

# Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid

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## Summary

In size-structured groups, conflict over rank, resources or access to breeding opportunities is expected to be greatest among individuals that are similar in size. We tested this general prediction using the cooperatively breeding African cichlid, *Neolamprologus pulcher*. We predicted that, when size differences between group members were small, we would observe some or all of: increased aggression, increased submissive behaviour, increased help by subordinates or avoidance of dominants by subordinates. We created standardised groups each with a breeder male and female and a large and small helper (both males). The size of all group members was kept constant, with the exception of the breeder males, which were either only slightly larger than the largest helper or much larger. This created either large or small size differences between breeder males and the large helper (the 2<sup>nd</sup> ranked male in the group). We found that large helpers showed more submissive behaviours, reduced affiliative behaviour and kept further from breeding sites when male breeders were small. We did not find a consistent influence of breeder size on aggression. Together, these results support the prediction that conflict between breeder and helper is increased when breeders are small, but that this conflict is expressed through changes in submissive and affiliative behaviours and in space use rather than aggression. In contrast to our predictions, large helpers increased helping (territorial defence) when the male breeder was large; the reasons for this are unclear.

**Keywords:** dominance hierarchy, cooperative breeding, Cichlidae, aggression, size asymmetry.

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## Introduction

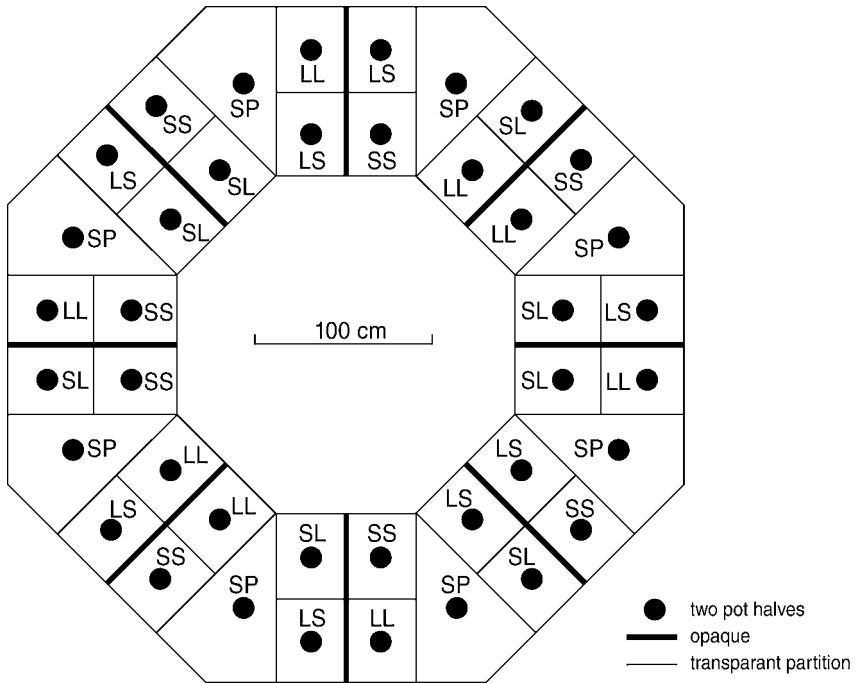
Group living can provide benefits such as reduced risk of predation (e.g., Pitcher & Parrish 1993; Roberts 1996), increased foraging efficiency (e.g., Pitcher et al., 1982; Packer & Ruttan, 1988), decreased costs of defence against intruders (Strassman et al., 1988) and, in cooperatively breeding species, increased help raising offspring (e.g., Taborsky 1984; Koenig & Dickinson 2004). However, group members compete with one another, and may come into conflict over rank, access to resources (including food, shelter and breeding opportunities) and group membership (for review, see Krause & Ruxton, 2002). In size-structured groups, conflict is often high between individuals that are similar in size (e.g., Enquist et al., 1987; Keeley & Grant, 1993; Huntingford et al., 1995; Jennions & Backwell, 1996; Nicieza & Metcalfe, 1999; Nathan et al., 2001). There may be several reasons for this. Conflict may be elevated between such individuals because of uncertainty regarding relative fighting ability (the sequential assessment hypothesis: Enquist & Leimar, 1983). Even if relative fighting ability is known, subordinates may be more likely to challenge the next ranking group member when the difference in fighting ability is small (Cant & Johnstone, 2000). Dominant group members may also increase aggression against or evict subordinates with high fighting ability (e.g., Taborsky, 1985; Reeve, 1992; Reeve & Nonacs, 1997; Balshine-Earn et al., 1998; Reeve et al., 1998), although both theoretical and empirical studies suggest this is not always the case (Poiani & Fletcher, 1994; Reeve 2000; Nonacs et al., 2004).

Commonly, the frequency or duration of aggression is used as an estimate of within-group conflict. While overt aggression is one potential outcome of conflict, group members may be able to escape aggression through submissive and pre-emptive behaviours (e.g., Balshine-Earn et al., 1998; Bergmüller & Taborsky, 2005) or avoidance (Werner et al., 2003). We tested the general prediction that conflict between group members would be greater when the difference in size between them was small, using a laboratory population of the cooperatively breeding Lake Tanganyika cichlid, *Neolamprologus pulcher*. We compared the interactions of large male helper *N. pulcher* with dominant breeding males, when the latter were only slightly larger than focal helpers and when they were much larger. We kept absolute size, breeding status, dominance rank and group size constant across all groups, and focal helpers differed only in their size relative to male breeders. In addition

to measuring changes in aggression, we also examined how other social behaviours, space use and helping behaviour changed with the relative size of adjacently ranked males.

