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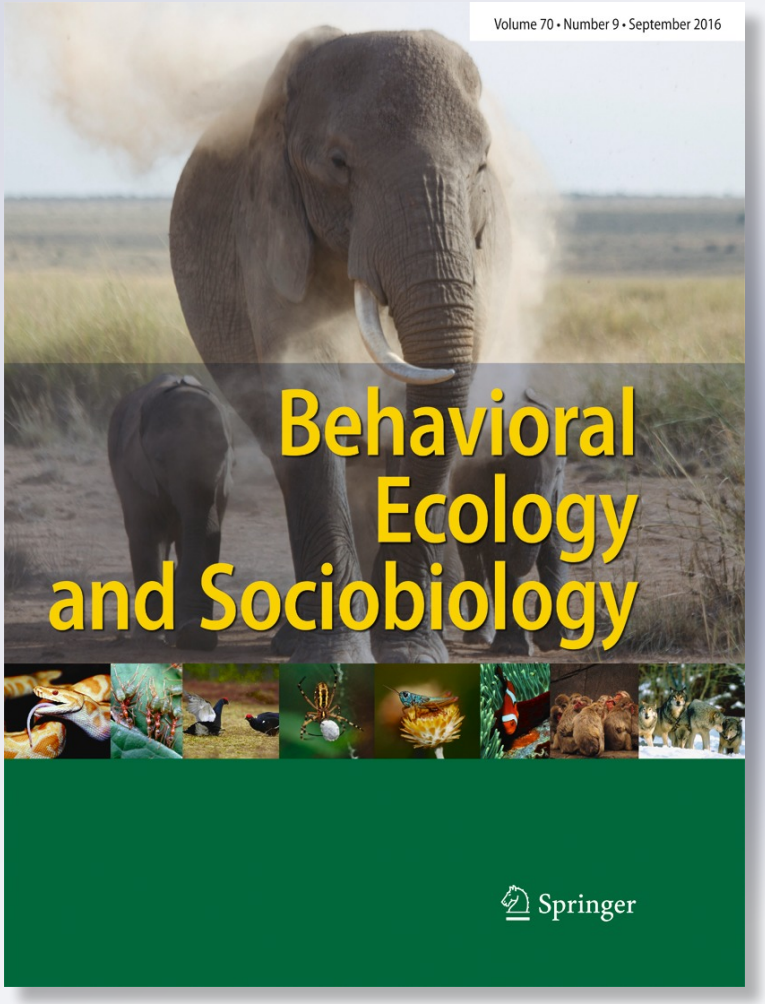

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ORIGINAL ARTICLE

The four elements of within-group conflict in animal societies: an experimental test using the clown anemonefish, *Amphiprion percula*

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Abstract
Conflicts of interest are part and parcel of living in a social group, yet actual conflict can be rare in established groups. Within limits, individuals can maximize the benefits of group living by resolving conflict with other group members. Thus, understanding what causes conflict, what determines its outcome, and how it is resolved holds the key to understanding the evolution and maintenance of sociality. Here, we investigate these questions using the clown anemonefish *Amphiprion percula*. Clownfish live in groups composed of a breeding pair and zero to four non-breeders that queue for breeding positions. Within groups, there is potential conflict over rank yet actual conflict is very rare. We staged contests in aquaria between pairs of non-breeding individuals over access to a key resource (an anemone), analogous to contests that would occur at the onset of group formation in the wild. The initial size ratio between individuals tended to predict the intensity, and predicted the outcome and resolution of conflict: conflict intensity was greater when individuals were more similar in size; the probability of the smaller individual winning was greater when individuals were more similar in size; and the loser of the contest grew less than the winner when individuals were more similar in size. These results provide a critical test of foundational assumptions upon which our understanding of clownfish and other fish societies has been built. More generally, the results show that one of the simplest and most effective ways for animals to resolve conflict is to modify the phenotype that triggers conflict.

