Aggression, segregation and stability in a dominance hierarchy

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Central to our understanding of social group formation and maintenance is the question of how within-group conflict resolution is achieved in the face of asymmetrical competition over resources and reproduction. A crucial yet implicit assumption of many conflict resolution models dealing with reproductive skew is that subordinates have perfect knowledge of the extent of conflict between themselves and their dominants, enabling behavioural responses on an individual rather than evolutionary scale. However, a mechanism enabling subordinates to accurately assess their relative conflict levels has yet to be empirically demonstrated. Here, we show in the angelfish *Centropyge bicolor* that the rate of overt mild aggression from dominants to subordinates acts as a signal of increasing rank conflict. The clarity of this signal can be reduced by spatial segregation, causing subordinates to be less able to respond appropriately by regulation of their foraging rates. A reduced signal ultimately leads to a less well-defined dominance hierarchy and destabilization of the social group. Our study suggests that, contrary to previous suggestions, dominant aggression rates play a crucial role as an accurate information signal required for the evolutionary stability of skew models.

Keywords: dominance hierarchies; social conflict; group stabilization; reproductive skew; aggression; threat signalling

1. INTRODUCTION

Reproductive skew models, which examine the resolution of conflict over reproduction, are popular for their simplicity and ability to make predictions relating parameters such as skew, relatedness, aggression and productivity; but they are built on assumptions that empirical work must test as well (Johnstone 2000). Kokko (2003) showed that the hidden assumption of perfect knowledge and the resulting ability to respond at an individual level to other group members is crucial, as the evolutionary equilibrium predicted by skew models rapidly loses stability if the assumption is relaxed. For stability, there must exist a mechanism to transmit accurate information within the group, for example to inform subordinates about the potential costs and benefits of staying in the group (from a concession model viewpoint, where subordinates stay only if benefits are high enough) or regulating their behaviour (from a restraint model viewpoint, where subordinates modify their behaviour in order to be allowed to stay). Empirical work has not elucidated this mechanism, despite theoretical suggestions that dominance displays and aggression may play a central role (Johnstone & Cant 1999; Cant & Johnstone 2009). Here, we use detailed behavioural studies on established groups of dwarf angelfish *Centropyge bicolor* to investigate mild chronic aggression as a mechanism to signal the extent of conflict between ranks.

Centropyge bicolor is a protogynous coral-reef angelfish that lives in harem groups of two to eight mature individuals, consisting of a large dominant male and several breeding females arranged in a linear dominance hierarchy with consistent stepwise decreases in body size

down the ranks (Aldenhoven 1984). The male guards a group territory of up to 200 m², within which the females have overlapping smaller home ranges. The hierarchy is also a breeding queue: when the male disappears, the top-ranked female will change sex and take over the harem, while the remaining females grow and move up in rank (Aldenhoven 1984). This type of body size-based linear dominance hierarchy has recently emerged as a model system useful for testing skew theory (Buston *et al.* 2007; Wong *et al.* 2007), partly because size relationships make it easy to measure dominance and the extent of conflict between ranks. Stability in these systems is achieved by means of maintaining clear size differences between adjacently ranked individuals, via the regulation of subordinate growth (Buston 2003; Heg *et al.* 2004; Wong *et al.* 2007) and foraging rates (Wong *et al.* 2008). However, the mechanism by which subordinates are able to assess the level of conflict between themselves and their immediate dominants, so as to be able to regulate their growth accordingly, is still unknown.

Aggression has long been suggested as a mechanism by which dominants can influence or coerce subordinates (Reeve 1992; Reeve & Nonacs 1997; Balshine-Earn *et al.* 1998) and is a key parameter in many reproductive skew models (Cant & Johnstone 2000; Cant *et al.* 2006; Fanelli *et al.* 2008). In this paper, we consider whether the rate of low-level aggression could be the signal used to express the extent of conflict between ranks. In a size-based linear hierarchy, we would then expect aggression rates from dominants to their immediate subordinates to escalate as they become closer in size. Previous work on this type of system has so far failed to find such an aggressive gradient (Hamilton *et al.* 2005; Wong *et al.* 2008), leading Wong *et al.* (2007, 2008) to