Within the general prediction that conflict would increase when size differences were small, we made several alternative, but not mutually exclusive, predictions regarding how within-group conflict would be expressed. The first of these was that conflict would lead to aggressive interactions, so that aggression between focal helpers and breeders would be more frequent or of longer duration when the size differences between them were small. However, aggressive conflict in *N. pulcher* can be circumvented through submissive displays (e.g., Balshine-Earn et al., 1998, Bergmüller & Taborsky, 2005). Thus, our second prediction was that helpers would show increased submissive behaviour alongside, or even instead of, an increase in aggression. Our third prediction was that subordinate *N. pulcher* would avoid conflict by altering patterns of space use (e.g., Werner et al., 2003); thus, we expected that subordinates would be observed further from breeding sites and engage in fewer affiliative interactions (e.g., swimming alongside dominants) when size differences were small.

Previous studies have also suggested that helping behaviour acts to appease conflict (Bergmüller & Taborsky, 2005) or is payment to be accepted in the group (Balshine et al., 2001; Bergmüller et al., 2005). For larger helpers, such as those used in this experiment, help consists primarily of defending the territory against conspecific and heterospecific intruders (Taborsky et al., 1986). Therefore, our fourth prediction was that territory defence would be more frequent or intense when conflict with breeders was high, that is, when size differences were small. Help as a mechanism to avoid conflict assumes that helping is beneficial for breeders. Experimental studies have shown that helpers increase breeders' egg production (Taborsky, 1984) and offspring survival (Brouwer et al., 2005). Since previous studies have shown that helping also reduces the workload of other group members (Balshine et al. 2001; Bergmüller & Taborsky, 2005), we predicted a negative correlation between defence by helpers and defence by breeders. If helping reduces within-group conflict, we also expected that our other measures of conflict (above) would be negatively correlated with investment in help, controlling for the potential for conflict (the size of the breeder).



**Figure 1.** Experimental set-up of the ring tank. All partitions were clear plexiglass, except for opaque plexiglass partitions between the eight sections. In each section, four groups (LL, LS, SL, SS, where L. or S. refer to the size of the breeder male in the first sequence, and .L and .S the same in the second sequence) and a single breeding pair (SP) were established. Groups contained a breeding male, breeding female, focal helper male and a small helper male. All individuals remained in their respective compartments for the duration of the experiment, except the breeding males in the groups, who were all exchanged after 30 days. Pot halves were used as breeding substrate.

## Methods

### *Experimental set-up*

We used one large 7200-litre ring tank divided into 8 sections, each with 5 group compartments (Figure 1), in a climate-controlled room at the Ethologische Station Hasli, University of Bern. The tank stood 60 cm high and was filled to a depth of 50 cm. The floor of the tank was covered with 30 mm sand (1 mm grain size). Two flowerpot halves were introduced per compartment as breeding substrate. Each compartment was fed ad libitum (2 feedings per day; 5 days TetraMin, 2 days fresh food with *Artemia* spp., *Daphnia* spp. and mosquito larvae each week). Water temperature was held constant at

28.0  $\pm$  0.4°C (SD), and water biochemical parameters were kept similar to Lake Tanganyika. The light:dark cycle was kept constant at 13:11h (lights on from 08:00 to 21:00h).

We created 32 artificial breeding groups (see Heg et al., 2004) of four fish each in 4 compartments of each section of the ring tank (Figure 1). In the fifth compartment in each section, we created a breeding pair without helpers (Figure 1). These fish were used in a different experiment (Heg et al., 2004) and we did not make behavioural observations on them. Groups were created as follows: first, a focal large helper male (standard length SL = 40-45 mm) and a small helper male (SL = 30-35 mm) were introduced in each compartment. Large helpers were reproductively mature; therefore, we expected conflict between them and male breeders over reproductive access, and the possibility of expulsion or rank reversals.

Two days later, a breeding female (SL = 55-65 mm) and, in half of the cases, a large and, in the other half, a small male breeder (SL = 70-75 mm or 46-51 mm) were added. In *N. pulcher*, breeding status is determined by size (Taborsky, 1984, 1985) and all of these individuals became breeders even though they were added later. All individuals were marked, and standard length and body mass measured. All group members were unrelated (as is sometimes found in the field, P. Dierkes & M. Taborsky, pers. comm.), to avoid complicating effects of relatedness. Helpers and breeders showed digging behaviour in the two pot halves, egg cleaning (both mainly by small helpers and female breeders) and territory defence along the partitions. Non-group members were visible through the partitions, and included one other group of four fish (breeders and helpers) and a pair of breeders without helpers (see Figure 1).

In the field, immigrants to the group often replace breeders that die (Balshine-Earn et al., 1998; Stiver et al., 2004). Helpers will accept new group members, even those that jump the queue to take the breeding position (Balshine-Earn et al., 1998). We took advantage of this to change the size composition of established groups midway through the experiment. After 30 days, all male breeders were replaced; half of the groups with a large male breeder now received a new large male breeder of similar size (27.4 mm larger than the focal helper on day 30, range 24.5-30.2 mm), the other half received a new small male breeder (6.8 mm larger than the focal helper on day 30, range 5.3-8.7 mm). Similarly, half of the groups with a small male breeder now received a new large male breeder (27.1 mm larger than the

focal helper on day 30, range 25.8–30.7 mm), the other half received a new small male breeder (6.3 mm larger than the focal helper on day 30, range 5.5–9.5 mm). Replacements of male breeders are sometimes accompanied by expulsion of existing helpers (Taborsky & Limberger, 1981; Balshine-Earn et al., 1998). In our groups, helpers were all accepted. The 30 day periods with the first and second male breeder are hereafter referred to as sequences 1 and 2, respectively.