Significance statement
The study provides a critical test of the foundational assumptions on which our understanding of conflict and its resolution in animal societies has been built. Importantly, this study highlights that four elements of conflict must be investigated for a complete understanding of societal maintenance, and broadens the taxonomic basis of empirical research of conflict (focused on terrestrial organisms) by examining these four elements in a fish society. Specifically, the study demonstrates the key importance of relative body size (competitive ability) in determining conflict intensity, contest outcome, and subsequent conflict resolution via the regulation of subordinate growth rates. The occurrence of strategic subordinate growth regulation is intriguing because it shows that the simplest and most effective way for animals to resolve conflict is to modify the phenotypes that trigger conflict in the first place.

Keywords Behavior · Conflict · Aggression · Size · Growth · Clownfish

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Introduction

Conflicts of interest between individuals over the distribution of reproduction are a ubiquitous feature of animal societies. These conflicts exist because individuals are not genetically identical, possessing different optima regarding the distribution of reproduction, and selection will have favored individuals that act in their own self-interest (Reeve and Ratnieks 1993; Godfray 1995; Bourke 2011). Although

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contesting may pay off in some circumstances and hence overt conflict be expressed, these inevitable conflicts must somehow be resolved for societies to be stabilized and maintained (Wiley and Rabenold 1984; Ratnieks et al. 2006; Bourke 2011). That is to say, selection will have favored individuals that efficiently minimize conflict so as to maximize the gains from being part of a cooperative society. A complete understanding of social group maintenance requires understanding four key elements of within-group conflict (Reeve and Ratnieks 1993; Ratnieks et al. 2006). First, what is the basis for conflict—the source of potential conflict? Second, under what conditions is conflict expressed—the occurrence of actual conflict? Third, whose interests prevail—what is the outcome of conflict? Fourth, what are the factors that reduce conflict—how is conflict resolved? Insect societies are undoubtedly the leading models for understanding these elements of conflict in animal societies (e.g., Frank 1995; Ratnieks et al. 2006; Bridge and Field 2007).

Despite substantial work on conflict and its resolution in vertebrate societies (e.g., Clake and Faulkes 2001; Clutton-Brock 2002; Buston and Cant 2006; Wong et al. 2007, 2008; Buston and Zink 2009; Cant and Johnstone 2009), there are still relatively few examples demonstrating all four elements in a vertebrate society using manipulative experimental approaches. Unlike social insects where many group members are sterile, most individuals have the capacity to reproduce in vertebrate societies. This capacity greatly increases potential conflict over reproduction since any adult within a group could replace their dominant breeders (Bridge and Field 2007; Maruska and Fernald 2010), become additional breeders (Keane et al. 1994; Woodroffe and Macdonald 1995; Wolff et al. 2001), or leave the group to breed elsewhere (e.g., Field et al. 1999; Spinks et al. 2000; Stiver et al. 2007). It also increases the expression of actual conflict over reproduction, for example, when subordinates fight to become the new breeder following death of a dominant (Clarke and Faulkes 1997; Wong and Balshine 2010), when dominants use aggression to suppress subordinate reproduction or evict them from the group (Clutton-Brock et al. 1998; Hackländer et al. 2003; Ang and Manica 2010a; Nichols et al. 2012), or when infanticide occurs within the group (Clutton-Brock et al. 1998; Cant 2000; Young and Clutton-Brock 2006). In vertebrate societies, the outcome of conflict is often dependent on traits correlated with competitive ability, such as relative body size (e.g., Fournier and Festa-Bianchet 1995; Schuett 1997; Reddon et al. 2011). Additionally, other factors such as genetic influences (Craig et al. 1965; Kikkawa et al. 1986), age (Sprague 1998; Valderrábano-Ibarra et al. 2007; Wittemyer and Getz 2007), and, in some cases, coalition formation (e.g., Silk et al. 2004; East and Hofer 2001) can also play a role. The final element, how conflicts are resolved or minimized, likely depends on a combination of kinship, coercion, and constraint (Ratnieks et al. 2006) which essentially reduces the pay-offs from costly conflict within groups and in some cases promotes subordinate cooperation (e.g., Balshine-Earn et al. 1998; Johnstone and Cant 1999; Buston and Cant 2006; Wong et al. 2007, 2008; Cant 2011).