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suggest a mechanism of subordinate growth restraint in response to an invisible threat of punishment by eviction by dominants should subordinates exceed a threshold size ratio. Their hypothesis did not posit any candidate overt signal enabling subordinates to assess how close they are to the threshold. In our study on *C. bicolor*, we consider whether the initial failure to find the expected gradient might reflect not the actual lack of an overt signal, but the confounding effect of spatial segregation on the aggressive pattern (Nonacs *et al.* 2004; Hamilton *et al.* 2005). When clear, an aggressive gradient could act as a signal to subordinates of the relative location of the punishment threshold, enabling them to restrain their growth accordingly. We also go on to examine the effect of spatial segregation on the expected subordinate foraging response to aggressive patterns, and finally investigate whether segregation and the accompanying loss of an effective aggression signal leads to reduced group stability.

2. MATERIAL AND METHODS

(a) General methods

Groups of *Centropyge bicolor* at Lizard Island (14°40' S, 145°28' E) on Australia's northern Great Barrier Reef were studied between March 2007 and February 2009, based from Lizard Island Research Station. In total, 37 social groups consisting of approximately 150 mature fish were studied in four study sites spread around the island. Each social group typically consisted of one dominant male, one to eight mature females (greater than 5 cm standard length (SL)) and zero to four juveniles arranged in a strictly size-based linear dominance hierarchy. Mature fish were individually identifiable by location, size, distinctive patterns in the borders between blue and yellow body colouring and Visible Implant Elastomer tags (Northwest Marine Technology). Body sizes (SLs) of all fish were measured to the nearest 0.5 mm using vernier callipers, while the fish was held in a plastic bag underwater during temporary capture. Fish were assigned ranks based on their relative sizes in the group, and SL ratios between adjacently ranked fish calculated as the SL of the subordinate divided by the SL of the dominant.

(b) Field behavioural observation methods

Individual fish in the field were observed using a standardized focal watch method. Each individual was observed over a focal set of three 15 min focal watches, one each in the morning (before 11.00), midday (11.00–14.00) and afternoon (14.00 to 1 h before sunset). Three types of behaviour were recorded during focal watches.

(i) Foraging rates

The total number of feeding nips the focal fish was observed to take over the focal watch was recorded. A stopwatch was used to record the total amount of time the fish was visible to the observer to the nearest second. Foraging rate (nips min⁻¹) was calculated by dividing the number of feeding nips by the visible time.

(ii) Aggression

All aggressive interactions the focal fish was involved in during a focal watch were recorded. In the great majority of cases, these were mild displacement interactions, where the aggressor would rapidly swim towards the receiver, causing the receiver to move away a short distance before resuming

foraging. For each interaction, the direction of the aggression (aggressor or receiver) and the identity of the other fish involved were recorded. Data were combined for the entire focal set for each fish owing to low rates of aggression.

(iii) Home ranges

During a focal watch, the observer would follow the focal fish, remaining directly above it at all times. This observer carried or towed on a taut line a Garmin GPS 72 unit attached to a surface buoy, which continuously recorded location fixes every 10 s, yielding up to 810 fixes over three 15 min focal watches. GPS data from the three focal watches were combined for use in calculations of the focal fish's home range.

As recommended by Getz *et al.* (2007), we used the 'adaptive sphere-of-influence' α -LoCoH method (standardizing $\alpha = 20$) to calculate home range. This is a non-parametric kernel-based method of home range estimation particularly useful in patchy environments with hard habitat-type edges, such as a coral reef. LoCoH is a nearest neighbour convex hull method. It produces home ranges by first considering each observed location and identifying all the neighbouring points within a radius a such that the distances of all points within the radius to the reference point sum to a value less than or equal to a . It then produces minimum convex polygons (local hulls) of each point and its selected neighbours. After arranging the hulls in increasing order of size, they are merged until the required proportion of points is included, so, for a 10th percentile isopleth, hulls are merged until 10 per cent of points are included. As hulls are merged in increasing order of size, the lower isopleths represent the most used part of the home territory (i.e. the densest area in terms of points). The radius a was selected following the 'minimum spurious hole covering' rule (according to Getz & Wilmsers 2004; Getz *et al.* 2007). We used the 50 per cent density isopleth throughout to estimate the home range (as recommended by Börger *et al.* 2006). Home ranges were calculated using the adehabitat package in R. Kernel shapefiles were exported to ArcView 9 (Environmental Systems Research Institute) to calculate the area of overlaps between individuals' home ranges. The overlapping area of adjacently ranked fishes' home ranges was expressed as a percentage of the subordinate's total home range area for analysis.

