

# The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish

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Social queues, in which subordinates wait for their turn to inherit dominant breeding status, are a familiar feature of many animal societies. However, little is known about the mechanisms stabilizing social queues given the inevitable conflict over rank between group members. Here, we report the role of punishment and cooperation in promoting the stability of size-based queues in a coral-dwelling goby, *Paragobiodon xanthosomus* (Gobiidae). Quantitative analysis of the size-structure of queues revealed that individuals of adjacent rank differ in size by a specific size ratio, and comparisons of individual growth rates within queues demonstrated that specific size ratios are maintained over time via the regulation of subordinate growth rates. Furthermore, contest experiments demonstrated that the specific size ratio represents a threshold above which the subordinates become a threat to their immediate dominant, and as a result, dominants evict subordinates that exceed this size ratio from the group. We propose that threshold size ratios are maintained by subordinates as a form of peaceful cooperation whereby they avoid inflicting costs on dominants, and that such cooperation arises in response to the threat of punishment in the form of eviction by dominants. Societal stability is therefore achieved through the effects of punishment and cooperation acting in concert to promote the resolution of conflict over rank between group members.

**Keywords:** social queue; eviction; growth regulation; conflict resolution; punishment; cooperation

## 1. INTRODUCTION

A fundamental question in the study of social behaviour is how social stability can be achieved in the face of conflict over reproduction between group members (Wiley & Rabenold 1984; Mesterton-Gibbons *et al.* 2006). In many animal societies, individuals are organized into dominance hierarchies that function as queues in which subordinates wait for their turn to inherit breeding status (Schwagmeyer & Parker 1987; Poston 1997; Field *et al.* 1999; East & Hofer 2001; Buston 2004a; Mitchell 2005). Although they stand to inherit breeding status in the future, subordinates often gain no current reproductive benefits while they wait and face the prospect of dying before attaining the top ranked breeding position (Field *et al.* 1999; Buston 2004a; Mitchell 2005). Under these circumstances, selection should favour a subordinate that managed to challenge and overtake its immediate dominant in rank (Wiley & Rabenold 1984; Cant *et al.* 2006; Mesterton-Gibbons *et al.* 2006). As a result, conflict over rank, and hence conflict over reproduction, should be particularly intense between the members of a social queue and have the potential to destabilize such

societies if left unresolved (Wiley & Rabenold 1984; Mesterton-Gibbons *et al.* 2006). Therefore, the key to understanding how social queues are stabilized over time lies in determining the mechanisms involved in resolving conflict over rank between group members. However, little is yet known about the nature of such mechanisms despite the prevalence of stable queues in animal societies.

Existing theoretical and empirical studies indicate that forcible eviction, where subordinates are expelled from a group by dominants, can promote conflict resolution through its effects on the behaviour of subordinates. For example, forcible eviction is one of the integral components of the 'restraint' model of the reproductive skew theory (Johnstone & Cant 1999; Johnstone 2000; Buston *et al.* in press). This model describes the factors responsible for variation in levels of reproductive sharing in animal societies when subordinates have full control over the partitioning of reproduction (Johnstone & Cant 1999; Johnstone 2000). According to the model, dominants will evict subordinates that obtain more than an upper limit of group reproduction. Given that being evicted is costly, the threat of eviction forces subordinates to behave cooperatively by restraining their own reproduction, which thereby promotes social stability (Johnstone & Cant 1999; Johnstone 2000). In addition, the 'pay-to-stay' mechanism for the evolution of helping behaviour proposes that dominants will forcibly evict unhelpful subordinates from the group where they suffer reduced

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fitness relative to the remaining in the group (Gaston 1978; Kokko *et al.* 2002; Hamilton & Taborsky 2005). As a result, the threat of eviction forces subordinates to behave cooperatively by providing help to dominants, thereby promoting social stability (Mulder & Langmore 1993; Balshine-Earn *et al.* 1998; Bergmüller *et al.* 2005). In these cases, eviction can be viewed as an extreme form of punishment—an evicted subordinate either dies or is unlikely to encounter its original dominant again and is thereby prevented from repeating the selfish action in the future (Clutton-Brock & Parker 1995). Clearly, the threat of being punished, in the form of eviction from the group, has the potential to serve as a general mechanism promoting subordinate cooperation, the resolution of conflict between group members and thus the stability of animal societies over time.

