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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.

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 ± 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