(c) Statistical analyses

All statistical analyses were conducted using R. We used the lme4 package to build generalized linear mixed models (GLMMs), enabling us to control for the effect of random factors such as site, group, individual, observer and focal set. In the models presented here, we retained only those random factors that were significant. However, including all the non-significant random factors that we dropped resulted in no qualitative change in the results. We tested the significance of model terms using ANOVA to compare alternative models with and without each term. For normal error structure models, we also used an alternative test by MCMC sampling the posterior distribution of the coefficient values generated from the model algorithm (using the function mcmcsm from lme4), and checking that the 95% confidence interval for the coefficients did not include zero, indicating a significant effect. Only the ANOVA test results are presented, as the two approaches always gave the same results.

(d) The dominant aggression response to size differences and spatial patterns

(i) Open spatial conditions—in the field

To investigate whether dominants might use overt aggression against relatively large subordinates in natural established groups in the field, we tested for a relationship between aggression rates from females to their immediate subordinates and the SL ratio between each such dyad, using a Poisson error structure GLMM. To account for the possibility of spatial patterns in the field mitigating any aggressive gradient, we also fitted to the model the spatial overlap between the home ranges of aggressor and receiver, and the interaction between this overlap and the SL ratio. We used aggression rate data from 112 focal sets on 86 females in 35 groups for the original non-spatial model, and 102 focal sets for the spatial model owing to a small number of cases where the GPS spatial data failed. Site, group, individual and focal set were initially fitted as random factors, but only group was retained as a significant random effect.

(ii) Confined spatial conditions—in aquaria

Staged contests in aquaria were conducted to assess whether aggression was escalated between similarly sized fish in spatially confined conditions. Twenty-four females were collected from the reef and individually housed in separate flow-through sea water aquaria. Random pairs of fish from different original groups with varying SL ratios were placed together in empty flow-through sea water aquaria ($25 \times 38 \times 60$ cm) for 15 min and observed for the number and direction of aggressive events. The larger fish was designated the dominant, and the smaller fish the subordinate. Each fish was used in only one contest in any given day. One hundred and fifteen contests were conducted over 18 days. Aggression was almost always directed from the dominant to the subordinate, except when the two fish were very similarly sized. On these occasions, the subordinate might act as the aggressor for part of the 15 min contest. Dominant to subordinate aggression rate was calculated as the total number of aggressive interactions directed from the dominant to the subordinate, divided by the number of minutes the dominant was acting as aggressor (usually 15, but occasionally less when the fish were similarly sized). The relationship between the dominant to subordinate aggression rate and the SL ratio between the two fish was tested using a GLMM controlling for the random effect of observer, with the SL ratio and the dominant's SL as fixed terms. Aggression rate was square-root transformed for normality.

(e) The subordinate foraging response to size differences and spatial patterns

To investigate whether relatively large subordinates show regulated foraging rates in the field, we tested for a relationship between female foraging rates and the SL ratio between the focal fish and its immediate dominant, using a GLMM. To account for the possibility of spatial patterns in the field mitigating any foraging regulation, we also fitted to the model the spatial overlap between the home ranges of aggressor and receiver, and the interaction between this overlap and the SL ratio. We used foraging data from 676 focal watches on 163 females in 37 groups in four sites over three field seasons. Site, group, individual, observer and focal set were fitted as significant random factors.

Figure 1. Core home ranges as estimated by LoCoH 50% isopleth kernels for two example groups. The extent of home range overlap between adjacently ranked females in a group can vary widely: here from (a) 64% in the high-overlap group to (b) 26% in the low-overlap group. Choice of the 50% isopleth meant that the kernel for some individuals could have multiple patches, indicating multiple areas of intensive use within the larger contiguous home range. Blue shaded area, rank 1; pink shaded area, rank 2; yellow shaded area, rank 3. Scale bar, 1 m.