In some animal societies, particularly those seen in fish, social rank and hence position in the queue to inherit breeding status is based on an individual's body size relative to other members of the same group i.e. larger individuals are competitively superior, more dominant and further ahead in the queue than smaller individuals (Forrester 1991; Balshine-Earn *et al.* 1998; Buston 2004a; Hamilton *et al.* 2005; Mitchell 2005). Within such size-based queues, conflict over rank would occur if a subordinate grew so that the size and thus competitive difference between itself and its immediate dominant was sufficiently reduced (Buston 2004a; Hamilton *et al.* 2005). Only then would the subordinate be capable of successfully challenging and overtaking its immediate dominant in rank (Buston 2004a; Buston & Cant 2006). Consequently, the mechanisms involved in promoting the resolution of conflict over rank within size-based queues would necessarily entail mechanisms promoting the regulation of subordinate growth rates over time such that subordinates always remain sufficiently small and unthreatening (Buston 2004a; Heg *et al.* 2004; Buston & Cant 2006).

Here, we propose that the threat of punishment by dominants, in the form of forcible eviction from the group, could be responsible for the regulation of subordinate growth rates and hence the resolution of conflict over rank within size-based queues. Specifically, when a subordinate grows beyond a specific size ratio with respect to its immediate dominant, it becomes capable of challenging and overtaking its dominant in rank. Consequently, the dominant would punish its immediate subordinate beyond this ratio by evicting it from the group. The specific size ratio therefore represents a threshold above which subordinates face the threat of punishment by eviction. Provided that being evicted is costly, subordinates would be forced to regulate their growth so that they maintain the threshold size ratio with respect to their immediate dominants. By doing so, subordinates avoid inflicting costs on dominants since they would remain incapable of overtaking their dominants in rank. As a result, growth regulation by subordinates can be viewed as a cooperative act since it enhances the fitness of dominants relative to if subordinates did not regulate their growth and thereby posed a threat to dominants (Bergmüller *et al.* in press; Buston & Balshine in press). Such cooperative behaviour, whereby subordinates actively avoid imposing costs they would otherwise inflict on dominants (Kokko *et al.* 2002), has recently been defined as peaceful cooperation (Buston 2004b; Buston & Balshine in press). Therefore, the

stability of social queues would ultimately be achieved through the effects of the threat of punishment and peaceful cooperation acting in concert to ensure the regulation of subordinate growth rates and hence the resolution of conflict over rank between group members. Although various studies of social fishes have demonstrated that subordinate growth rates are influenced by the size of their immediate dominant (Buston 2003, 2004a; Heg *et al.* 2004) and that dominants sometimes evict subordinates that are large (Taborsky 1985; Balshine-Earn *et al.* 1998), there is currently no experimental demonstration of the combined effects of dominant punishment by eviction, and subordinate cooperation by growth regulation, on the stability of size-based queues in any species.