Among vertebrates, coral reef fishes have become a useful model for understanding conflicts and their resolution (reviewed in Wong and Buston 2013; Buston and Wong 2014). Their use as model species of social evolution originated in part from observations of the clown anemonefish *Amphiprion percula* (Buston 2003a). Groups of clownfish are confined to sea anemones that provide protection from predators (Allen 1972; Mariscal 1970). Within each anemone, there is a single group of clownfish composed of a breeding pair and zero to four non-breeders organized into a size-based dominance hierarchy, all inhabiting a single anemone (Buston 2004a). Within each group, there is a size-based dominance hierarchy: the female is largest, the male is second largest, and non-breeders get progressively smaller as the hierarchy is descended (Buston 2003a). The size hierarchy represents a queue for breeding positions: if the female of the group dies, then the male changes sex and assumes the position vacated by the female, and the largest non-breeder inherits the position vacated by the sex changing male (Buston 2004b). Groups form or grow when larvae settle to the reef and recruit to an anemone (at approximately 18 mm in standard length): if entering an uninhabited anemone, recruits will compete with each other for dominance; if entering an inhabited anemone, recruits will join the back of the queue (Elliott et al. 1995; Buston 2003b).

Within clownfish groups, potential conflict over reproduction exists because all individuals have the capacity to reproduce yet only the largest female and male are breeders (Buston 2003a). Actual conflict is rarely expressed in stable groups however (PMB personal observation). This lack of overt conflict suggests that mechanisms exist to resolve conflict. Buston (2003a) hypothesized that potential conflict is resolved by the maintenance of well-defined size differences between individuals adjacent in rank, which ensure that subordinates do not become a threat to their dominants. This hypothesis was based on three untested assumptions: (1) actual conflict would be highest when individuals are similar in size, (2) the outcome of conflict would be dependent on relative size, and (3) that conflict would be resolved by subordinates regulating their growth to maintain the well-defined size differences. While there was plenty of indirect evidence for these assumptions (Buston 2003a; Buston and Cant 2006), and some of these assumptions were subsequently verified in other social fishes (Heg et al. 2004; Hamilton et al. 2005; Wong et al. 2007; Ang and Manica 2010a; Matthews and Wong 2015), there have still been no direct tests of these assumptions in clown anemonefish themselves.

Here, we investigate actual conflict, the outcome of conflict, and the mechanism of conflict resolution in the clown

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anemonefish, *A. percula*. Specifically, we frame what were initially assumptions into four testable predictions that enable us to examine the intensity, dynamics, outcome, and resolution of conflict: (1) actual conflict will be more intense when individuals are more similar in size, (2) the intensity of conflict will decrease over time as conflict becomes resolved, (3) larger individuals will be more likely to win contests when the two individuals are more dissimilar in size but this advantage will decline when the two individuals become more similar in size, and (4) losers of conflict will regulate their growth leading to the formation and maintenance of well-defined size differences between themselves and their dominant.

Methods

Study population

We studied the clown anemonefish, *A. percula*, for 3 months (June to August 2012) at Boston University, USA. Fish were wild-caught from Papua New Guinea and supplied to us by Quality Marine. All fish were less than 30 mm in standard length at which size they would be non-breeders in the wild. No fish began breeding for more than a year after the end of the experiment. Two fish were randomly assigned to each of twenty-three, 30-gallon, aquaria (36 × 18 × 12 in.). To enable recognition of individual fish, natural variation in body markings (color and/or band pattern) was also noted. Individuals have been shown to vary substantially in their natural markings such that they can be reliably identified on a regular basis (Nelson et al. 1994; Buston 2003a).

Each aquarium received a continuous flow of re-circulating seawater (Instant Ocean® Sea Salt) maintained under controlled conditions throughout the experiment (average temperature ± SE = 27.3 ± 0.01; average pH ± SE = 8.36 ± 0.2; average salinity (ppt) ± SE = 32.5 ± 0.03). The light cycle was maintained for a total of 12 h dawn until dusk. The light was ramped up and down, slowly increasing and decreasing the lux value to mimic the natural daylight cycle. The light for the tanks consisted of two T5 24-W bulbs whose spectra color mimics that of the natural environment. Fish were fed once a day, 6 days a week with New Life Spectrum marine formula 1-mm pellets.

