Fight for your breeding right: hierarchy re-establishment predicts aggression in a social queue

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Social aggression is one of the most conspicuous features of animal societies, yet little is known about the causes of individual variation in aggression within social hierarchies. Recent theory suggests that when individuals form queues for breeding, variation in social aggression by non-breeding group members is related to their probability of inheriting breeding status. However, levels of aggression could also vary as a temporary response to changes in the hierarchy, with individuals becoming more aggressive as they ascend in rank, in order to re-establish dominance relationships. Using the group-living fish, *Neolamprologus pulcher*, we show that subordinates became more aggressive after they ascended in rank. Female ascenders exhibited more rapid increases in aggression than males, and the increased aggression was primarily directed towards group members of adjacent rather than non-adjacent rank, suggesting that social aggression was related to conflict over rank. Elevated aggression by ascenders was not sustained over time, there was no relationship between rank and aggression in stable groups, and aggression given by ascenders was not sex-biased. Together, these results suggest that the need to re-establish dominance relationships following rank ascension is an important determinant of variation in aggression in animal societies.

Keywords: aggression; dominance hierarchy; conflict over rank; *Neolamprologus pulcher*

1. INTRODUCTION

Social aggression between group members is a universal characteristic of animal societies. A key hurdle to understanding social aggression within dominance hierarchies lies in answering two questions: (i) why are individuals aggressive? and (ii) what are the causes of inter-individual variation in aggression? In many animal societies, dominants and subordinates both reproduce—under these circumstances, aggression has been linked to conflict over the division of immediate direct reproduction [1]. However, in societies where subordinates are non-reproductive and queue to inherit breeding status, the function of

aggression and causes of its variation remain unclear. Recent theory suggests that social aggression represents an underlying conflict over rank between group members, and inter-individual variation in low-level aggression reflects variation in the probability of inheriting breeding status [2]. Specifically, individuals are expected to become more aggressive as they ascend in rank and approach the front of the queue, since the profitability of investing in aggressive dominance testing and deterrent displays increases with an individual's expectation of future fitness ([2]; here termed the 'future fitness hypothesis').

Levels of aggression may also increase upon rank ascension because individuals use aggression to re-establish dominance relationships after they have been promoted in rank (here termed the 'hierarchy re-establishment hypothesis'). Specifically, the death or disappearance of dominants is expected to trigger a temporary spike in aggression as newly promoted individuals re-establish their rank positions within the group [3,4]. Like the future fitness hypothesis, conflict over rank is still the underlying reason for aggression under the hierarchy re-establishment hypothesis, since the motivator for aggression is the consolidation of rank positions within the hierarchy. Unlike the future fitness hypothesis, levels of aggression are expected to decline back to previous levels once dominance relationships have been reinforced [4]. Both hypotheses are not mutually exclusive despite generating different predictions about aggression following rank ascension.

Here, we address the function and causes of variation in social aggression using the group-living cichlid fish, *Neolamprologus pulcher*. This species provides a useful model with which to investigate patterns of aggression within hierarchies. Groups comprise two breeders and 0–20 subordinate helpers of both sexes, with helpers organized into a size-based dominance hierarchy in which there is conflict over rank ([5]; see electronic supplementary material). Subordinate helpers achieve breeding status by queueing to inherit the breeding position (mainly female helpers) or dispersing to take over elsewhere (mainly male helpers; [6]). First, we determined whether aggression is related to conflict over rank. If so, we predicted that: (i) ascending helpers should become increasingly aggressive towards adjacent rather than non-adjacent ranked group members, because conflict over rank is the greatest among adjacent ranks and (ii) female ascenders should exhibit more aggression than males because the female route to reproduction depends more on position in the queue. Second, we tested whether variation in aggression owing to conflict over rank is better explained by the future fitness or hierarchy re-establishment hypotheses. The future fitness hypothesis would predict: (i) a positive correlation between helper dominance rank and aggression, (ii) increased aggression after rank ascension that remains elevated over time, and (iii) increased aggression towards same-sex group members following rank ascension. In contrast, the hierarchy re-establishment hypothesis would predict: (i) no correlation between helper dominance rank and aggression, (ii) a temporary spike in aggression after rank ascension that declines over time, and (iii) no sex-bias in aggression following rank ascension.