Here, we test this 'punishment-cooperation' hypothesis in a coral-dwelling goby, *Paragobiodon xanthosomus* (Gobiidae). Individuals of this species are specialized on living in just one species of coral, *Seriatophora hystrix* (Pocilloporidae), which provides a source of food, shelter and breeding sites (Lassig 1976). Coral colonies are spatially discrete units and within each colony, there is a group of gobies consisting of a breeding pair and up to 15 non-breeding females (Thompson *et al.* in press; Wong *et al.* in preparation). The breeding male and female (ranks M and F, respectively) are the largest group members and similar in size (Wong *et al.* in preparation). The remaining females (rank 3 upwards) are smaller than the breeding pair, and exhibit a stepwise reduction in body size throughout the group indicating the presence of a size hierarchy (Wong *et al.* in preparation). The size hierarchy reflects a dominance hierarchy, initiators of dominance displays are always larger than receivers, and dominance displays always elicit subordinate displays in the smaller group member (Wong *et al.* in preparation). Subordinate non-breeders appear to provide no assistance to the dominant breeders (Lassig 1977) and are unlikely to be related to dominants given that newly hatched larvae spend several weeks in a well-mixed pelagic environment before recruiting to the benthic coral habitat (Sale 1991). *Paragobiodon xanthosomus* is also a protogynous hermaphrodite, if the male of a group dies, the female changes sex to become the breeding male and the largest non-breeder will become the breeding female (Lassig 1977).

Specifically, we demonstrate that the size-based hierarchy in *P. xanthosomus* groups acts as a queue to inherit breeding status, and test four key predictions arising from the punishment-cooperation hypothesis: (i) there should be a prevalence of a specific size ratio found between group members of adjacent rank in natural groups, and this ratio should differ significantly from that obtained from an expected random distribution of size ratios, (ii) the growth rates of subordinates should be regulated such that the specific size ratio is maintained between themselves and their immediate dominants over time, (iii) subordinates should be capable of challenging and evicting their immediate dominants if they have breached the specific (threshold) size ratio, and (iv) dominants should punish immediate subordinates that breach the specific (threshold) size ratio by evicting them from the group. By testing these predictions, we would be able to ascertain whether the interplay of punishment and cooperation serves to resolve conflict over rank and enhance the stability of these societies over time.

## 2. MATERIAL AND METHODS

### (a) *Study site*

All fieldwork was conducted at Lizard Island (14°40' S, 145°28' E) on the northern Great Barrier Reef, Australia, and aquarium experiments were conducted using facilities the Lizard Island Research Station, between November 2004 and May 2005.

### (b) *Do size-based hierarchies act as queues to inherit breeding status?*

To test whether the size-based hierarchy acts as a queue for breeding, courtship and reproductive behaviour were compared between experimental groups where the breeding female was removed ( $n=10$ ) and control groups where the breeding female was present ( $n=10$ ). Gobies from each group were anaesthetized by placing them in a small beaker containing a clove oil solution (Munday & Wilson 1997). The gobies were then measured (standard length (SL) to nearest 0.1 mm) using calipers, sexed under a dissecting microscope by the shape of their genital papillae (Lassig 1977) and uniquely tagged by injecting fluorescent elastomer (Northwest Technologies) just under the surface of their skin. These tags have high retention rates with no adverse effects on individual growth or survival (Malone *et al.* 1999). Gobies were released back onto their original coral colony with the exception of breeding females removed from the 10 experimental groups. Ten minute observations of the behaviour of group members were subsequently conducted every other day for two weeks on SCUBA. The occurrence of courtship behaviour, defined as the occurrence of reciprocal shivering and energetic activity by partners around the nest site, and reproductive behaviour, defined by the presence of eggs in the nest site (Lassig 1976), was recorded as well as the identity of the group members exhibiting those behaviours.

### (c) *Is there a prevalence of a specific size ratio?*

To assess whether a specific size ratio exists between group members of adjacent rank, a total of 420 individuals from 54 natural groups were collected and used to create a frequency distribution of body size ratios. Ratios between the breeding male and female within each group were excluded from the frequency distribution since they are effectively of equivalent rank and are no longer queuing for breeding positions. Ratios between ranks 8 upwards were also excluded since these individuals represent the most recently arriving group members that have not yet established a regular size-based hierarchy among themselves (M. Y. L. Wong 2005, personal observation). The body size of each group member was measured (SL to nearest 0.1 mm) in order to calculate size ratios between group members of adjacent rank (SL rank  $N+1$ /SL rank  $N$ ). However, body size measurements were found to be subject to measurement error since there were considerably more body size measurements to the nearest whole number than to the first decimal place, suggesting that measurement accuracy was not to the nearest 0.1 mm (see electronic supplementary material, figure 1). To correct for any effects of this measurement error on the size ratio calculations and resulting size ratio frequency distribution, each value was rounded to its nearest whole number and a random number between  $-0.5$  and  $+0.5$  mm was added to the rounded value (see electronic supplementary material, figure 1). Size ratios were then calculated using this corrected data and a frequency distribution of the corrected ratios generated. The whole procedure was iterated 100 times,