### *Behavioural observations*

Focal behavioural observations were conducted using 'The Observer 3.0' (Noldus, Wageningen, the Netherlands). The target was to conduct four 15-minute focal observations during each 30-day sequence, twice when eggs were present and twice with no eggs present ( $N = 4$  observations  $\times$  2 sequences  $\times$  32 focal individuals = 256 observations). However, four groups did not have broods at all during one sequence (three during sequence 1, one during sequence 2), two groups produced only one brood in one of the two sequences (once during sequence 1 and once during sequence 2), and in one group the observation during the presence of the second brood in sequence 1 failed. Therefore, the total number of observations was 235. Eggs were removed after the observations to prevent the presence of a brood interfering with the rest of the experiment. All observations were conducted by DH.

Three classes of behaviour were recorded for each focal helper. First, the focal helper's minimum estimated distance (to the nearest 5 cm) from the pots during the 15 minutes was recorded (hereafter referred to as 'distance'). Second, the social behaviour displayed by the focal helper was recorded, following the outline in Coeckelberghs (1975), Kalas (1975) and Taborsky (1982, 1984), see also Buchner et al. (2004). Aggressive displays were summed into two categories: (1) overt aggression (i.e., with body contact: ramming, biting, mouth-fighting, tail-beating) and (2) restrained aggression (fast approach, opercula spreading, head jerking, head down display, S-shaped bend, fin raising). In addition, the following social behaviours were recorded: (3) submissive behaviour (tail quivering, hook display), (4) affiliative behaviour (joining other fish), (5) slow approach toward other fish, (6) bumping (i.e. soft-touching the body of the recipient) and (7) group display (Limberger, 1982). The recipient of these behaviours was also recorded (e.g., breeder male, other group members, members of other groups). Third, the social behaviours (above) received from other fish were recorded, along with the identity of the actor.

### *Statistical analyses*

We tested whether distance to the breeding site (the flowerpots) differed with the size of the male breeder. First, we performed a logistic regression to test for a difference in whether helpers would enter the breeding site depending on the size of male breeder, the presence of eggs and sequence. For those that did not enter the breeding site, we used a mixed-model GLM, using the square-root transformed minimum distance to the pots at which the helper was observed as the dependent variable. The sequence (1<sup>st</sup> or 2<sup>nd</sup>), the presence of eggs and the size of the male breeder (large or small) were used as fixed effects in the model. Group and section of the ring tank (Figure 1) were included as random variables. Variance components were estimated by Restricted Maximum Likelihood (REML) using the MIXED procedure in SPSS 11.0. The final model presented is that which minimised the value of Akaike's Information Criterion (AIC), with all main effects included and redundant random variables removed.

In order to simplify the analysis of a large number of non-independent variables, we used principal component analysis to extract components that explained a large proportion of the variance in the behavioural data. These were rotated using varimax rotation and Kaiser normalization to aid in interpretation. We present here the results only for those variables that were normally distributed and without outliers. Principal components analysis is robust to violation of the assumption of normality, so we also performed several other principal component extractions, varying the variables included. In all cases, the number and general structure of components that we extracted were robust to the addition or removal of variables (results not presented).

We performed separate principal component analyses for interactions between the focal helpers and male breeders and between focal helpers and members of other groups. Behavioural variables included in the analyses differed, as some behaviours were rare for some combinations of actors (Table 1, Appendix). We then separately compared the extracted factors scores using mixed-model GLMs, with sequence, presence of eggs and male breeder size as fixed factors, and group and section as random factors. Variance components were estimated by REML using the MIXED procedure in SPSS 11.0. In one set of analyses, we included distance to the breeding site as a covariate because it may influence opportunities for interactions, as fish that approach the breeding site more closely will encounter other group members more

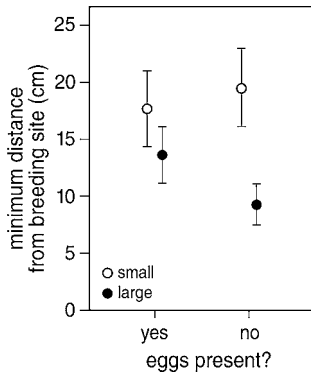
**Table 1.** Significant components (eigenvalues > 1) in two separate principal component analyses of interactions between focal helpers and male breeders or non-group members, respectively. Variables included in each analysis differed because some behaviours were rare or non-existent for some combinations of actors (see Appendix). In all cases, variance explained and loadings refer to components after varimax rotation. Italics indicate loadings > 0.50.