2. MATERIAL AND METHODS

The investigation was conducted between February 2008 and April 2010 using a colony of *N. pulcher* housed at McMaster University, Canada. All fish used were F1 or F2 progeny originating from wild-caught breeders collected from Lake Tanganyika, Zambia. A total of 38 social groups was used for the experiment, each comprising a breeding pair plus 3–12 helpers. Before manipulations, each group member was tagged, sexed, measured and placed back with its original group. Dominance rank of helpers was assigned based on body size and behavioural differences. Eighteen groups were randomly allocated to the 'ascending' treatment, and 20 groups allocated to the 'non-ascending' treatment. One helper per group was chosen as the focal helper if it was larger than 3.5 cm (to ensure reproductive capacity, [7]) and subordinate to at least one other same-sex helper within their group. On day 1 (before removal), focal helpers were observed for 10 min between 08.00 h and 17.00 h during which time the frequencies of aggressive acts were recorded (see electronic supplementary material). Following behavioural observations, the more dominant, same-sex helper was caught and permanently removed from groups in the ascending treatment, and caught but re-released immediately from groups in the non-ascending treatment. Therefore, the focal helper (and all others subordinate to the removed individual) ascended in rank in the ascending treatment but did not actually acquire breeding status. On days 2 and 12 (i.e. 1 and 11 days post-removal), behavioural watches of focal helpers in both the ascending and non-ascending treatments were repeated as for day 1 to document any changes in the aggressive behaviours of focal helpers.

To determine whether dominance rank and aggression were correlated, a linear regression between helper rank and the frequency of aggression given was performed using data from stable groups only (i.e. from non-ascending and ascending treatment groups on day 1). To analyse the effects of rank ascension on aggression over time, the change in frequency of aggression by ascending and non-ascending helpers was calculated for day 2 (= frequency of aggression on day 2 − day 1) and for day 12 (= frequency of aggression on day 12 − day 1). General linear models were then used to assess the effect of treatment, helper body size, sex, initial rank and group size on change in aggression (see electronic supplementary material). χ^2 tests were used to investigate any changes in the relative frequency of aggression directed towards different group members before (day 1) versus after (days 2 and 12) ascension.

3. RESULTS

There was no significant correlation between levels of aggression given and the dominance rank of helpers in stable groups (linear regression: $r = 0.045$, $n = 38$, $p = 0.789$; figure 1a), nor when males and females were considered separately (males: $r = 0.264$, $n = 25$, $p = 0.202$; females: $r = -0.209$, $n = 18$, $p = 0.492$).

Ascending helpers were more aggressive than non-ascending helpers by day 2 (GLM: treatment, $F_{1,30} = 8.0$, $p = 0.008$; figure 1b). Aggression was unaffected by helper body size ($F_{1,30} = 0.2$, $p = 0.66$), group size ($F_{1,30} = 1.97$, $p = 0.17$) or helper rank ($F_{1,30} = 1.02$, $p = 0.32$). The increased aggressiveness of ascenders on day 2 was driven by an increase in aggression by female rather than male helpers (treatment × sex, $F_{1,30} = 5.59$, $p = 0.025$; figure 2a). Ascenders became more aggressive towards group members adjacent in rank (immediately above or below them in the dominance hierarchy), rather than to group members of non-adjacent rank (two or more ranks above or below them; $\chi_1^2 = 3.93$, $n = 38$, $p = 0.047$). There was no difference in aggression directed towards adjacent dominants versus adjacent subordinates ($\chi_1^2 = 0.21$, $p = 0.64$). Ascenders did not direct more aggression towards same-sex group members ($\chi_1^2 = 0.73$, $p = 0.39$).