Initially, each aquarium contained one anemone and an opaque plastic barrier that divided the aquarium into two equal sized halves. The two fish assigned to an aquarium were initially isolated from each other on either side of the barrier, resulting in one fish being housed with the anemone and the other fish being housed without the anemone for a period of approximately 1 month. The barrier prevented the exchange of visual cues between fish during this time. Chemical cues circulated throughout all of the aquaria in each system; therefore, individual fish were exposed to chemical cues from many fish and anemones just as they would be in the wild. After approximately 1 month, the positions of the two fish were switched such that the fish that had been residing without the anemone was housed with the anemone (and vice versa) for approximately one more month. Importantly, we randomized whether it was the larger or smaller of the two fish that resided in the anemone last (i.e., just prior to the commencement of the trial) to control for any potential biases caused by which fish was most recently associated with the anemone. When the barrier was removed, after 2 months, a contest ensued that is analogous to the kind of interactions that occur between non-breeders when groups form or grow (Buston 2003b).

Size and growth

Just prior to a contest trial (day 0), each fish was captured using hand nets, measured using calipers [standard length (SL) to the nearest 0.1 mm]. Initial size ratio between the two fish was calculated as SL of smaller fish/SL of larger fish, following a previous definition (Wong et al. 2007) [note this is the inverse of Buston and Cant (2006)'s ratio calculation, but more intuitive]. After all video recordings were completed (next section), each fish was captured and its body size and mass re-measured, and final body size ratios and growth rates (percent change in SL over 6 weeks) calculated.

Aggression and submission

At the start of a contest trial (day 1), the opaque barrier was gently lifted out of the water allowing the two fish to interact. Each contest was recorded using a video camera (Kodak Play Sport 1080p) mounted on a tripod facing the aquarium, beginning from the start of the first interaction and ending 12 min later. The first 2 min of each video was disregarded as acclimation time and the remaining 10 min used to score various behavioral traits (see below). Each pair was recorded in the morning only (0900–1200) to avoid any biases due to time of day. These recordings were repeated on days 3 and 5 to obtain a temporal picture of the contest (i.e., three recordings per pair over the course of 5 days post-introduction). Further, each pair was recorded in the morning and afternoon of days 8, 15, 22, 29, and 36, making a total of 16 recordings per pair over the course of 6 weeks.

From each video, we scored all aggressive (head bites, body bites, darts, and aggressive displays) and submissive behaviors (flees and submissive displays) between the two fish (for more detailed ethogram, see Wong et al. 2013). The sum of all aggressive and submissive behaviors within 10 min was used as a measure of the intensity of conflict (e.g., Hamilton et al. 2005). The winner of the contest was defined as the fish that managed to first acquire residence within the

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anemone—although not always the largest fish at the start, in all cases this fish was the larger, dominant individual by the end of the 6-week period. This individual who won the contest was assigned the "rank 1" or "dominant," and the individual who lost the contest was assigned the "rank 2" or "subordinate." To minimize observer bias, observers were blind to the size ratios of contestants when behavioral data was analyzed.

Statistical analyses

All statistical analyses were conducted using Statistics version 21.0 (IBM Corp., Armonk, NY). To investigate hypothesis 1 and 2, we analyzed the effect of initial size ratio and time since the beginning of the contest on the intensity of conflict. We used a Generalized Linear Mixed Model with Poisson distribution and log link function since intensity of conflict was a non-normally distributed count variable. Initial size ratio between contestants was entered as a continuous covariate, time since the initial contest ($n = 8$ time points) was entered as a categorical variable, and tank ID was entered as a random factor to account for the lack of independence between multiple measures of the intensity of conflict made in the same tank at different times.