generating 100 size ratio frequency distributions. The final observed frequency distribution was obtained by taking the mean  $\pm$  s.d. of the 100 ratio frequency distributions.

To test whether our observed ratio frequency distribution differed from a random distribution of size ratios, a random distribution of size ratios expected under a null model was constructed using a Monte Carlo procedure programmed in MATLAB. This procedure involved the random selection of individuals from the pool of 420 size-corrected individuals and combining them into groups based on the exact distribution of group sizes found in our sample. The randomly selected individuals allocated to each group were then ranked according to relative size and the size ratios between group members of adjacent rank calculated. This procedure was iterated 100 times, generating a final expected ratio frequency distribution against which the observed distribution was compared using a Kolmogorov–Smirnov test (see electronic supplementary material). This null model design was appropriate since it excludes the factor of interest (social interactions between adjacent ranked individuals) while retaining all other factors (body size and group size distribution; Gotelli & Graves 1996).

### (d) *Is subordinate growth being regulated to maintain the specific size ratio?*

To determine whether subordinates regulate their growth to maintain the specific size ratio between themselves and their immediate dominant, the growth rates of subordinates and dominants were assessed in relation to the initial size ratio between them. If it is only the growth of subordinate members of a rank dyad that is being regulated to maintain the specific size ratio between individuals then: (i) the growth of subordinates (percentage increase in size per day) through time should be negatively correlated with the initial size ratio between themselves and their immediate dominant and (ii) there should be no correlation between the growth of dominants (percentage increase in SL per day) and the initial size ratio between themselves and their immediate subordinate. Furthermore, if the growth of subordinate members of a rank dyad is being regulated to maintain a specific size ratio with respect to their immediate dominant, subordinate growth rate (percentage increase in SL per day) should be equal to that of their immediate dominant when the initial size ratio between them is at the specific size ratio.

Twelve social groups were collected and each fish removed from its coral, measured, sexed, uniquely tagged and replaced into its original coral. Size ratios between 'subordinates' (ranks 3–7) and their immediate dominants (ranks 2–6) were then calculated and termed 'initial size ratios'. Fish were left undisturbed in the field for six months when they were recaptured and remeasured to determine growth rates. Growth rates of subordinate and dominants (percentage increase in SL per day) were calculated from the increase in body size that occurred within this six-month period and square-root transformed to reduce skew in the data.

We predicted that an individual's growth rate would not only be affected by initial size ratio, but also by the growth rates of other group members, particularly those closest to them in rank. Therefore, an autoregressive order 1 covariance structure (AR(1)) was incorporated into a linear mixed effects model (LME) to more accurately test the relationship between individual growth rate and initial size ratio. The AR(1) assumes that ranks are autocorrelated with their adjacent ranks with an exponentially diminishing correlation