Interactions with:	Male breeders			Non-group members	
	PC 1	PC 2	PC 3	PC 1	PC 2
Component					
Variance explained (%)	38.1	25.7	11.1	46.5	23.9
Factor loadings					
Join	<i>0.85</i>	0.42	-0.10		
Bump	<i>0.66</i>	0.21	0.19		
Slow approach	<i>0.92</i>	0.11	-0.09	<i>0.86</i>	0.16
Submissive	0.32	<i>0.83</i>	0.21		
Overt aggression				<i>0.55</i>	<i>0.71</i>
Display aggression				<i>0.84</i>	0.42
Group displays				0.02	<i>0.73</i>
Duration joining	<i>0.87</i>	0.18	-0.10		
Duration slow approach	<i>0.87</i>	0.10	-0.05	<i>0.73</i>	0.18
Duration submissive	-0.08	<i>0.89</i>	0.15		
Duration overt aggression				0.27	<i>0.81</i>
Duration display aggression				<i>0.72</i>	<i>0.52</i>
Received overt aggression	-0.04	0.04	<i>0.95</i>	<i>0.73</i>	0.18
Received display aggression				<i>0.87</i>	0.37
Received bumps	0.29	<i>0.69</i>	-0.28		
Received slow approach	0.31	<i>0.59</i>	-0.06	<i>0.71</i>	0.05
Received submissive					

often. On the other hand, distance to the breeding site may be a result of aggression or other interactions, and including it in the model could obscure these patterns, as much of the variation in aggression (or other behaviours) would be attributed to an effect of distance. Therefore, we always present results of analyses with and without distance included as a covariate. The final model presented is that which minimised AIC values and which included all main effects (and the covariate, distance, if appropriate), and with redundant random variables (i.e., those for which covariance parameters could not be estimated by REML) removed.

To test whether defence by helpers influenced defence by breeder males, we compared overt and display aggression directed at other groups by male breeders with a similar model to that described above. We included the





**Figure 2.** Effects of male breeder size and the presence of eggs on mean ( $\pm$  SE) minimum distance that large male helpers approached the nest site. Results shown are for those helpers that did not enter the nest site. Symbols denote the sizes of male breeders.

factors extracted from our analyses of focal helpers' interactions with other groups as covariates. Interactions were removed from the models if doing so improved (minimised) AIC values.

Finally, to test whether help performed by helpers influenced interactions with breeders, we also re-ran our analyses of interactions with male breeders, incorporating focal helpers' interactions with other groups as covariates. Because we were interested in how these interactions influenced breeder-focal helper interactions, they were retained in the final model even when removing them would improve AIC values. Otherwise, model selection was performed as in previous analyses.

## Results

Median values for interactions between focal helpers and other group members or members of neighbouring groups are listed in the Appendix. Interactions with breeder females and small helpers did not differ significantly with treatment (results not presented).

### *Distance to breeding site*

The size of breeder males did not influence the likelihood that helpers would enter the breeding site (25% of helpers in each treatment entered it; Wald statistic = 0.0,  $df = 1$ ,  $p = 1.0$ ). For those helpers that did not enter it,

**Table 2.** Results of SPSS MIXED procedure for interactions between focal helpers and male breeders. The dependent variables are the three significant principal components obtained from analysis of interactions between male breeders and focal helpers (see Table 1). In (a), the size of male breeders, presence of eggs, sequence and retained interactions among these were included as fixed effects. In (b), the minimum distance that focal helpers were observed from the nest site was also included as a covariate.

(a)

Component	<i>F</i>	df <sub>num</sub>	df <sub>denom</sub>	<i>p</i>
PC 1 (Affiliativeness)				
Male breeder size	2.71	1	31.66	0.11
Presence of eggs	2.26	1	15.74	0.15
Sequence	9.45	1	6.86	0.018
Sequence * male size	6.08	1	22.95	0.022
PC 2 (Submissiveness)				
Male breeder size	4.25	1	29.55	0.048
Presence of eggs	0.04	1	4.54	0.84
Sequence	0.09	1	8.59	0.77
Eggs * male size	1.20	1	12.99	0.29
Sequence * male size	0.02	1	17.15	0.88
Eggs * sequence	0.64	1	29.42	0.43
Eggs * sequence * male size	0.58	1	12.88	0.46
PC 3 (Aggression Received)				
Male breeder size	0.01	1	8.52	0.94
Presence of eggs	1.62	1	6.82	0.24
Sequence	4.06	1	9.33	0.074
Eggs * male size	8.76	1	30.53	0.006
Sequence * male size	0.01	1	11.03	0.93
Eggs * sequence	3.09	1	40.77	0.087
Eggs * sequence * male size	5.58	1	29.99	0.025

there was a tendency for focal helpers to approach nearer to the breeding site when breeder males were large ( $F = 3.92$ ,  $df = 1$ ,  $26.03$ ,  $p = 0.06$ ). However, there was a significant effect of the interaction between the size of male breeders and the presence of eggs on distance (Figure 2, male size \* eggs:  $F = 12.58$ ,  $df = 1$ ,  $15.30$ ,  $p = 0.003$ ). When eggs were present, there was little difference in distance to the breeding site whether male breeders were large or small. When eggs were absent, focal helpers approached the breeding site more closely when male breeders were large. There was also

**Table 2.** (Continued).

(b)