(f) Size hierarchy destabilization in response to spatial segregation

To investigate whether highly spatially segregated individuals displayed less rigid size differentiation, we tested for a relationship between the SL ratio and the home range overlap between adjacently ranked individuals using a GLMM. We used data from 157 pairs of fish in 37 groups from four sites. Site, group, individual and focal set were fitted as random factors, but only site was retained as a significant random effect.

We also investigated whether less rigid size differentiation—higher SL ratios between adjacently ranked individuals—was linked to long-term destabilization of groups. We compared SL ratios from groups that were stable over our study period with groups that underwent fission into separate groups or displayed a 'branching' harem structure with some females clearly spatially segregated from others, indicating imminent fission (Sakai & Kohda 1997), using a Welch's *t*-test.

3. RESULTS

(a) The dominant aggression response to size differences and spatial patterns

(i) Open spatial conditions—in the field

In our initial test for the predicted increase in aggression from dominants to their immediate subordinates as the two fish became closer in size, we found no aggressive gradient (Poisson GLMM: $\chi^2 = 2.93$, $p = 0.087$, $n = 112$; the trend was in the opposite direction from the expected, showing decreasing aggression with increasing similarity in size). However, the use of aggression rates as a measure of conflict in established groups can be confounded by the amount of time the focal individuals actually spend encountering each other, or their spatial relationships (Nonacs *et al.* 2004; Hamilton *et al.* 2005). We therefore incorporated spatial information into our model of aggression rates between adjacently ranked individuals, in the form of the extent of overlap between the home ranges of each pair of individuals (figure 1). We found that spatial overlap significantly mitigated the relationship between aggression rates and size ratios (Poisson GLMM, interaction effect: $\chi^2 = 8.07$, $p < 0.005$, $n = 102$); when

Figure 2. There is a significant interaction of SL ratio of adjacently ranked pairs and home range overlap extent between those pairs in determining aggression rates (plotted as $\log(x+1)$) from dominants to their immediate subordinates in the field (Poisson GLMM, interaction effect: $\chi^2 = 8.07$, $p < 0.005$, $n = 102$). Data are split into high overlap ((a) $\geq 30\%$), where there is a significant increase in aggression with the SL ratio (Poisson GLMMs on data subset: $\chi^2 = 4.23$, $p = 0.040$, $n = 31$), but no such relationship was found for medium ((b) between 5 and 30%: $\chi^2 = 2.92$, $p = \text{n.s.}$, $n = 36$) or low overlap ((c) $< 5\%$: $\chi^2 = 3.69$, $p = \text{n.s.}$, $n = 35$). SL ratio is calculated as the SL of the subordinate/SL of the dominant; aggression rates are corrected for group effects as estimated by the mixed models.

the spatial overlap between the two fish was low, no aggressive gradient with size ratios could be discerned, whereas when the spatial overlap was high, the expected aggressive escalation between similarly sized fish was revealed (figure 2).

(ii) *Confined spatial conditions—in aquaria*

To further test the hypothesis that gradients of overt, visible aggression can be revealed in high overlap conditions, we conducted staged contests in confined spatial conditions in aquaria between randomly allocated pairs with varying size differences. As predicted, dominant to subordinate aggression rates increased with increasing size similarity between the pair (GLMM: $\chi^2 = 29$, $p < 0.001$, $n = 115$).

(b) *The subordinate foraging response to size differences and spatial patterns*

We tested for regulation of subordinate foraging rates with SL ratios to their immediate dominants, incorporating spatial overlap information. We found that spatial overlap significantly mitigated the relationship between foraging rates and size ratios (GLMM, interaction effect: $\chi^2 = 8.54$, $p < 0.005$, $n = 676$); when the spatial overlap between the two fish was low and the aggression signal dampened, no foraging gradient with SL ratios could be discerned, whereas when the spatial overlap was high allowing for an accurate aggression signal, the expected foraging reduction of relatively large subordinates was revealed (figure 3).

(c) *Size hierarchy destabilization in response to spatial segregation*

In our *C. bicolor* study population, high spatial segregation between adjacently ranked fish was correlated to higher—or less clearly differentiated—SL ratios (GLMM controlling for random effect of site: $\chi^2 = 4.19$, $p = 0.041$, $n = 157$).