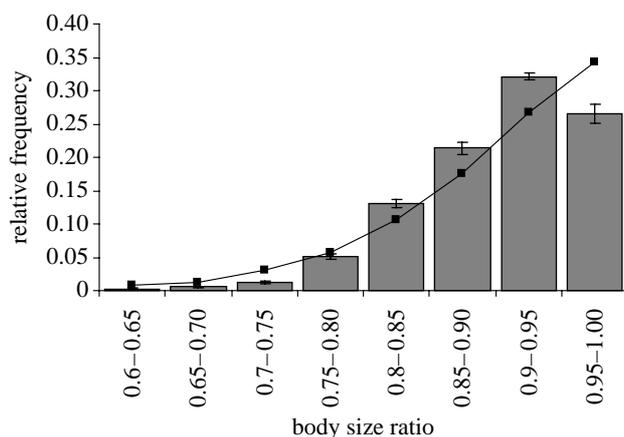


Figure 1. Frequency distributions of size ratios between group members of adjacent rank. Size ratios are expressed as: (SL rank  $N + 1$ /SL rank  $N$ ). Mean relative frequency  $\pm$  s.d. of ratios for individuals adjacent in rank after correction for measurement error (bars) and the expected frequency distribution of ratios generated under a null model by a Monte Carlo procedure (line).

with ranks further away. Thus, we accounted for any variation due to the growth rate of other group members on the final relationship between growth rate and initial ratio. The equation for the LME model was

$$\text{growth rate} = \text{initial ratio} + \text{group}_{\text{AR}(1)} + \text{error},$$

with the fixed effect being initial ratio and the random effects being  $\text{group}_{\text{AR}(1)}$  (the autocorrelated group effect) and error (random error).

**(e) Can subordinates evict their immediate dominant at ratios above the threshold?**

If subordinates regulate their growth to maintain threshold size ratios as a form of cooperation whereby they avoid becoming a threat to their immediate dominant, we predicted that subordinates would be capable of evicting their immediate dominant from the group at ratios above the specific size ratio (found to be 0.93). To test this, staged contest experiments were conducted to determine the size ratio at which subordinates could evict their dominant. Seven coral colonies, each containing four to five gobies were collected and transferred to separate aquaria filled with continuously running seawater. Gobies from each group were removed, measured, sexed and uniquely tagged. The breeding male and female were placed back into the coral colony. Pairs of contestants were generated from the pool of available gobies (or from newly collected gobies). Contestants were matched so they fitted into one of four categories of size ratio: 0.85, 0.9, 0.95 and 1. The ratios between contestants were always assigned randomly. The larger fish was designated the dominant and the smaller the subordinate. Contestants were always immature females with no prior experience of each other, and not differing in their original rank by more than 1 rank distance. The paired contestants were then released into a trial coral in which neither had prior residence. Contestants were observed continually for 15 min from the start of their first interaction, and the occurrence of subordinate eviction, dominant eviction or no eviction was then scored. Contest outcome (i.e. eviction or no eviction) is usually resolved within this period of time (M. Y. L. Wong, personal observation). Eviction was scored whenever one

contestant left the live part of the coral and either entered the dead base of the coral or a piece of coral rubble placed at the other end of their tank. The contestants were left in their corals overnight and contest outcome re-scored the following morning.

**(f) Do dominants punish their immediate subordinate at ratios above the threshold?**

If subordinates regulate their growth in response to the threat of eviction by dominants, subordinates should suffer higher probabilities of being evicted at ratios above compared to below the specific size ratio. To test this, we used the stage contest experiment described above to ascertain the size ratio at which subordinates face a significant threat of being evicted from the group by their immediate dominant.

### 3. RESULTS

**(a) Do size-based hierarchies act as queues to inherit breeding status?**

If the size-based dominance hierarchy acts as a queue for inheriting breeding status, removal of the breeding female from the group should result in courtship and reproduction between the largest non-breeder (initial rank 3) and the male. In all experimental groups where the breeding female was removed ( $n = 10$  groups), courtship between the initial rank 3 and the male was observed within 2 days, and egg clutches were observed within two weeks in six groups. In no experimental group was the breeding vacancy usurped by a non-breeder from another coral head, neither was there any evidence of courtship or reproduction between non-breeders of initial rank 4 and upward. In control groups where the breeding female was not removed ( $n = 10$  groups), there was no evidence of courtship or reproduction between the male and non-breeders rank 3 or upwards. These results demonstrate that *P. xanthurus* forms a strict queue for breeding positions within groups. Queuing is likely to be favoured over dispersing to breed elsewhere owing to the low probability of successfully moving among coral heads in this and other habitat-specialist reef fish (Lassig 1981; Munday 2002).