To investigate hypothesis 3, we analyzed the data in two ways; firstly, we investigated the effect of initial size ratio on the outcome of conflict using a logistic regression analysis when initial size ratio was considered as a continuous predictor variable and contest outcome (larger individual wins or loses) as the binary response variable. Secondly, we considered initial size ratio as a categorical variable with two levels, "small" and "large." To create these levels, we split the total of 22 initial size ratio values in half, considering the $n = 11$ lowest ratios as "small" and the $n = 11$ highest size ratio values as "large." A chi-squared test was then used to analyze the association between initial size ratio category and the frequency of wins and losses.

To investigate hypothesis 4, we analyzed the relationship between initial size ratio and change in size ratio (final size ratio − initial size ratio) using a linear regression to determine whether smaller size ratios became larger and larger size ratios became smaller over time. As change in size ratios are manifested through variations in growth rate, and to disentangle whether winners and/or losers of contests regulated their growth, we investigated the effect of initial size ratio and final rank (rank 1 or 2) on the percent change in standard length, using a General Linear Mixed Model. Initial size ratio was entered as a continuous predictor and final rank as a categorical predictor, incorporating tank ID as a random factor.

Results

Hypothesis 1

We tested the hypothesis that size similarity will influence the intensity of conflict, with the expectation that fish of similar size would experience a greater intensity of conflict than fish of dissimilar size. Initial size ratio between individuals tended to be related to the intensity of conflict (Table 1). Specifically, the intensity of conflict between individuals was greater when individuals were initially more similar in size (when size ratios were higher) (Fig. 1). This result confirms the relationship between size difference and conflict intensity, previously assumed for this species.

Hypothesis 2

We tested the hypothesis that a relationship exists between the intensity of conflict and the time of interaction, predicting that the intensity of conflict between two individuals would decline over time. Time since initial pairing was significantly related to the intensity of conflict—the passage of time had a negative effect on conflict intensity, and by day 3 post-introduction, conflict was nearly nonexistent (Table 1; Fig. 1). There was also a significant interaction between initial size ratio and time on the intensity of conflict, with initial size ratio being positively related to conflict intensity on day 1 but not at any other times (Table 1; Fig. 1).

Hypothesis 3

We tested the hypothesis that relative size will influence the outcome of conflict, predicting that as the initial size ratio approaches unity, smaller fish would be more likely to assume the rank 1 position compared to when the initial size ratio differed greatly from unity. A logistic regression analysis with initial size ratio as a continuous predictor variable indicated that the outcome of conflict was not significantly related to initial size ratio, although there was a trend in the predicted

Table 1 Predictors of conflict intensity: summary of the results of a Generalized Linear Mixed Model analysis that investigated the effect of initial size ratio (covariate) between individuals and time since the start of conflict on the intensity of conflict

Effect	*ndf*, *ddf*	*F*	*P* value
Initial size ratio	1, 21	4.27	0.052
Time	7, 159	4.65	<0.0001
Initial size ratio × time	7, 159	3.61	0.001

ndf numerator degrees of freedom, *ddf* denominator degrees of freedom

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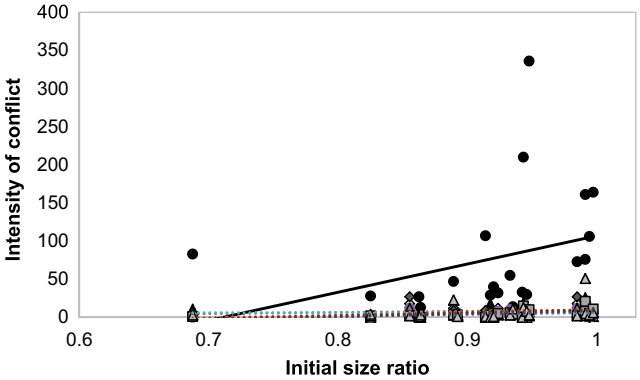

Fig. 1 Intensity of conflict between individuals. Intensity of conflict as a function of the initial size ratio between contestants and time since the beginning of the conflict (day 1 = *black line*, *solid circles*; days 3, 5, 8, 15, 22, 29, 36 = all other *dotted lines* superimposed and *open shapes*). *Fitted lines* show the relationships estimated by the mixed model analysis

direction (logistic regression—$\chi^2 = 2.598$, $df = 1$, $P = 0.107$; Fig. 2). The alternate analysis, considering initial size ratio as a categorical predictor variable (small ratios, $n = 11$; large ratios, $n = 11$), indicated that the outcome of conflict was significantly related to initial size ratio (chi-squared test—$\chi^2 = 4.889$, $df = 1$, $P = 0.027$). Taken together, these results provide mixed support for the hypothesis that smaller fish were more likely to win the fight for dominance when they were more similar in size.