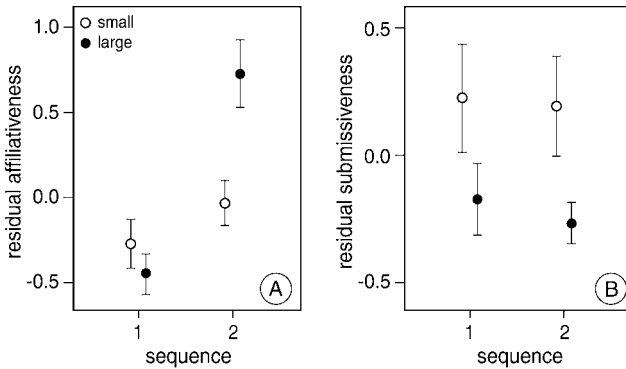
Factor	<i>F</i>	df <sub>num</sub>	df <sub>denom</sub>	<i>p</i>
PC 1 (Affiliativeness)				
Male breeder size	1.88	1	30.05	0.18
Presence of eggs	2.11	1	11.74	0.17
Sequence	15.10	1	24.64	0.001
Eggs * male size	1.58	1	21.09	0.222
Sequence * male size	6.30	1	22.20	0.020
Minimum distance to nest	19.23	1	34.03	<0.001
PC 2 (Submissiveness)				
Male breeder size	3.60	1	31.85	0.067
Presence of eggs	0.03	1	5.38	0.86
Sequence	0.34	1	7.47	0.58
Eggs * male size	0.56	1	17.83	0.47
Sequence * male size	0.02	1	21.68	0.88
Eggs * sequence	0.32	1	37.21	0.57
Eggs * sequence * male size	0.75	1	17.43	0.40
Minimum distance to nest	3.28	1	33.22	0.079
PC 3 (Aggression Received)				
Male breeder size	0.10	1	9.68	0.77
Presence of eggs	1.74	1	8.16	0.22
Sequence	3.07	1	9.71	0.11
Eggs * male size	5.60	1	27.89	0.025
Sequence * male size	0.05	1	11.14	0.83
Eggs * sequence	1.81	1	36.38	0.19
Eggs * sequence * male size	5.65	1	26.93	0.025
Minimum distance to nest	5.46	1	41.09	0.024

Group, section and interactions with main effects were included as random effects. Variance components were estimated with Restricted Maximum Likelihood (REML). Results for fixed effects only are shown.

a significant interaction between the presence of eggs and sequence on the distance that focal helpers approached the breeding site (sequence \* eggs:  $F = 7.14$ ,  $df = 1$ ,  $16.85$ ,  $p = 0.016$ ).

#### *Interactions with male breeders*

In our principal components analysis, we extracted three components with eigenvalues greater than one (Table 1). The first of these had high loadings on the frequency and duration of joining and slow approaches, and the fre-



**Figure 3.** Effects of male breeder size and sequence on the mean ( $\pm$  SE) (a) affiliative interactions and (b) submissive interactions between focal large male helpers and male breeders. Values are rotated component scores for the 1<sup>st</sup> (a) and 2<sup>nd</sup> (b) principal components for interactions between male breeders and focal helpers (see Table 1). Shown are residuals of SPSS MIXED procedures, with the presence of eggs as a fixed effect, and group and section as random factors. Symbols denote the sizes of male breeders. In (a), the interaction between sequence and male breeder size is significant (see Table 2). In (b), there is no effect of sequence on submissiveness, but there is an overall significant effect of male breeder size.

quency of bumping performed by focal helpers. The second component had high loadings on receipt of bumping and slow approaches from the male breeder, and on frequency and duration of submissive behaviour displayed by the large helper. Bumping and slow approaches can be difficult to interpret. Bumping by focal helpers, directed at breeders, has been suggested to be affiliative or conciliatory (R. Bergmüller, pers. comm.). Bumping by breeders, however, may occur in aggressive contexts (D. Heg, pers. obs.). Slow approaches may be terminated bumps or initiate affiliative joining, but may also grade into more aggressive fast approaches. Therefore, we interpret the first of these axes as a measure of affiliative behaviour within the group, and the second as a measure of submissiveness by the focal helpers. The third component was highly correlated with the number of attacks received. We therefore interpret this axis as a measure of aggression directed by the male breeders toward the focal helpers.

There was a significant interaction between sequence and the size of male breeders on affiliativeness scores of focal helpers, both with and without minimum distance to the breeding site included as a covariate (Table 2). Affiliativeness scores of focal helpers were higher in groups with large male breeders than in those with small male breeders, but only in the second se-

quence (Figure 3a). Affiliativeness scores were also higher overall in the second sequence. When distance was included, it was negatively correlated with affiliativeness. In other words, more affiliative focal helpers were observed closer to the breeding site than were less affiliative ones.

Focal helpers tended to be more submissive toward small male breeders (Figure 3b). This effect was significant when distance was not included in the model (Table 2a). When distance was included, submissiveness increased, although not significantly so, with increasing distance from the pots (Table 2b). Other effects in the model were not significant (Table 2).

There was a significant effect of the three-way interaction among sequence, the presence of eggs and male breeder size on aggressive behaviour received by focal helpers (Table 2a). In the first sequence, aggression received from small male breeders was higher than that received from large male breeders when eggs were absent, but the opposite was found when eggs were present. In the second sequence, there was little difference in aggression received from large or small male breeders or when eggs were present or absent. Distance significantly influenced aggression (Table 2b); there was a positive correlation between aggression received from breeders and minimum distance from the breeding site.

### *Interactions with other groups*

For interactions with members of other groups, two principal components were extracted (Table 1). The first loaded highly upon receipt of attacks and aggressive displays, receipt and use of slow approaches and aggressive displays. The second loaded highly upon the frequency and duration of attacks and the frequency of group displays. Hereafter, we refer to these components as 'display defence' and 'escalated defence'.

Both of these components were greater when male breeders were large, although this was significant only for escalated defence (Table 3). There was also a significant influence of the three-way interaction among sequence, the presence of eggs and male breeder size on escalated defence (Table 3). In the first sequence, there was a stronger effect of male size on escalated defence when eggs were absent than when eggs were present. When distance was included as a covariate, it was negatively correlated with both factors (Table 3).