Ascenders remained more aggressive than non-ascenders on day 12 (GLM: treatment, $F_{1,25} = 4.62$, $p = 0.041$; figure 1b). In contrast to day 2, the high
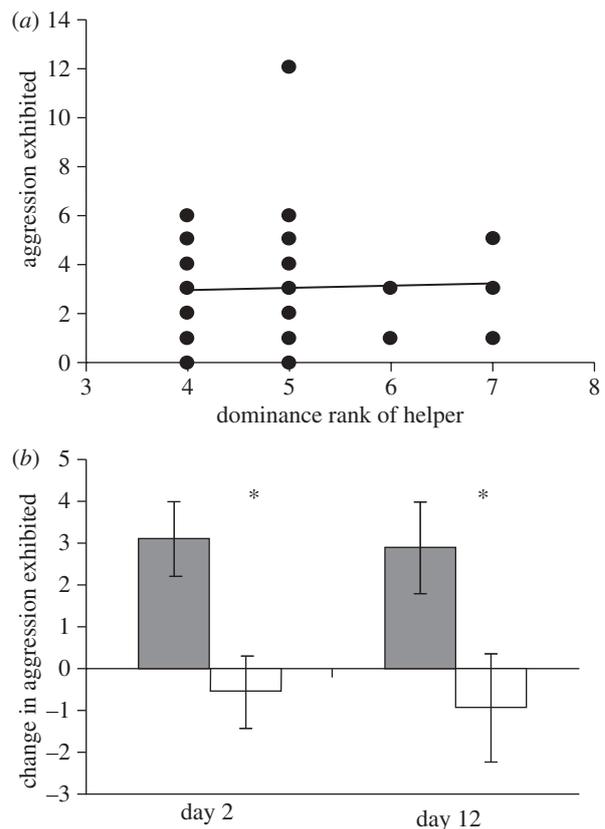

Figure 1. (a) Aggression exhibited (per 10 min) in relation to dominance rank of focal helpers within stable groups. Solid line represents a linear regression of aggression on dominance rank ($y = 2.44 + 0.115x$). (b) Change in aggression exhibited by ascenders (grey) and non-ascenders (white). Change in aggression exhibited by day 2 and day 12 is expressed as the frequency of aggression on these days minus frequency of aggression on day 1. Plotted are least-square means ± s.e. Asterisks represent a significant difference between helpers in ascending versus non-ascending treatments.

levels of aggression by ascenders was driven by an increase in aggression by male rather than female helpers (sex, $F_{1,25} = 4.77$, $p = 0.038$; figure 2b). To assess whether male helpers would have sustained these increased levels of aggression, we compared levels of aggression by male and female helpers in stable groups (i.e. from non-ascending and ascending treatment groups on day 1). Males were not more aggressive than females overall (Mann–Whitney U test: $Z = 0.3$, $p = 0.76$), suggesting that the elevated levels of aggression by male helpers was not likely to be sustained. Ascenders remained more aggressive towards adjacent rather than non-adjacent ranked group members on day 12 ($\chi_1^2 = 5.77$, $n = 32$, $p = 0.02$), and were equally aggressive towards adjacent dominants and adjacent subordinates ($\chi_1^2 = 0.17$, $p = 0.68$). As on day 2, ascenders did not direct more aggression towards same-sex group members ($\chi_1^2 = 0.813$, $p = 0.37$).