Hypothesis 4

We tested the hypothesis that changes in size similarity are associated with conflict resolution, predicting that size ratios would converge via large ratios becoming smaller and small ratios becoming larger over time. More specifically, we predicted that the growth of subordinates but not dominants would be regulated in response to the initial size ratio. The size similarity changed over time, with small size ratios (far from unity) becoming larger and large size ratios (close to unity) becoming smaller over time (linear regression—$N = 23$, $R^2 = 0.5446$, $P = 0.0006$). The percent change in the standard length of individuals was significantly related to initial size ratio and the interaction between initial size ratio and whether they won or lost the conflict, but not the main effect of winning or losing per se (Table 2). Specifically, the growth of the rank 1, or winner of the contest, was independent of initial size ratio; however, growth of the rank 2, or loser, was altered in order to reduce conflict and achieve a stable size ratio of approximately 0.92 (Fig. 3). Above this specific size ratio, the subordinate grew slowly relative to the dominant; below this specific ratio, the subordinate grew quickly relative to the dominant (Fig. 3).

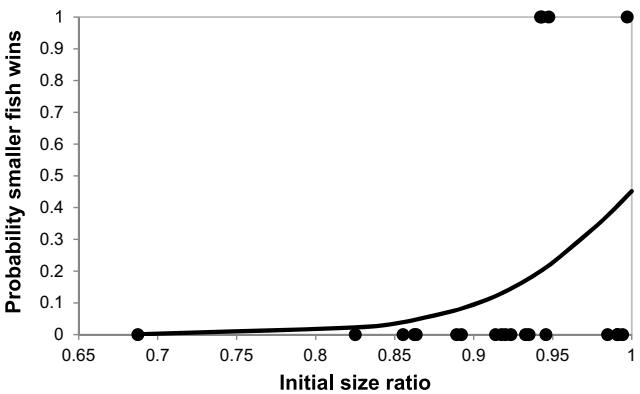

Fig. 2 Outcome of conflict between individuals. Probability that the smaller fish won a contest as a function of the initial size ratio between the contestants (0.65 to 1). *Fitted line* shows the relationship estimated by a logistic model analysis

Discussion

Conflicts of interest are part and parcel of living in a social group, but all elements of conflict need to be elucidated to generate a complete picture of social group maintenance. In the well-studied system of the clown anemonefish *A. percula*, potential conflict arises because both subordinates and dominants want to breed within the group yet only dominants gain access to reproduction (Buston 2003a). In this species, actual conflict, expressed as the intensity of conflict, has long been assumed to relate to the relative body size of individuals, with actual conflict increasing with decreasing size difference between individuals. Further, it has been assumed that actual conflict is resolved via the regulation of subordinate growth, i.e., that aggression declines as growth adjustments and hence conflict resolution takes place (Buston 2003a; Buston and Cant 2006).

Here, we conducted the critical experimental test of these assumptions and link all four elements of conflict in a fish, or indeed any vertebrate, society for the first time. Firstly, we found that the intensity of conflict tended to increase with initial size ratio between individuals; in other words, when individuals were more similar in size, there tended to be more aggressive and submissive interactions—indicators of

Table 2 Predictors of percent growth: summary of the results of a General Linear Mixed Model analysis that investigated the effect of initial size ratio between individuals, and whether or not an individual won or lost the battle for dominance, on their percent change in standard length

