

Sex differences in the effect of social status on the growth of subordinates in a co-operatively breeding cichlid

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Social influences on the growth of the co-operatively breeding cichlid *Neolamprologus pulcher* were studied by examining the size structure of existing laboratory groups and the responses of males and females to removals of higher-ranked fish, which created larger size differences with more dominant fish. The size differences between adjacently ranked group members were predicted to differ from expected based on random size distributions of group members. Both males and females were predicted to respond to removals by increasing growth rate. In previously established groups, the size difference between dominant and highest-ranked subordinate males was greater than expected based on random group-assembly rules. The size difference between dominant and subordinate females did not differ from the null expectation. Third-ranked subordinate males increased their growth rate upon moving up one place in the dominance hierarchy (after the removal of higher-ranking fish) relative to fish that did not change rank. Contrary to predictions, however, females did not increase growth upon increasing rank.

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INTRODUCTION

In many dominance-structured groups, the growth of previously subordinate group members increases with attainment of the dominant, breeding position, e.g. meerkats *Suricata suricatta* (Schreber) (Russell *et al.*, 2004), limpets *Crepidula norrisiarum* (Williamson) and *Crepidula fornicata* L. (Collin, 1995; Warner *et al.*, 1996) anemonefish *Amphiprion percula* (Lacepede) (Buston, 2003) and several species of cichlids *Neolamprologus pulcher* (Trewavas & Poll) and *Neolamprologus brichardi* (Poll) (Taborsky, 1984; Heg *et al.*, 2004) and *Haplochromis burtoni* (Gunther) transitioning from non-territorial to territorial status (Hofmann *et al.*, 1999), a phenomenon which has been referred to as ‘status dependent growth’ (Heg *et al.*, 2004). Growth rates may change as newly

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dominant individuals gain access to hitherto unavailable resources or increase in size to better defend territories or attract mates. Recently, it has been proposed that the relatively slow growth of subordinate group members is a strategic response to conflict with higher-ranked group members (Taborsky, 1984; Buston, 2003; Heg *et al.*, 2004; Wong *et al.*, 2007), so that rapid growth after attaining dominant position is at least in part a response to release from this conflict. This 'strategic growth' hypothesis (Buston, 2003; Heg *et al.*, 2004) predicts that growth of low-ranking individuals in groups is lower than expected based on food availability and initial size, and that growth of the lower-ranked individual is positively correlated with the size difference between adjacently ranks. In several species of fishes, growth is positively correlated with the size difference with the next highest-ranked individual, *e.g.* anemonefish (Buston, 2003), cichlids (Heg *et al.*, 2004) and gobies (Wong *et al.*, 2007), consistent with these predictions. Socially influenced growth regulation or strategic growth has been implicated as an important influence on group size and structure in group-living fishes, *e.g.* *Amphiprion ocellaris* Cuvier (Mitchell & Dill, 2005), *A. percula* (Buston & Cant, 2006), *Paragobiodon xanthosomus* (Bleeker) (Wong *et al.*, 2007) and *Gobiodon histrio* (Valenciennes) (Munday *et al.*, 2006), leading to size-structured queues and setting a maximum limit to group size.

Socially influenced growth restriction or strategic growth may arise through direct dominant suppression of growth or subordinate self-inhibition, as a response to the threat of dominant 'punishment' that allows subordinates to avoid risking injury or expulsion. Direct suppression of growth or expulsion of larger helpers are self-serving punishments (Cant & Johnstone, 2006), because it is in the interest of dominant group members to remove costly subordinates. Self-inhibition of growth is analogous to reproductive restraint (Johnstone & Cant, 1999; Hamilton, 2004) and paying-to-stay (Kokko *et al.*, 2002; Hamilton & Taborsky, 2005), in which costly co-operation evolves in response to punishment. By analogy to these other forms of coerced co-operation, the probable occurrence of subordinate growth restriction can be predicted. Both self-serving punishment and a co-operative response require that subordinates are costly in some way to dominants [as in pay-to-stay models (Kokko *et al.*, 2002; Hamilton & Taborsky, 2005) and in self-serving punishment (Cant & Johnstone, 2006)]. If punishment and restraint are based on relative size, then these costs must be size dependent. Dominant individuals must also have to power to detect costs and impose punishment (Hamilton, 2004). Finally, multiple mechanisms may resolve size related conflict, so the net payoffs of imposing punishment and restricting growth alone or in combination with other mechanisms must exceed those of exclusively using alternative mechanisms such as helping or leaving the group.

