups only when they could join that group at a high rank. The sex differences in the preference for large groups in the first experiment did not stem from a general difference in sociability between the sexes as males and females spent a similar amount of time socializing during both experiments. Given the highly social nature of *N. pulcher*, it is not surprising that both sexes preferred to be near conspecifics.

Deciding which group to join is critically important in *N. pulcher* as the social group is organized into a size-based linear dominance hierarchy with the most dominant pair monopolizing reproductive output (Wong & Balshine 2011a). In our first experiment, all of the stimulus fish were larger than the focal fish. Therefore, the focal fish would be in a relatively better social position by affiliating with the single stimulus fish (rank 2) rather than the group of three stimulus fish (rank 4). On the other hand, there is good evidence to suggest that one of the primary benefits of group living in *N. pulcher* is the abatement of predation (Balshine et al. 2001; Heg et al. 2004). By affiliating with a larger group, the focal fish may be choosing greater safety over improved social standing. In a previous study, Jordan et al. (2010a) found that *N. pulcher* preferred to associate with groups that had larger helpers over groups with smaller helpers. By choosing a group with small helpers, the focal fish could have improved its social standing, but groups with large helpers were preferred presumably because these groups provided greater safety from predators. In larger groups, individuals have lower per-individual risk of predation than they do in small groups (Balshine et al. 2001), possibly due to shared vigilance, selfish herd effects, predation risk dilution and/or predator confusion effects (Krause & Ruxton 2002). Alternatively or additionally, larger groups may be better buffered against predation because mutualistic territory defence is more effective in these groups (Krause & Ruxton 2002; Wong & Balshine 2011a). *Neolamprologus pulcher* helpers stage a more vigorous defence against predators than they do against unfamiliar intruding conspecifics (possible joiners and rank competitors) and prioritize defence against predators over defence against conspecific intruders (Desjardins et al. 2008a). Taken together with our results, these findings suggest that *N. pulcher* subordinates, particularly males, may prioritize safety over rank.

Preference for larger groups may also relate directly to the evolution of cooperative breeding in *N. pulcher*. The group augmentation hypothesis predicts that helpers provide help in cooperative breeding systems in order to produce helpers that will assist their own breeding efforts when they eventually assume the breeding position (Woolfenden 1975; Woolfenden & Fitzpatrick 1978; Kokko et al. 2001). If group augmentation is an important force in the evolution of helping behaviour in this species, then *N. pulcher* individuals may prefer to join large groups rather that small ones because large groups are more likely to be large when these joining fish eventually ascend to the breeding position (Kokko et al. 2001). Larger *N. pulcher* groups are more productive than smaller ones, and breeders with more helpers have reduced workloads and increased feeding rates compared to those with fewer helpers (Balshine et al. 2001). Heg et al. (2005) found that territories with large groups in one year continued to contain large groups in the next year, suggesting that large groups are less likely to go extinct (Heg et al. 2005). Future research with marked individuals and territory quality controls would provide further confirmation of this result.

The sex difference we observed in our first experiment could be a result of male-biased dispersal in *N. pulcher* (Stiver et al. 2004,

2006, 2007). Males may be more attuned to assessing group composition because they often leave home and choose a strange group with which to affiliate, so joining is a normal part of male life history and developmental trajectory. In contrast, females rarely join unfamiliar groups, and remain in or near their natal territory; hence, females may not as readily make use of group size cues. However, our second experiment suggests that females do in fact pay attention to cues of group size but are also concerned with their rank when joining a group. When joining rank and group size were in conflict, females showed no clear preference, indicating they may consider both parameters (Wong & Rosenthal 2005). When joining rank was held constant though, females preferred the large group. Female philopatry may have selected females to be more sensitive to their rank position within a group as they lack any alternative route to breeding position. Males by contrast are able to disperse and breed in another group if their current situation is unfavourable upon reaching breeding size.

Male and female *N. pulcher* are equally susceptible to predation (Balshine et al. 2001) and experience similar levels of within-hierarchy conflict (Wong & Balshine 2011b), so differences in predation risk or costs of being subordinate are unlikely to explain the sex difference we observed. Females, being philopatric, may benefit more from group augmentation than do males because they spend a larger portion of their life in the group in which they eventually breed (Kokko et al. 2001). As a result we might expect females to have a stronger preference for large groups; however, we found the opposite, suggesting that sex differences in the benefits of group augmentation do not account for our results. Similarly, there is some evidence that high-ranking male subordinates may be able to secure some reproduction within the group, at least in laboratory settings (Heg et al. 2006). Subordinate reproduction may increase the value of being a high-ranking male subordinate; however, we found that females pay more attention to social rank than males did. Future experimentation is required to conclusively rule out these alternative explanations.

When the importance of dominance rank has been investigated, dominance rank has been shown to affect grouping decisions. For example, Gómez-Laplaza (2005) found that juvenile angelfish, *Pterophyllum scalare*, preferred to associate with socially subordinate individuals from their own shoal. Wong & Rosenthal (2005) found that female swordtails (*Xiphophorus birchmanni* × *Xiphophorus malinche*) preferred to associate with large groups over small groups and with similarly sized individuals over differently sized individuals, but when preferred group size and preferred body size were placed in conflict, swordtails showed no clear choice, suggesting they valued both parameters equally. This result mirrors our findings in females, where conflicting preferences between group size and composition can lead to indecisiveness or individual variation in group-joining preferences. In contrast, Krause & Godin (1994) found that banded killifish, *Fundulus diaphanous*, prefer large to small groups and like-sized individuals to differently sized individuals, but these fish prioritize body size over group size when making grouping decisions. The results of the banded killifish study illustrate that group joiners may differentially value the characteristics of a social group. This may be the case with *N. pulcher* males that appear to place a higher value on group size than on joining rank. Neither swordtails nor banded killifish have rigid dominance hierarchies, and these results together with the current study show that group choice decisions may be handled differently between sexes and across species with different social systems, suggesting that social context plays an important role in group size preferences. The neural basis of group-joining preferences (e.g. neuropeptides in the oxytocin family; Goodson et al. 2009) appears to be highly conserved between taxa (Goodson 2005), and different social

systems may evolve through the modulation of these systems (Goodson 2008).

In conclusion, males and females did not differ in their general preference to be near conspecifics, suggesting that the sex differences in grouping decisions are not due to sex differences in desire to be near conspecifics. Males appear to base group-joining decisions on concerns for safety rather than social position, whereas females seem to consider both rank and safety. Females may be more sensitive to concerns over their rank because they typically inherit a dominance position and have less opportunity to pursue alternative options. Future research should examine how cues of predation risk affect group-joining decisions. If grouping is primarily an antipredator response, then predation risk cues should increase preference for large groups. Ultimately, the structure of the group is modulated by the preferences of both joining and current members (Jordan et al. 2010b). Investigating how individuals within a group make the decision to admit new members would nicely complement our current study and would be a productive avenue for future research.

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