Effect	*ndf*, *ddf*	*F*	*P* value
Initial size ratio	1, 21	13.0749	0.0016
Winner or loser	1, 21	0.0034	0.9541
Initial size ratio × winner or loser	1, 21	22.0030	0.0001

ndf numerator degrees of freedom, *ddf* denominator degrees of freedom

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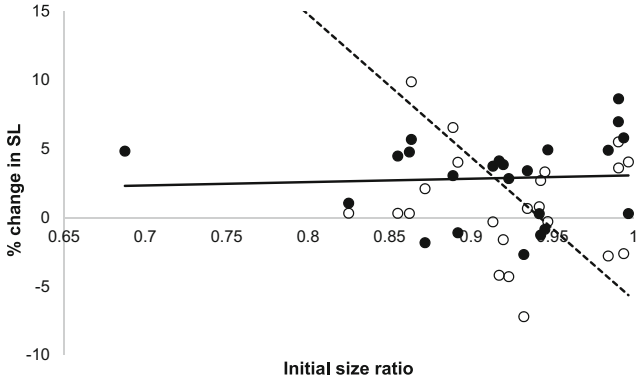

Fig. 3 Conflict resolution via size ratio and growth regulation. Percent change in standard length (SL) of individuals as a function of the initial size ratio between them and whether they were the winner (*solid circles*) or loser (*open circles*) of the battle for dominance. *Fitted lines* show the relationships estimated by the mixed model analysis

elevated conflict. This pattern was particularly apparent on day 1 when contestants were unfamiliar with each other. Even so, conflict was resolved very quickly—after the first day, not only was there markedly less conflict but conflict became unrelated to initial size ratio. Secondly, we found that the winner of the conflict tended to be the larger individual, but that the probability of the smaller individual winning increased toward 0.5 as the size ratio increased to unity. Finally, we demonstrated that growth of the rank 2 (the loser of the contest) but not the rank 1 (the winner of the contest) was regulated over the 6-week period to maintain a specific size ratio between individuals adjacent in rank, reinforcing the resolution of conflict and stability of the hierarchy.

Conflict was more intense when individuals were more similar size. This simple yet key result confirms the relationship between size difference and conflict intensity which previously had not been established despite Buston (2003a) and Buston and Cant (2006)'s suggestion that a precise size hierarchy is established to minimize conflict between individuals of adjacent rank. Direct evidence for a relationship between size similarity and intensity of conflict reflects that found for other social fishes (Heg et al. 2004; Hamilton et al. 2005; Ang and Manica 2010a; Matthews and Wong 2015). For example, in the cooperatively breeding African cichlid fish, *Neolamprologus pulcher*, subordinate helper males showed more submissive and reduced affiliative behaviors—indicative of increased conflict—when there was a small size difference between themselves and breeder males (Hamilton et al. 2005). In addition, Ang and Manica (2010a) reported increases in aggression between group members as the size ratio between them increased to unity, although only for groups where there was substantial spatial overlap. Therefore, our study adds to the growing consensus that actual conflict in social species is expressed and intensified when size and hence competitive asymmetries between individuals in the hierarchy are reduced.

The outcome of conflict was also likely influenced by relative body size, as the likelihood that the smaller fish won access to the anemone increased with size similarity. However, since the two methods of analysis provided different degrees of support for the hypothesis, this result should be interpreted with caution. Nevertheless, in conjunction with the fact that aggression was greater between similarly sized fish, the result suggests that conflict intensified between similarly sized individuals because the competitive ability of the smaller fish increased such that it became capable of winning the contest with some non-zero probability. Further support for this notion is the fact that this non-zero probability of winning a contest is precisely what has been proposed in another species to lead to dominants imposing a threat of eviction on subordinates to ensure that they regulate their growth to avoid becoming too similar in size (*Paragobiodon xanthosomus*, Wong et al. 2007, 2008). Importantly, the process of subordinate growth regulation in response to heightened conflict has remained but an assumption for *A. percula* since the original formulation of the hypothesis (Buston 2003a). Therefore, our study which demonstrates that subordinate (loser) *A. percula* subsequently regulated their growth in relation to the initial size ratio between themselves and their dominant (winner), and that aggression was related to initial size ratio, represents a valued test of the generality of Wong et al. (2007)'s finding and provides further support for the punishment-cooperation hypothesis as a mechanism of conflict resolution in social fishes.