In this study, the influence of social status on the growth of a co-operatively breeding cichlid *N. pulcher* (sister species of, or conspecific with *N. brichardi*; Taborsky & Grantner, 1998) was examined. Previously, subordinate male helpers were found to grow faster in standard length (L_S), but not mass, when they were in a group with a large dominant male than when with a small dominant male (Heg *et al.*, 2004). The aims of this study were to examine the effects of social status on size-based hierarchy structure in unmanipulated laboratory groups, to confirm the effects of increasing the size difference between

dominant and subordinate fish on subordinate growth by removing individuals from the hierarchy and to investigate whether social status also influenced growth in females. Because attainment of dominant status is associated with changes in growth (Heg *et al.*, 2004), second-ranked fish (*i.e.* large subordinates) were removed, and the growth rates of fish transitioning from third to second rank were compared with those that remained in second and third rank, so that all fish retained subordinate status. Based on the strategic growth hypothesis, the size differences between adjacently ranked individuals were predicted to differ from those under random group assembly rules (Buston & Cant, 2006) and the removal of higher-ranked fish was predicted to lead to more rapid growth of lower-ranked ones.

Subordinate females were also predicted to show strategic growth. Subordinate female *N. pulcher* are costly to dominant females in at least two ways. The growth of dominant females is reduced when subordinate female helpers are present (unpubl. data). Although successful reproduction by subordinate females is rare (Dierkes *et al.*, 1999; Dierkes *et al.*, 2005; Heg *et al.*, 2006), breeding attempts by subordinates are accompanied by a loss of alloparental care of the offspring of dominants when subordinate females use and defend different breeding shelters than the dominant female (unpubl. data). These costs may be related to size. Use and defence of a different breeding shelter is more likely when subordinate females are relatively large compared to (but still smaller than) dominant females (unpubl. data). Size may also be a better cue of reproductive competition in females than in males. In female fish, body size and fecundity are usually closely linked, while in males, smaller individuals may allocate resources to gonads rather than growth, allowing successful parasitic spawning, although Fitzpatrick *et al.* (2006) found evidence of suppression of gonadal development in male subordinate fish. The benefits of remaining in the group are also high for females. In *N. pulcher* females may inherit their natal territory, while males rarely, if ever, inherit (Balshine-Earn *et al.*, 1998; Dierkes *et al.*, 2005).

MATERIALS AND METHODS

Twenty-nine previously established laboratory groups of *N. pulcher* were used in April to July 2004. All groups were maintained in 100 l or one half of 200 l tanks at the Ethologische Station Hasli (Hinterkappelen, Switzerland), under a 13L:11D cycle. Water temperature was monitored at 1200 hours each day and varied from 24.5 to 28.3° C. Water biochemical variables were kept similar to Lake Tanganyika. Groups were fed *ad libitum* (two feedings per day; 5 days TetraMin, 2 days fresh food with *Artemia* spp., *Daphnia* spp. and mosquito larvae each week). All tanks were filled to *c.* 30 mm with sand (1 mm grain size) and equipped with filter, airstone and two breeding shelters, consisting of bottomless flowerpot halves.

EXISTING SIZE DIFFERENCES

Groups were established >1 year previous to the observation period, and ranged in size from two to 14 individuals >15 mm standard length (L_S). At the start of the observation period, L_S and mass (M) of every fish in pre-existing groups were measured. Length was measured twice and averaged. Fish were also marked with dorsal fin clips to assist in identification.