**(b) Is there a prevalence of a specific size ratio?**

There was a highly significant difference between the observed and the expected frequency distributions (Kolmogorov–Smirnov test:  $p = 0.0007$ ; figure 1 and see figure 2 of electronic supplementary material). Most noticeably, in the observed frequency distribution of body size ratios, there was a peak in ratios of 0.90–0.95 but fewer ratios above 0.95, when compared with the expected distribution (figure 1). This result demonstrates that the distribution of body size ratios of individuals adjacent in rank is non-random and suggests that the growth of individuals is being regulated such that group members adjacent in rank converge onto specific size ratios of 0.90–0.95 over time.

**(c) Is subordinate growth being regulated to maintain the specific size ratio?**

As predicted, there was a significant negative relationship between subordinate growth and initial size ratio (linear mixed effects model:  $n = 38$ ,  $t = -4.79$ , d.f. = 26,  $p < 0.0001$ ; figure 2 and table 1a of electronic

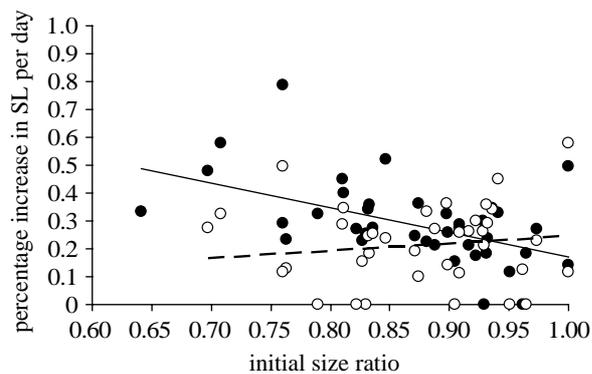


Figure 2. Percentage change in SL of group members adjacent in rank. Growth rates of subordinates (filled circles, solid line) and dominants (open circles, dotted line) are shown in relation to the initial size ratio between themselves and their immediate dominant or subordinate, respectively. Growth rates are square root transformed. Regression lines show the relationship between initial ratio and subordinate ( $y = 1.0602 - 0.8911x$ ) (solid line) and dominant ( $y = -0.00878 + 0.2534x$ ) (dashed line) growth rates estimated by a linear mixed effects model.

supplementary material) and a non-significant relationship between dominant growth and initial size ratio (linear mixed effects model:  $n = 39$ ,  $t = 1.07$ , d.f. = 21.5,  $p = 0.297$ ; figure 2 and table 1*b* of electronic supplementary material), after controlling for the growth rate of other group members (see table 1*c,d* of electronic supplementary material). In addition, the model predicts that the initial size ratio at which the growth of subordinates is equal to that of their immediate dominants was 0.93 (figure 2), within the range of predominant size ratios of 0.90–0.95 observed in natural groups. This suggests that the growth of subordinates is being regulated so that they converge onto the specific size ratio of approximately 0.93 with respect to their immediate dominants.

**(d) Can subordinates evict their immediate dominant at ratios above the threshold?**

Dominants were never evicted by their immediate subordinate when the size ratio between them was less than 0.95, but suffered a significantly higher risk of eviction at ratios of 0.95 and above (Chi-squared test:  $\chi^2_1 = 12.5$ ,  $p = 0.0004$ ; figure 3). Subordinates therefore pose a threat to their immediate dominants at ratios of 0.95 and above, thus by regulating their growth to maintain size ratios below 0.95, subordinates are peacefully cooperating by avoiding inflicting costs on dominants.