We expect that groups with high levels of spatial segregation may eventually fission into smaller groups, owing to the instability caused by similarly sized adjacently ranked individuals. In our study, two groups underwent fission, and four further groups displayed a 'branching' harem structure (Sakai & Kohda 1997) with some females clearly spatially separated from the remaining females, indicating a potential imminent fission event. SL ratios in these six groups were significantly higher than in the rest of the study population (Welch's *t*-test: $t = 4.93$, $p < 0.001$, $n = 6$ groups about to fission, 36 stable groups, figure 4).

4. DISCUSSION

(a) *Aggression as a stabilizing signal of conflict intensity*

Our results demonstrate for the first time in a size-based linear dominance hierarchy that low-level dominant aggression gradually escalates towards immediate subordinates as the size difference between the individuals decreases and rank conflict intensifies. This expected aggressive pattern has previously proved elusive (Hamilton *et al.* 2005; Wong *et al.* 2008), perhaps due partly to the confounding effect of spatial relationships between individuals on aggression rates. By combining field aggression data with spatial home range overlap information, we were able to reveal the expected aggressive pattern when spatial overlaps were high. This field result was further backed up by a similar aggressive pattern from our staged contest experiments in aquaria where contestants were forced to spatially overlap, a finding consistent with a number of previous staged contest experiments with other species (Enquist *et al.* 1987; Keeley & Grant 1993; Huntingford *et al.* 1995; Jennions & Backwell 1996). Combining data from the field and aquaria, we have strong evidence that when spatial segregation is low, low-level aggression from dominants to their

Figure 3. There is a significant interaction of SL ratio of adjacently ranked pairs and home range overlap extent between those pairs in determining foraging rates of the subordinates in the field (GLMM, interaction effect: $\chi^2 = 8.54$, $p < 0.005$, $n = 676$). Data are split into high overlap ((a) $\geq 30\%$), where there is a significant decrease in foraging with SL ratio (GLMMs on data subset: $\chi^2 = 4.57$, $p = 0.033$, $n = 258$), but no such relationship was found for medium ((b) between 5 and 30%: $\chi^2 = 0.44$, $p = \text{n.s.}$, $n = 216$) or low overlap ((c) $< 5\%$: $\chi^2 = 0.097$, $p = \text{n.s.}$, $n = 185$). SL ratio is calculated as the SL of the subordinate/SL of the dominant; foraging rates are corrected for site, group, individual identity, observer and focal set effects as estimated by the mixed models.

Figure 4. Average SL ratios between adjacently ranked individuals in groups that were stable over the length of the study and those in groups that later underwent fission or displayed a branching harem structure indicating imminent fission. Average SL ratios were higher in groups about to undergo fission (t -test: $t = 4.93$, $p < 0.001$, $n = 6$ groups about to fission, 36 stable groups).

immediate subordinates increases with the size ratio between them. We propose that the rate of aggression is thus a good candidate for a signal that subordinates can use to assess the intensity of conflict between themselves and their dominants, so as to be able to adjust their behaviour accordingly and avoid punishment by eviction.

If overt aggression rate is the signal used by subordinates to assess conflict levels, we would expect that subordinates will adjust their behaviour accordingly, but only when the aggression signal is clear. The obvious behavioural mechanism by which subordinates can regulate their growth rates to achieve clear size differentiation is via the adjustment of their foraging rates. We found that subordinates reduced their foraging rates when they were too large, a novel result from established groups in the

field (Wong *et al.* 2008). However, this foraging regulation was only apparent in spatially overlapped dominant–subordinate pairs, strongly suggesting that spatial segregation and the resulting loss of a clear aggressive gradient signal led also to the loss of the appropriate foraging response.