**Table 3.** Results of SPSS MIXED procedure for interactions between focal helpers and members of other groups. The dependent variables were obtained from principal component analysis of these interactions (see Table 1 for variance explained and factor loadings). The size of male breeders, presence of eggs, sequence and retained interactions among these were included as fixed effects, and group and section as random effects. Results are shown with and without minimum distance that focal helpers approached the nest site as a covariate. Variance components were estimated by REML. Results for fixed effects only are shown.

Factor	<i>F</i>	df <sub>num</sub>	df <sub>denom</sub>	<i>p</i>
<b>Without distance</b>				
PC 1 (Display & received aggression)				
Male breeder size	4.45	1	6.91	0.073
Presence of eggs	3.67	1	9.03	0.087
Sequence	4.02	1	4.79	0.10
Eggs * male size	0.03	1	22.71	0.87
Sequence * male size	0.62	1	40.71	0.44
Eggs * sequence	0.95	1	80.18	0.33
Eggs * sequence * male size	0.97	1	22.83	0.34
PC 2 (Escalated aggression)				
Male breeder size	8.08	1	0.599	0.030
Presence of eggs	0.84	1	14.63	0.38
Sequence	0.34	1	11.30	0.57
Eggs * male size	0.55	1	29.66	0.47
Sequence * male size	0.80	1	25.20	0.38
Eggs * sequence	1.69	1	43.05	0.20
Eggs * sequence * male size	4.89	1	29.75	0.035
<b>With distance</b>				
PC 1 (Display & received aggression)				
Male breeder size	2.63	1	8.59	0.14
Presence of eggs	3.58	1	10.27	0.087
Sequence	7.98	1	3.02	0.066
Eggs * male size	0.37	1	25.21	0.55
Sequence * male size	0.96	1	29.27	0.33
Eggs * sequence	0.13	1	84.51	0.72
Eggs * sequence * male size	0.89	1	25.19	0.36
Minimum distance to nest	18.27	1	40.90	<0.001
PC 2 (Escalated aggression)				
Male breeder size	6.06	1	6.35	0.047
Presence of eggs	0.75	1	17.45	0.40
Sequence	0.03	1	10.34	0.86

**Table 3.** (Continued).

Factor	<i>F</i>	df <sub>num</sub>	df <sub>denom</sub>	<i>p</i>
PC 2 (Escalated aggression)				
Eggs * male size	0.00	1	34.74	0.99
Sequence * male size	0.77	1	28.96	0.39
Eggs * sequence	0.57	1	44.07	0.46
Eggs * sequence * male size	6.02	1	34.04	0.019
Minimum distance to nest	15.13	1	49.59	<0.001

### *Defence by male breeders*

Defence by male breeders was negatively correlated with defence by focal helpers. Male breeders attacked other groups less often when focal helpers engaged in frequent interactions with other groups (display defence by focal helpers:  $\beta = -0.16 \pm 0.061$ ,  $F = 6.80$ ,  $df = 1, 24.40$ ,  $p = 0.015$ ; escalated defence by focal helpers:  $\beta = -0.036 \pm 0.059$ ,  $F = 0.37$ ,  $df = 1, 18.38$ ,  $p = 0.55$ ). Male breeders also displayed less toward members of other groups when focal helpers defended more (display defence by focal helpers:  $F = 7.08$ ,  $df = 1, 67.54$ ,  $p = 0.010$ ; escalated aggression by focal helpers:  $F = 1.34$ ,  $df = 1, 52.93$ ,  $p = 0.25$ ).

Defence by breeders was also influenced by size, the presence of eggs and sequence. Large male breeders attacked members of other groups significantly less often than did small male breeders ( $F = 11.24$ ,  $df = 1, 13.17$ ,  $p = 0.005$ ). Attacks by large breeders were higher when eggs were absent ( $F = 9.12$ ,  $df = 1, 6.40$ ,  $p = 0.022$ ) and in the second sequence ( $F = 10.06$ ,  $df = 1, 13.77$ ,  $p = 0.007$ ). Display defence by large male breeders was influenced by the three-way interaction among sequence, male size and the presence of eggs and display defence by focal helpers (eggs \* sequence: \* male size:  $F = 6.23$ ,  $df = 1, 49.30$ ,  $p = 0.016$ ). In the first sequence, large male breeders engaged in more frequent display defence than did small male breeders when eggs were present, but less frequent display defence when eggs were absent. In the second sequence, large male breeders engaged in less frequent display defence, regardless of whether eggs were present.

### *Correlations between help and interactions with male breeders*

Interactions between focal helpers and male breeders were correlated with defence by the helpers. Affiliativeness toward breeder males increased significantly with increases in both display defence ( $\beta = 0.18 \pm 0.086$ ,  $F = 4.60$ ,

df = 1, 33.02,  $p = 0.039$ ) and escalated defence against other groups ( $\beta = 0.22 \pm 0.087$ ,  $F = 6.31$ , df = 1, 29.64,  $p = 0.018$ ). Submissiveness toward breeder males was not significantly influenced by interactions between helpers and members of other groups (display defence:  $\beta = -0.024 \pm 0.10$ ;  $F = 0.06$ , df = 1, 36.34,  $p = 0.82$ ; escalated defence:  $\beta = 0.053 \pm 0.10$ ,  $F = 0.26$ , df = 1, 26.77,  $p = 0.61$ ). Effects were similar if distance was included (not shown). All other effects in the models were qualitatively similar to those in Table 2.