**(e) Do dominants punish their immediate subordinate at ratios above the threshold?**

The probability of a subordinate being evicted by its immediate dominant increased as the size ratio increased (figure 3), but more importantly, subordinates were approximately twice as likely to be evicted by their immediate dominant when the size ratio between them was 0.95 and above when compared with below 0.95 (Chi-squared test:  $\chi^2_1 = 4.52$ ,  $p = 0.0335$ ; figure 3). The threat of eviction serves as an effective form of punishment for dominants since dominants had significantly greater chances of evicting their subordinate than subordinates had of evicting their dominant, when the size ratio

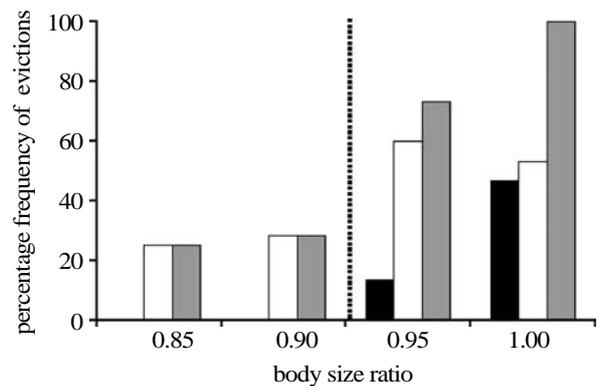


Figure 3. Percentage frequency of dominant, subordinate and any evictions in relation to the size ratio between contestants. White, subordinate evicted; black, dominant evicted; grey, any eviction. Number of trials per ratio category: 0.85,  $n = 12$ ; 0.9,  $n = 14$ ; 0.95,  $n = 15$  and 1,  $n = 15$  trials. Vertical dotted line indicates trials occurring above and below the predicted threshold size ratio (0.93).

between them was 0.95 (Chi-squared test:  $\chi^2_1 = 6.8$ ,  $p = 0.0092$ ; figure 3).

#### 4. DISCUSSION

Conflict over rank within social queues raises the perplexing evolutionary problem of how queues can be stable, since any subordinate that managed to increase its rank by contesting would gain a selective advantage over a subordinate that waited its turn (Wiley & Rabenold 1984). Pay-offs from queue-jumping would be particularly high, and thus conflict particularly intense, in societies such as *P. xanthosomus* where subordinates gain no direct or indirect reproductive benefits while they queue, and face the prospect of dying before they reach the top ranked position. In accordance with the punishment–cooperation hypothesis, the results of this study demonstrate that the threat of punishment by dominants in the form of forcible eviction from the group, promotes cooperation by subordinates in the form of growth regulation, such that a threshold size ratio of approximately 0.93 is maintained between individuals of adjacent rank over time. The maintenance of this threshold ensures that subordinates are unable to challenge and overtake their immediate dominant in rank and thereby promotes the resolution of conflict over rank between group members.

Clearly, conflict resolution through the joint effects of dominant punishment and subordinate cooperation promote the stability of *P. xanthosomus* societies through time. In the presence of punishment and cooperation, subordinate *P. xanthosomus* would grow to approach ratios of 0.93 relative to their immediate dominant. At or below this size ratio, queues are relatively stable given the low frequency of subordinate evictions and the absence of dominant evictions at ratios of 0.9 and below. However, in the absence of punishment and cooperation, subordinates would grow to approach the size of their immediate dominant, since growth in fishes is usually asymptotic and small fish grow more rapidly than large fish (Calder 1984). Consequently, this would lead to increasing size similarity between subordinates and their immediate dominants, and given the increased frequency of subordinate and dominant evictions at ratios of 0.95 and above, would lead to the breakdown of societal stability.