Kokko (2003) suggests that lack of an accurate signal would lead to instability of the social group. In our study population of *C. bicolor*, the regulation of subordinate sizes to maintain clear size differentials between adjacently ranked individuals does seem to break down in highly spatially segregated situations, with segregated dominant–subordinate pairs displaying greater size similarity, a pattern also found in *Centropyge ferrugatus* (Sakai & Kohda 1997). Loss of a well-defined size hierarchy then appears to destabilize the group overall, as groups with closely sized ranks were more likely to undergo fission during our study period. Harem fission has been previously observed in *C. bicolor* (Aldenhoven 1984) and several other harem fishes (Robertson 1974; Moyer & Zaiser 1984; Lutnesky 1994; Sakai 1997). We note that although spatial segregation may cause instability for the group, the individuals concerned might benefit from fission: low-ranking females move up in rank and size, while high-ranking females may ascend to the dominant male position significantly sooner (albeit with a smaller number of subordinate females to mate with), in addition to saving the energetic costs associated with aggressive coercion of oft-encountered relatively large subordinates.

(b) Caveats

Thus far, we have suggested that spatial segregation reduces the clarity of the aggressive signal, causing subordinates to fail to regulate their foraging, finally resulting in too much subordinate growth and destabilization of the hierarchy. Two alternative interpretations of the data

might be raised. Firstly, relatively large subordinates might actively segregate from dominants in order to escape aggression, rather than segregation allowing growth. If avoidance were the main reason for segregation to occur, we would expect that all segregated dyads would have high size ratios. However, a large range of size ratios occurs at all levels of overlap, with low size ratios common even in segregated situations (figures 2 and 3), suggesting that segregation can occur first with consequent adjustment of subordinate size ratios over time. Furthermore, we observed that segregation was most common in one study site that had a different substrate type to the other sites, suggesting that environment may encourage segregation regardless of current size ratios. Even when avoidance does occur, the resulting lack of aggressive regulation and consequent further growth and destabilization described above would still be expected to follow.

Secondly, rather than segregation unavoidably reducing the clarity of the aggressive signal and causing overly high-rate subordinate growth, it might be suggested that in highly spaced groups, dominants are willing to tolerate smaller size differences towards their subordinates because there is reduced competition. We suggest that this latter interpretation is unlikely if group members are competing primarily for rank in the reproductive benefits queue (with the disproportionately beneficial male position at the top), rather than for spatial resources such as food and shelter. Even in a segregated situation, dominants would then be selected to guard against small size differences that increase the risk of rank challenges that would push the dominant further from the male position. To conclusively test between hypotheses of reduced signal clarity versus reduced competition, spatially limited resources such as food and shelter might be experimentally enhanced in unsegregated groups: the resulting mitigation of the aggressive pattern would favour the reduced competition hypothesis, whereas a continued strong aggressive signal would favour the hypothesis of segregation-caused signal clarity reduction.

Support for the segregation-caused signal clarity reduction hypothesis depends, in this paper, on correlations from field and aquaria data on aggression rates, size ratios and foraging rates. Further studies should focus on manipulative experiments demonstrating that subordinate foraging restraint occurs in response to an aggressive signal of the extent of rank conflict. Experimental manipulations of the extent of rank conflict might be achieved by introducing subordinates of varying size ratios into a social group, or supplementally feeding existing subordinates away from dominants (Wong *et al.* 2008), and measuring the resultant changes in dominant aggression rates and subordinate foraging rates. A direct link between dominant aggression rates and subordinate foraging rates would also help to further support the aggressive signal hypothesis.

5. CONCLUSION

The assumption of perfect knowledge is common to many theoretical models of animal behaviour, but in nature, this assumption is only occasionally likely to hold true. In particular, skew theory carries a crucial implicit assumption of accurate information transmission between individual

group members (Kokko 2003; Cant & Johnstone 2009). Our findings demonstrate for the first time that in dominance hierarchies, variation in overt mild aggression rates may act as a simple but effective mechanism for subordinates to assess the extent of conflict between themselves and their dominants, enabling appropriate individual responses as predicted by the skew theory. Where this mechanism is compromised, here by spatial segregation, the skew theory may no longer be meaningfully applied and groups may become unstable (Kokko 2003). Overt aggression from dominants to subordinates is common in various animal taxa and social systems beyond fish linear hierarchies (Emlen 1982; Reeve 1992; Forkman & Haskell 2004; Cant *et al.* 2006), and we expect that it may play a similar role as the crucial signal of rank conflict in a wide range of animal societies.

All procedures were conducted according to institutional guidelines and approved by the Animal Ethics Committee of James Cook University in Australia where the work was carried out.

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