To test whether the size difference between adjacently ranked individuals of the same sex differed from that expected under the null hypothesis of random group assembly, the following Monte-Carlo procedure was used (Buston & Cant, 2006). Length measurements for all individuals in question (*e.g.* all dominant females and largest female helpers prior to any removal or manipulation for that comparison) were pooled and random pairs selected from that pool. The largest individual in the pair was designated as the top-ranked individual (*i.e.* in the above example, the dominant), the smaller as the second-ranked individual (*i.e.* in the above example, the helper), regardless of their actual status. The size ratio for each new group and the median size ratio for all newly created groups were determined. The median size ratio of observed groups was compared against the distribution of median size ratios generated by 500 randomization trials. Restricting data to the relevant focal ranks (*i.e.* using only fish ranked first and second in their existing groups in the above example) allowed the examination of whether observed size ratios between particular ranks differed from expected, controlling for other rank-related effects on size. Medians were used to avoid making assumptions about the distribution of size ratios in the population. Other methods of generating the null distribution of size ratios could also be used (Buston & Cant, 2006). Extensive preliminary modelling, however, supported the use of the method presented here, which consistently correctly classified rank-specific size ratios in simulated data sets as random or non-random (unpubl. data). Separate comparisons were performed for each of: first- and second-ranked females, first- and second-ranked males, second- and third-ranked females and second- and third-ranked males.

REMOVAL EXPERIMENT

Ten second-ranked fish of one sex were removed from 10 pre-existing tanks (five females and five males). One second-ranked male died in a tank in which removal of a female fish had occurred early in the experiment, and was also considered a 'male removal'. No fish were removed in another 12 tanks for comparison. Removed fish did not differ significantly in L_S from retained fish of the same sex and rank (ANOVA, F , d.f. = 1, 32, $P > 0.05$). The growth of the fish immediately below the removed fish in the hierarchy (*i.e.* fish that moved from rank 3 to rank 2) was compared with the growth of fish that remained in rank 2 and those that remained in rank 3 with a mixed model general linear model (GLM) in SPSS 14.0. Group was included in the model as a random variable, with removal treatment (change rank, remain at rank 2, remain at rank 3) and sex, and the interaction between sex and treatment as fixed effects. The dependent variable was change in L_S or M per day⁻¹. Initial L_S or M was included in the model as a covariate. This is equivalent to using change in size per initial size but avoids the use of ratios. Other possible comparisons (controlling for initial rank by using fish that changed rank *v.* fish remaining in rank 3 only; controlling for changes in group size by limiting comparisons to only those groups in which a fish was removed; not including the dead male) yielded the same qualitative results as the final model, but were limited by small sample sizes.

To increase sample size, a similar analysis was performed, including data from a second period of 30 days, during which two females and three males of second rank died in groups in which no removals had occurred previously. These were treated as removals. Data were also included from this second period for males and females in remaining tanks if the second-ranked fish of that sex had not been removed in the first period. This added five groups in which removal occurred and 16 groups in which removal did not. In all analyses, sequence (first or second 30 day period) was added as a main effect; group and interactions between group and main effects were retained as a random effect in the models to account for multiple observations of the same groups. Tanks in which mortality occurred may have differed from those in which it did not and sample sizes for removals and intact groups differed greatly in the second sequence; therefore, both these results and the more conservative results for removals in the first sequence as described above are presented.

ETHICAL NOTE

Removed fish were placed in 'aggregation' tanks, in which breeding substratum was not provided and fish did not defend territories. Therefore, these fish did not experience aggressive reactions from other fish in these tanks. In experimental tanks, opaque plastic tubes located near the water surface were provided as shelters for subordinate fish, so that they could avoid escalated aggression from other group members. During the second sequence, a number of subordinate fish died and one fish died in the first sequence. With the exception of the fish in the first sequence, mortality occurred exclusively in tanks which had not experienced removals, suggesting that it was not the manipulation that caused mortality of fish. Injured fish, including those that eventually died, were isolated from other group members in small nets within their group tank to avoid further injury from group-mates. The experiment was approved by the Swiss Federal Veterinary Office (Department of Economic Affairs).

RESULTS

SIZE STRUCTURE IN EXISTING GROUPS

In pre-existing laboratory groups, the size ratios of top-ranked (dominant or breeding) and second-ranked (largest helper) females and of second- and third-ranked females prior to any manipulation of group structure did not differ significantly from those expected if females were assigned randomly to groups [Fig. 1(a), (b)]. The size ratio of first- and second-ranked males, however, was significantly larger than expected [Fig. 1(c)]. The size ratio of second- and third-ranked males did not differ significantly from that expected by chance [Fig. 1(d)].