The threat of punishment has increasingly been invoked as a key factor promoting the evolution of cooperative and altruistic behaviour among non-relatives in human societies (e.g. Fehr & Gächter 2002; Gardner & West 2004; Henrich *et al.* 2006). However, there are relatively few convincing demonstrations of the link between punishment and cooperation in animal societies (e.g. Bshary & Grutter 2005). In addition, a complete understanding of punishment and cooperation in animal societies would require explanation of how punishment initially evolved in the population (Cant & Johnstone 2006) and how it coevolves with cooperation (Lehmann & Keller 2006). Recently, Cant & Johnstone (2006) suggested that the initial evolution of punishment can be facilitated if its function is 'self-serving', i.e. if it provides immediate fitness benefits to the punisher regardless of the response of the opponent. Eviction in *P. xanthurus* appears to bear the hallmarks of self-serving punishment, since a dominant that evicts a large subordinate is spared from eviction itself. Self-serving punishment is predicted to coevolve with cooperation if (i) the costs of being punished are sufficiently high, (ii) the costs of punishing are smaller than the fitness gained from punishing, and (iii) non-cooperative counterstrategies against punishment cannot be developed (Lehmann & Keller 2006). All the three conditions appear satisfied in *P. xanthurus*: (i) an evicted subordinate has an extremely low probability of moving to another coral, owing to intense predation during movement (Lassig 1981) and a low and unpredictable availability of alternative coral colonies (Munday 2002), (ii) the costs to dominants of evicting subordinates (e.g. due to injury or energy expenditure) are low in relation to the benefits accrued from ensuring that they themselves are not evicted (Buston 2004a; Buston & Cant 2006), and (iii) the costs of retaliation against dominants are high because the physical confines of a coral colony, high rates of mortality outside colonies (Lassig 1981), and the size and thus competitive differences between individuals (current study) ensure that dominants can usually maintain a complete control over their subordinates.

Growth regulation by subordinates can be viewed as a form of cooperation since it serves to enhance the fitness of dominants by minimizing threats to their rank, and enhance the fitness of subordinates by allowing continued membership within the queue. Such peaceful cooperation, whereby subordinates offset the costs of their presence in exchange for group membership (Kokko *et al.* 2002; Buston & Balshine *in press*), contrasts with more typical forms of helpful cooperation in which subordinates provide benefits to dominants above and beyond being alone in exchange for group membership (Gaston 1978; Mulder & Langmore 1993; Balshine-Earn *et al.* 1998; Buston & Balshine *in press*). Subordinates therefore need not 'pay-to-stay' by providing help to dominants (Gaston 1978), but can instead 'pay-to-stay' within the group by ensuring that they remain small and unthreatening. Thus, there appears to be a continuum in the forms of cooperative behaviour, ranging from helpful to peaceful (Buston & Balshine *in press*). Establishing the conditions under which helpful versus peaceful cooperation should evolve is still in its infancy. However, additional benefits from helping, e.g. kin-selected benefits may predispose subordinates to do more than just offset the costs they

inflict (Kokko *et al.* 2002). In the majority of fishes, including *P. xanthurus*, the dispersive larval phase means that kin-selected benefits rarely apply (Sale 1991), which may in turn reduce the incentives for helpful cooperation.

We expect a similar interplay of punishment and cooperation to be involved in promoting conflict resolution and stability in a wide range of animal societies, particularly those in which group members are unrelated. Furthermore, future studies are expected to reveal increasing occurrences of peaceful cooperation in queues that are not necessarily size-based, for example those seen in social insects (Field *et al.* 1999), birds (Poston 1997), mammals (East & Hofer 2001) and even humans. Within these societies, peaceful cooperation is more likely to manifest itself as the self-regulation of subordinate behaviour or body weight, as opposed to body size as may be more prevalent in fishes (Buston 2004a; Heg *et al.* 2004; current study). As demonstrated in the current study, investigations into the occurrences of peaceful cooperation in other species would require the experimental manipulation of the costs imposed on dominants by subordinates by varying the extent to which potentially peaceful cooperative behaviour is expressed by subordinates, followed by measurements of the behavioural responses of both parties to the varying costs. Such investigations are likely to reveal a greater diversity of cooperative behaviours than is currently appreciated, and increase our understanding of the mechanisms promoting conflict resolution and social stability within both human and animal societies.

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