Receipt of aggression from male breeders was not correlated with either display defence or escalated defence when distance was included in the model (display and received aggression:  $\beta = 0.048 \pm 0.099$ ,  $F = 0.24$ , df = 1, 23.40,  $p = 0.63$ , escalated aggression:  $\beta = -0.14 \pm 0.10$ ,  $F = 1.84$ , df = 1, 18.83,  $p = 0.19$ ). Removing distance from the model, the negative correlation between escalated defence and aggression received from the male breeder became significant ( $\beta = -0.21 \pm 0.092$ ,  $F = 5.00$ , df = 1, 19.84,  $p = 0.037$ ). Display defence was not significantly correlated with aggression received from male breeders when distance was removed ( $\beta = -0.033 \pm 0.089$ ,  $F = 0.14$ , df = 1, 21.10,  $p = 0.72$ ).

## Discussion

The size of male breeder *N. pulcher* strongly influenced interactions between them and large male helpers in their social group. As predicted, focal helpers increased submissive behaviour toward small male breeders. Changes in affiliative and spacing behaviour indicate that helpers also avoided small male breeders. In the second sequence, helpers engaged in fewer affiliative interactions (joining, bumping and approaching) with small male breeders. When eggs were absent, focal helpers were also observed further from the breeding site when male breeders were small. We found that focal helpers that received high levels of aggression tended to stay further from the nest site. The direction of causation for the latter two effects is unclear. It may be that increased aggression leads to avoidance (e.g., Werner et al., 2003) or that individuals that have been excluded from the group are not tolerated when they encounter breeders. In aquaria, distance to the nest site may be evidence of eviction; permanently or temporarily evicted focal helpers cannot leave the group (because of the partitions), but, at the same time, cannot approach the



nest site without being chased. In contrast to our predictions, we found no consistent effect of relative size on aggression. However, rates of aggression were low (Appendix). In a separate analysis, we also found effects of breeder size on the growth of helpers (see Heg et al., 2004). Helpers grew more slowly when male breeders were small.

In other experimental studies with *N. pulcher*, subordinates placed in conflict with breeders (by being prevented from helping) increased their rates of submissive displays (Balshine-Earn et al., 1998; Bergmüller & Taborsky, 2005) and help (Bergmüller & Taborsky, 2005). Submissive behaviour also may act as appeasement against or pre-emption of aggression (Balshine-Earn et al., 1998; Bergmüller et al., 2005; Bergmüller & Taborsky, 2005). There appear to be several ways that subordinate *N. pulcher* can resolve conflicts with dominants, including aggression, appeasement, avoidance, and possibly by restraining growth (Heg et al., 2004).

Conflict within established hierarchies is hypothesised to be a critical element of social behaviour. It plays a key role in concessional, restraint and tug-of-war models of reproductive skew (reviewed in Johnstone, 2000) and aggression (Cant & Johnstone, 2000; Reeve, 2000), pay-to-stay explanations for helping (Kokko et al., 2002; Hamilton & Taborsky, 2005), self-restraint in growth or reproduction (Buston 2003; Hamilton, 2004; Heg et al., 2004), and the maintenance of hierarchy structure (Broom, 2002). However, in established groups, the expectation of repeated interactions allows players to use a variety of tactics, such as appeasement, pre-emption or expulsion, in addition to or instead of aggressive and submissive behaviours to resolve conflict, enforce dominance or challenge for status. Our results and those of others (Balshine-Earn et al., 1998; Werner et al., 2003, Bergmüller & Taborsky, 2005) indicate that aggression alone may be a poor measure of within-group conflict in *N. pulcher*.

Our aggression results are inconsistent with those of many other studies, including those using other cichlids, which have found escalated aggression among individuals that are similar in size. In the cichlid, *Nannacara anomola*, overt aggression was never observed when size differences between opponents were large but was when differences were smaller (Enquist et al., 1987). In convict cichlids, *Archocentrus nigrofasciatum*, aggression increased when size differences were small (Keeley & Grant, 1993). In fiddler crabs, encounter duration increased when intruders were relatively large (Jennions & Backwell, 1996). In the swimming crabs, *Necora puber* and

*Liocarcinus depurator*, small size differences led to extended and escalated contests (Huntingford et al., 1995). However, all of these studies were conducted to test the sequential assessment model (Enquist & Leimar, 1983), which assumes uncertainty over fighting ability, and were performed with unfamiliar individuals. In established groups, uncertainty regarding relative fighting ability should be diminished, although some may remain. The effects of relative competitive ability or size on aggression are less clear in established groups (e.g., *Polistes* wasps: Reeve & Nonacs, 1997; Nonacs et al., 2004). Again, this may be because size differences do not influence conflict or because conflict between members of established groups can be expressed in several ways. In our experiment, changes in behaviours other than aggression suggest that size differences did influence conflict between large helpers and male breeders.

We did not find support for our prediction that helpers would help more when male breeders were small. Indeed, focal helpers were more aggressive toward members of other groups when the male breeder in their own group was large. There is evidence that this aggression did help breeders. We found a negative correlation between one measure of helper defence (PC 1, display and received aggression) and both attacks and displays directed at other groups by male breeders. Male breeders defended less when their focal helpers defended more. This relationship is correlational, but is consistent with the results of other studies that showed that the presence of helpers reduced breeder workload (Balshine et al., 2001) and that, when focal helpers were prevented from defending, other groups members increased defence (Bergmüller & Taborsky, 2005).