REMOVALS AND GROWTH

In the removal comparison, there was a marginally significant interaction between sex and status change on change in L_S , adjusted for initial L_S (Table I). For females, fish changing status from rank 3 to rank 2 grew less than did fish that remained in rank 2 or rank 3. For males, fish changing status grew more than fish that did not change status (Fig. 2). There was a similar tendency for M , although the effect of the interaction between sex and status change was not significant.

Adding data from the second sequence, fish that increased in rank because of removal and those that increased because of death of a higher-ranked fish did not differ in growth (ANOVA, both L_F and M : F , d.f. = 1, 12, $P > 0.05$). Comparing the growth of fish that changed rank *v.* those that did not, the sex by status change interaction remained significant for L_S (mixed model GLM, F , d.f. = 2, 77.50, $P < 0.05$) and was also significant for changes in M (mixed model GLM, F , d.f. = 2, 61.25, $P < 0.05$). The main effects of sex, sequence and status change did not significantly influence change in L_S (mixed model GLM, sex: F , d.f. = 1, 78.50, $P > 0.05$; sequence: F , d.f. = 1, 67.52, $P > 0.05$; status change: F , d.f. = 2, 52.35, $P > 0.05$) or M (sex: F , d.f. = 1, 68.53, $P > 0.05$; sequence: F , d.f. = 1, 25.21, $P > 0.05$; status change: F , d.f. = 2, 34.08, $P > 0.05$). A non-significant effect of the interaction between sex and sequence on change in L_S was retained in the final model (F , d.f. = 2, 71.79,

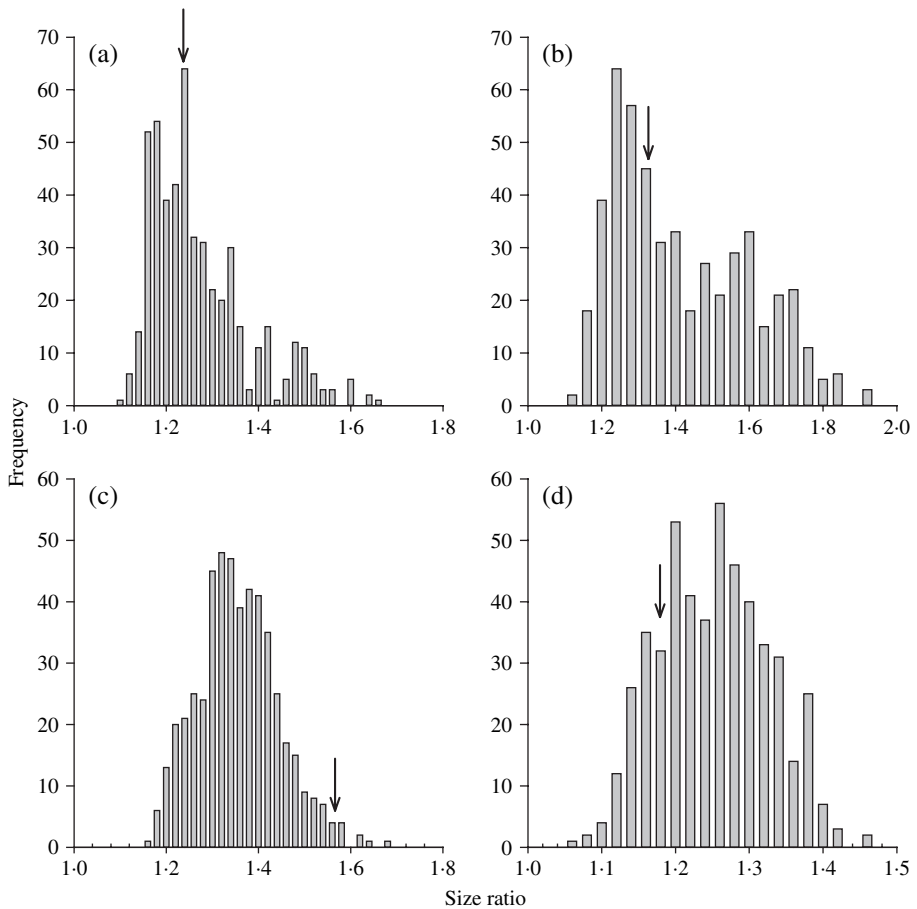


FIG. 1. Expected frequency distributions of median size ratios under random group assembly rules ($n = 29$). Results are for 500 randomly generated populations. (a) First- and second-ranked females (probability that observed ratio = expected: $P > 0.5$), (b) second- and third-ranked females ($P > 0.5$), (c) first- and second-ranked males ($P < 0.05$) and (d) second- and third-ranked males ($P > 0.05$). ↓ the observed median size ratio in the population in pre-existing tanks.