The size ratio that was regulated over time in *A. percula* was approximately 0.92 (intersection of the dominant and subordinate growth curves), whereas size ratios in a wild population of *A. percula* were most frequently in the range of 0.8 (Buston and Cant 2006, reported as ratios of 1.2–1.3). This difference may either reflect an influence of laboratory conditions, given that individuals in aquaria did not experience the full range of potential environmental or ecological factors that could influence group structure or social interactions in the wild (Wong 2011). Alternatively, this difference could reflect existences of adaptive differences in threshold size ratios occurring between populations. Therefore, the next challenge for our understanding of conflict resolution, and patterns of social organization more broadly, requires attempts to understand variation in size ratios in natural populations (e.g., Ang and Manica 2010b; Wong 2011). In particular, investigating size ratio variation both between species and between populations of a given species would be helpful, as would detailed investigations into the causes and consequences of variation in both actual and threshold size ratios (Buston and Cant 2006; Wong et al. 2007; Ang and Manica 2010b; Wong 2011).

Given the importance of growth regulation in conflict resolution, we would have expected growth and hence size adjustments to temporally coincide with the dramatic

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reduction in conflict intensity observed by just day 3 post-introduction. However, the regulation of growth and the creation of distinct size differences arising from growth regulation clearly took place over a much longer period. Therefore, the rapid decline in aggression is likely to reflect other mechanisms promoting more immediate conflict resolution, which could include processes such as winner or loser effects (Dugatkin 1997; Chase et al. 2002; Dugatkin and Earley 2004) or spatial segregation (Ang and Manica 2010a), and testing these possibilities would be an intriguing area of future research. Whatever the mechanism and its associated proximate cues, our results enable us to advance our current understanding of conflict resolution mechanisms by indicating that different mechanisms of conflict resolution are likely to prevail in terms of relative importance depending on the timeframe. In light of this, the regulation of growth and hence the creation of defined size differences is likely to have greater importance for long-term conflict resolution, which in turn leads to the continued maintenance of hierarchy and group stability over time.

As a caveat, we note that each contest involved only two fish and a single anemone in an isolated and protected laboratory environment where the threat of leaving the anemone is not nearly as fatal as in the wild. This lack of perceived risk (or more accurately, a lack of ecological constraints) may have altered inherent aggression and submission levels and hence actual conflict expressed among the individuals. A replication of the experiment in a more natural habitat would be important to increase the robustness of our findings. Nevertheless, we provide the first experimental verification of all elements of conflict in this animal society. In the future, determining the influence of social dynamics and proximate cues that serve to rapidly resolve conflict in advance of the more graduated effects of size modification would enable us to address the finer scale details of conflict resolution, and hence society stabilization, in an animal society.

Our study also complements a growing number of reports documenting the regulation of growth in other vertebrate societies, e.g., mole-rats and meerkats (Russell et al. 2004a; O'Riain and Jarvis 1998; Young and Bennett 2010). In these terrestrial vertebrates, the emphasis is usually placed on explaining why dominant females are large, the fitness benefits of which—namely bigger litters, heavier offspring, and the ability to dominate—are relatively obvious (O'Riain et al. 2000; Russell et al. 2004b; Young et al. 2015). On the other hand, insights from fish societies emphasize the alternative perspective, which focuses on the conundrum of why subordinates remain small (Buston and Wong 2014). It seems possible that subordinate mole-rats and meerkats remain small for the same reason as subordinate anemonefish and coral gobies—because growing would bring them into conflict with the dominant female leading to a potentially lethal fight that the subordinate is likely to lose (Buston and Cant 2006; Wong et al. 2007, 2008; current study). Regardless of the ultimate reasons for growth modification in social vertebrates, elucidating the underlying proximate mechanisms may be a fascinating avenue of research. These social vertebrates, whose growth we can turn on and off by altering their social context, may ultimately prove useful to medical researchers attempting to understand which genes are expressed in various organs as growth is turned on and off.

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