4. DISCUSSION

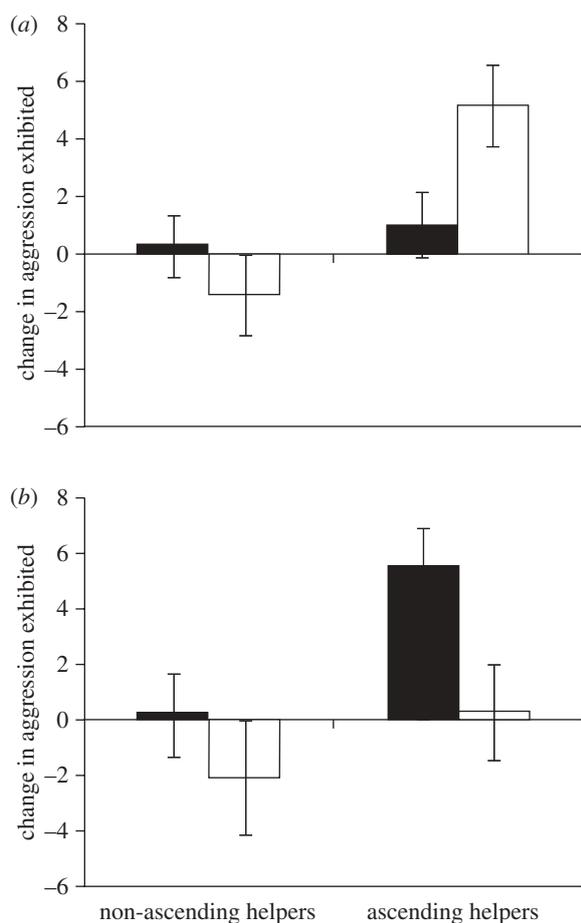Explaining why non-breeding group members are aggressive and why levels of aggression vary is central

Figure 2. Change in aggression exhibited by male (black bars) and female helpers (white bars) in non-ascending and ascending treatments by (*a*) day 2 and (*b*) day 12. Change in behaviour is expressed as: frequency of aggression on day 2 or day 12 minus frequency of aggression on day 1. Plotted are least-square means $\pm$ s.e.

to understanding the nature of underlying conflicts within social groups. Here, we show that aggression by ascending helpers was primarily directed towards adjacent ranks, suggesting that conflict over rank promotes social aggression in *N. pulcher*. We had also expected that females, being the queueing sex, would exhibit more aggression in response to ascension than males, being the dispersing sex, if conflict over rank promoted aggression. However, we found that both males and females became more aggressive after rank ascension, but the response was more immediate for females than males. This suggests that both sexes experienced conflict over rank, but that females were more sensitive to changes in rank position than males and thus responded to rank ascension more rapidly. Further work determining which aspects of rank conflict promote aggression in males and females, and the timeline over which such aggression occurs, would therefore be enlightening.

The fact that female helper aggression spiked on day 2 and then declined supports the hierarchy re-establishment hypothesis. Although it is not known whether the increased aggression by male ascenders on day 12 eventually subsided, the fact that

aggression levels of males and females in stable groups did not differ suggests that aggression in males would also have declined back to pre-ascension levels. Further support for the hierarchy re-establishment hypothesis comes from the lack of relationship between dominant rank and aggression in stable groups, and lack of sex-bias in aggression given by ascenders. Thus, following rank ascension, individuals are likely to become more aggressive as a means of re-establishing their rank position following disruption of the hierarchy. Our study therefore builds on an existing body of empirical research that investigates the influence of hierarchical disruption and re-establishment on changes in agonistic behaviour (e.g. [8–10]), by demonstrating that one of the fitness consequences of such changes in behaviour is the maintenance of social rank within a breeding queue.

Why the future fitness hypothesis does not explain patterns of aggression in *N. pulcher* may rest on its emphasis on the benefits individuals attain from increasing and maintaining elevated levels of aggression as they approach the front of the queue. It is possible that the costs of doing so may prohibit the maintenance of high aggression levels, and this possibility should be addressed in future studies. Finally, future research comparing the aggressive responses of all group members ranked below and above the removed individual would be useful for examining within-hierarchy variation in aggressive responses to rank ascension and their associated fitness consequences in animal societies.

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