$P > 0.05$), in which females grew faster than males in the first sequence, but grew more slowly than males in the second sequence.

DISCUSSION

Male and female *N. pulcher* differed in the initial size structure of their dominance hierarchies and in their responses to manipulation of this structure. At the start of the measurement period, the median size ratio between dominants and the largest helpers was greater than expected for males, but did not differ from expected for females. Size differences between second- and third-ranked fish did not differ from expected for both sexes. Males responded to a removal of more dominant fish by growing more quickly, while females did not. Although sample sizes were small, there was a marginally significant interaction

TABLE I. Factors in the final general linear models that influenced change of standard length (L_S) and mass (M) of second- and third-ranked subordinate males and females used in the removal comparison ($n = 23$). Three levels of status change are possible: remaining at rank 2, changing from rank 3 to rank 2 and remaining at rank 3

Source*	L_S				M^\dagger			
	F	d.f. _{num}	d.f. _{denom}	P	F	d.f. _{num}	d.f. _{denom}	P
Sex	1.66	1	25.73	>0.05	0.01	1	30.94	>0.05
Status change	0.27	2	28.09	>0.05	0.39	2	27.28	>0.05
Sex \times status change	3.38	2	25.10	0.05	2.84	2	27.28	>0.05
Initial L_S	9.42	1	35.92	<0.01				

*Group \times sex also included as a random variable in all models.

†Initial M removed from final model to improve AIC value. Inclusion does not change qualitative results or significance.

between sex and the effects of social status on growth. Females not only differed from males in the effects of removals on growth, but tended to grow more slowly when a higher-ranked fish was removed, which was the opposite direction from that predicted and from that observed in males. Including removals due to natural mortality during a subsequent observation period did not change qualitative results, and the effect of the interaction between sex and treatment on growth remained significant. Growth did not differ between tanks from which fish were removed and those in which a fish died. Together, these results indicate that change in social status has little effect on growth of subordinate females, but does influence the growth of males, consistent with previous experiments (Heg *et al.*, 2004). These results are also consistent with observations of multiple breeding females in naturally occurring groups of *N. brichardi* and *N. pulcher* (Limberger, 1983).

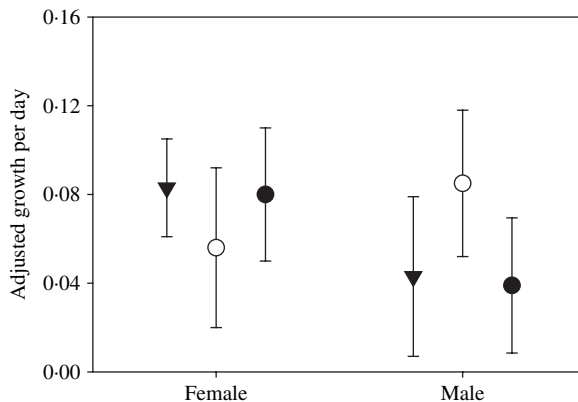


FIG. 2. Effects of sex and removals of second-ranked fish on the growth rate of second- and third-ranked *Neolamprologus pulcher* ($n = 29$). Results are adjusted means \pm 95% CL from a mixed general linear model incorporating sex and status change as fixed effects, initial standard length as a covariate and group by sex as a random effect. ○, Fish that changed rank from third to second upon removal of the previous second-ranked fish; ▼, ●, fish that did not change rank: ▼, fish that remained at second rank throughout the experiment and ●, fish that remained at third rank.