Why would focal helpers help more when male breeders are large? Helping may serve an appeasement function, as investment in help increases in fish that have previously been prevented from doing so (Bergmüller & Taborsky, 2005). However, in this experiment, help was greatest for helpers in groups with large breeders. These fish were also less submissive, more affiliative and were allowed nearer to the nest site, so there was little indication of increased need for appeasement. Another possibility is that fish were more likely to help if they expected to remain as helpers. Under the pay-to-stay framework (Gaston, 1978; Kokko et al., 2002; Hamilton & Taborsky, 2005), help is payment in exchange for being allowed to stay in the group or to avoid harassment. In support of this, we found that focal helpers that defended more received reduced aggression and engaged in more affiliative

interactions with dominants. However, the same logic dictates that a helper that is likely to take over the territory in the near future (because it is similar in fighting ability to the breeder) should not engage in costly help (Kokko et al., 2002; Hamilton & Taborsky, 2005). Finally, breeders may simply have been better able to enforce demands for help when they were large.

An alternative explanation for our general results is that the age or size of breeder and helper males, rather than the difference in size between them, influenced conflict within groups. This is a problem for studies of relative size and conflict in general (Taylor & Elwood, 2003). To tease apart the effects of absolute and relative size, we would need to manipulate helper and breeder size, as well as the difference in size between these. Some evidence for the importance of relative size comes from our analysis of interactions with other groups. Display and received aggression was significantly related to the difference in size between focal helpers and male breeders (using  $\ln[\text{length male breeder} - \text{length focal helper} + 1]$  as a covariate, rather than male breeder size as a fixed effect:  $F = 9.3$ ,  $df = 1, 38.7$ ,  $p = 0.004$ ), but not significantly influenced by the absolute size of male breeders (Table 3). In an analysis of growth data using the same fish (Heg et al., 2004), we also found a stronger effect using the difference in size between focal helpers and male breeders than using the size of male breeders (Heg et al., 2004, unpubl. data).

If size differences account for our results, this may have implications for the growth of helpers, contributing to the size structure of hierarchies. This appears to be the case in several salmonid species, in which subordinates that receive aggression from dominants grow slowly because they are excluded from food (e.g., Olla et al., 1992), have reduced feeding activity (Metcalf, 1989), experience reduced conversion efficiency (Abbott & Dill, 1989) and have lowered disease resistance (Salonius & Iwasa, 1993). This leads to compensatory growth and an increasingly skewed size distribution over time (Ryer & Olla, 1996). In several systems, it has been suggested that reduced growth of subordinates and increased growth of dominants may be beneficial to both because of reduced conflict, and consequently, reduced risk of costly aggression and expulsion (e.g., Taborsky, 1984; Buston, 2003; Heg et al., 2004; Russell et al., 2004).

Our results imply that the cost of subordinate growth, in terms of increased conflict, to subordinate group members is greater when differences in size between them are small. We suggest that this will lead to reduced growth for subordinates in groups with small male breeders. During this experiment, we

found that difference in size between breeder and helper males influenced the growth of the latter (reported in Heg et al., 2004). Focal helpers paired with smaller breeders grew more slowly. Buston (2003) reported similar results for clownfish. The mechanism for this adjustment is not known; focal helpers may restrain their own growth to avoid expulsion and harassment, breeders may suppress the growth of subordinates, or both. Previous studies have found that submissive behaviour can be energetically very costly (Grantner & Taborsky, 1998). Avoidance of aggression is also likely to be energetically costly. Thus, one mechanism for the observed differences in growth may result from increased energetic expenditure on submissive behaviour and escaping from aggression. Our results are consistent with dominant suppression playing at least some role in growth adjustments in *N. pulcher*.

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## Appendix

Interactions between focal large helpers and members of their own and other groups. Medians and ranges of frequencies or durations (s) per 15 min observation are presented separately for interactions with male breeders and members of other groups, and for groups with large or small male breeders.

	Interactions with:							
	Male breeders				Non-group members			
	Large		Small		Large		Small	
	Med	Range	Med	Range	Med	Range	Med	Range
Join	47	4-116	41	1-119	0	0-1	0	0-2
Bump	6.5	0-30	2	0-21	n/a		n/a	
Slow approach	17	0-65	13.5	0-50	9.5	0-46	7	0-30
Submissive	21.5	0-59	26	0-98	0	0-1	0	0-1
Overt aggression	0	0	0	0-4	6	0-36	3	0-14
Display aggression	0	0-11	0	0-29	88	0-280	42	0-171
Group displays	n/a		n/a		2	0-18	1	0-10
Duration joining (s)	6.6	0.7-19.9	4.9	0.2-15.5	0	0-0.5	0	0-0.8
Duration slow approach (s)	1.0	0-3.0	0.8	0-2.6	0.7	0-3.1	0.2	0-1.5
Duration submissive (s)	0.9	0-3.2	1.3	0-7.2	0	0-0.1	0	0-0.2
Duration overt aggression (s)	0	0	0	0-0.4	0.32	0-1.6	0.14	0-0.8
Duration display aggression (s)	0	0-0.4	0	0-1.9	11.5	0-31.7	5.4	0-19.5
Received overt aggression	1	0-13	1	0-7	3	0-31	1	0-19
Received display aggression	0	0-1	0	0-17	38.5	0-99	24	0-87
Received bumps	1	0-7	1	0-11	n/a		n/a	
Received slow approach	6	1-24	6	0-27	6	0-25	4.5	0-17
Received submissive	0	0	0	0-2	0	0-2	0	0-1