Based on restraint and payment models of co-operation, there are several potential explanations for the lack of social growth restriction in females. It is unlikely that subordinate females benefit less from grouping than do males, because females are more likely to inherit group territories (Balshine-Earn *et al.*, 1998; Dierkes *et al.*, 2005). In other studies, subordinate females impose apparent costs on dominant females and these costs are size related (unpubl. data). The net inclusive fitness costs of subordinate female presence on dominant females, however, may be low because of higher average relatedness among females (Dierkes *et al.*, 2005; Stiver *et al.*, 2005) and low costs of sharing male parental care (such as defence against egg predators and other intruders; Taborsky *et al.*, 1986). Additionally, the costs of suppressing or restraining growth may be high relative to other mechanisms of conflict resolution. Dominant females can directly control subordinate reproduction by eating eggs (unpubl. data). For subordinates, a number of other mechanisms may resolve conflicts, including helping (Bergmüller & Taborsky, 2005; Bergmüller *et al.*, 2005a), submissive behaviour and avoidance (Hamilton *et al.*, 2005), although these are also available to and used by males which do show growth restriction. Finally, anecdotal evidence suggests that dominant females may lack the power to impose costs on subordinate females. Males, who presumably benefit from the presence of several large, potentially reproductive females in the group, interfere in conflict between females over egg laying (pers. obs.) and such male 'peacekeeping' has been observed in other lamprologine cichlids, *e.g.* *Neolamprologus multifasciatus* (Boulenger) (Schradin & Lamprecht, 2000) and *Lamprologus ocellatus* (Steindachner) (Walter & Trillmich, 1994). Without further experiments, it is not possible to distinguish among these effects.

An alternative interpretation of these results is that females that move into second rank reduce their growth rate in anticipation of either future reproduction (for example, because of allocation to gonadal development) or the onset of dominant punishment (as expected under the strategic growth hypothesis). This is supported by the finding that the growth rate of transitioning females was lower than that of stationary females. The present results from existing groups, however, contradict this hypothesis. Gaps between dominant and second-ranked females and between second- and third-ranked females did not differ from expected values. If females slow down growth upon attaining second rank, regardless of the pre-existing size difference, the size difference between first- and second-ranked females should be large while that between second- and third-ranked females should be small, a pattern that was evident in males but not females.

Larger than expected size ratios were only found in males when comparing top-ranked (breeding) individuals with the largest helpers. Conflict between breeding males and large helping males is expected to be high. Large helpers and dominant males may compete for dominant position and reproductive opportunities. As well, dominant males may gain from rapid growth irrespective of the presence and size of helpers, such that the large size gap between dominant males and the largest male helpers may result from both reduced growth of subordinates and enhanced growth of dominant males. The results of this and previous experiments (Heg *et al.*, 2004; Hamilton *et al.*, 2005), indicate that the size and presence of more dominant fish do influence the growth and

behaviour of subordinate ones. Previous experiments, however, have shown status dependent growth in *N. pulcher* and *N. brichardi*, with a substantial increase in growth rate upon achieving breeding position (Taborsky, 1984; Heg *et al.*, 2004).

In *A. percula* and *A. ocellaris* and the coral-dwelling *P. xanthosomus*, size gaps are larger than expected throughout the dominance hierarchy with the exception of new arrivals, and queues are structured so that larger gaps than expected exist between all ranks (Buston, 2003; Mitchell & Dill, 2005; Buston & Cant, 2006; Wong *et al.*, 2007). This size structure appears to be maintained through growth modification rather than emigration. Such size structure may influence group size in *A. percula* and *A. ocellaris*, as the size of gaps sets a maximum boundary on the number of individuals that can fit below the breeding pair while maintaining minimum size ratios (Mitchell & Dill, 2005; Buston & Cant, 2006). While dominant male size limits the size of immediately subordinate males in *N. pulcher*, the size of subordinate females and lower-ranked subordinate males is less influenced by the size of dominant individuals. Thus, growth modification would be expected to have less influence on group size and overall group structure than in *A. percula* or *P. xanthosomus* (Mitchell & Dill, 2005; Buston & Cant, 2006; Wong *et al.*, 2007). In a laboratory setting, however, fish are unable to leave the group. Stronger size structuring may develop in groups when emigration is possible because of movement of individuals from and between groups (Bergmüller *et al.*, 2005*b*).

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