



RESEARCH PAPER

Interactions Between Sabre-Tooth Blennies and Their Reef Fish Victims: Effects Of Enforced Repeated Game Structure and Local Abundance on Victim Aggression

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Abstract

The conditions under which humans benefit from contributing to a public good have attracted great interest; in particular the potential role of punishment of cheaters is hotly debated. In contrast, similar studies on other animals are lacking. In this study, we describe for the first time how the course of interactions between parasitic sabre-tooth blennies (the cheaters) and their reef fish victims can be used to study both punishment and the emergence of public goods. Sabre tooth blennies (*Plagiotremus sp.*) sneak up from behind to bite off small pieces of scales and/or mucus from other fish. Victims regularly show spontaneous aggression as well as aggressive responses to blenny attacks. In a between species comparison, we tested how the probability of chasing a blenny is affected by (1) the option of avoiding interactions with a blenny by avoiding its small territory, and (2) variation in local abundance of conspecifics. We found that resident victim species are more aggressive towards blennies than visiting species. This difference persisted when we controlled for victim size and territoriality, suggesting that it is the enforced repeated game structure that causes residents to chase blennies. In residents, we also found a negative correlation between aggression towards blennies and local abundance, which suggests that the benefits of chasing are diluted with increasing local abundance. We discuss the implication of these results for future studies.

Introduction

The existence of punishment where an individual decreases both its own and the target's immediate payoffs (Clutton-Brock & Parker 1995) has been a key topic in the recent literature on human cooperation. Humans readily use the option to punish cheaters even in one-shot public good games (Fehr & Gächter 2002) or when they just observe transgressions (Fehr & Fischbacher 2004). In the experiments on humans such punishment creates a public good, because it causes punished individuals to behave more cooperatively in the future with other partners (Fehr & Gächter 2002). Based on these results, the cultural group selection concept (Boyd et al. 2003;

Gintis et al. 2003) has been developed, which states that strong competition between human groups has selected for culturally transmitted punishment as a mechanism that benefits group survival. However, the notion that punishment increases group productivity has been contested (Rockenbach & Milinski 2006; Dreber et al. 2008; Egas & Riedl 2008). It seems that punishment can only be useful if it involves relatively low costs to the punisher and a high impact on the target (Egas & Riedl 2008) and if the same partners have many interactions (Gächter et al. 2008).

The evolution of punishment may be easier to understand in asymmetric games between two players where only one partner may cheat. For example,

in cleaner fish–client reef fish interactions, cleaners may cooperate by feeding on client ectoparasites and cheat by eating client mucus, whereas non-predatory clients lack the option to cheat cleaners (recent review by Bshary & Côté 2008). Some client species respond to cheating by cleaners with chasing, which causes cleaners to behave more cooperatively during future interactions with the punishing individuals (Bshary & Grutter 2002, 2005). While the self-serving role of punishment has been demonstrated in the cleaner fish system, the effects of punishment on third party individuals have not been explored. For example, punished individuals could be generally more cooperative in future interactions. In that case, the punishing individual would not only gain personal benefits but in addition produce a public good. The scenario would then be similar to n-player cooperation games where the benefits resulting from a contribution are so high that individual contributions become immanently self-serving: per unit given the contributor receives more than one unit in return, independently of what others are doing. Such contributions to public goods could yield immediate benefits, in which case the concept of by-product mutualism (Brown 1983) applies. Alternatively, contributions could be self-serving even if they are an investment (in the sense that the immediate consequences are a reduction in payoffs for the actor, Bshary & Bergmüller 2008). Investment may yield foreseeable future benefits if recipients will use it for self-serving actions that benefit the investor as a by-product. To such circumstances, the concept of pseudoreciprocity (Connor 1986) applies. An alternative term in the literature describing self-serving contributions to public goods is ‘weak altruism’ (Wilson 1990).

From a strategic point of view, it is easy to understand that contributions to public goods are stable if the contributions are self-serving. However, it is important to identify the ecological conditions that cause helping to be self-serving and thereby causing the unconditional contributions (Nowak & May 1992; Van Baalen & Rand 1998; Killingback et al. 1999; Kokko & Johnstone 1999; Taylor & Irwin 2000; Avilés 2002). Of particular importance has been the concept of group augmentation (Kokko et al. 2001), which was developed to understand apparently unconditional helping in cooperatively breeding species like meerkats *Suricata suricatta* (Clutton-Brock et al. 1999, 2000; Clutton-Brock 2002). Mutual dependency between group members (Roberts 2005) causes conditions where helping can be either a by-product mutualism or pseudoreciprocity.

Recently, Sherratt et al. (2009) developed a model where they assumed that an individual gets a disproportionate amount of the benefits derived from its own contribution. Such asymmetry greatly enhances stable contribution to a public good and may explain for example the production of extra-cellular substances in bacteria (Griffin et al. 2004; Dugatkin et al. 2005). Nevertheless, empirical studies on by-product public goods that explicitly test theoretical predictions and aim at identifying both ecological parameters and game structures are a clear lack.

Here, we describe in detail the nature of interactions in a system that appears to provide a setting for detailed additional studies on punishment and the possible emergence of public goods as a by-product. Our study species are parasitic sabre-tooth blennies, *Plagiotremus rhinorhynchus* and *P. tapeinosoma*, and their victim coral reef fish species. Sabre-tooth blennies defend small territories in which they attack many different types of fish species and bite off small chunks of skin, mucus and scales. This is their only way of gaining food (Smith-Vaniz 1976). *Plagiotremus rhinorhynchus* has attracted attention because it shows variation in colour, with one morph closely resembling juvenile cleaner wrasses (Kuwanura 1981; Côté & Cheney 2004, 2007; Moland & Jones 2004; Johnson & Hull 2006). To avoid possible effects of such aggressive mimicry on our results, we only included adult, non-mimetic blennies in our study. For our game theoretic approach, sabre-tooth blennies are the equivalent of ‘phenotypic defectors’ (Sherratt & Roberts 2001) or ‘always defect players’ (Axelrod & Hamilton 1981) in terminology used to evaluate the stability of cooperation. We noticed during preliminary observations that host fishes sometimes show spontaneous aggression as well as aggressive responses to successful and attempted blenny attacks. Such aggression may serve as punishment sensu Clutton-Brock & Parker (1995) because it may alter the target’s (blenny) future behaviour to the benefit of the punisher (the fish that was bitten). In contrast to a cooperative context, punishing in the blenny system cannot cause the target to behave more cooperatively in the future but punishment could be beneficial if it causes the blenny to attack other individuals.

Victim species differ with respect to two parameters that could have important effects on game structure and hence the probability of aggressive responses. First, some victim species are resident within a blenny’s territory and hence experience an enforced repeated game structure: they could be at permanent risk of being bitten by the blenny. In

contrast, visitor species have large home ranges and can in principle avoid a blenny by avoiding its territory. Second, local abundance varies greatly between species and sometimes also within species, ranging from one individual to hundreds. Both theory and experiments on humans propose that the efficiency of punishment relies on repeated interactions (Clutton-Brock & Parker 1995; Gächter et al. 2008). Therefore, we predicted that residents are more likely to respond aggressively to blennies than visitors. With respect to group size, we wanted to investigate whether aggression could be costly (i.e. reducing the direct fitness of the chaser) in larger groups. While the costs of chasing are presumably independent of group size, the benefits of chasing a blenny may well be reduced in larger groups: in larger groups it is more likely that a blenny will bite another group member if it decides to attack the same victim species again despite having been chased during its last encounter. Furthermore, if the blenny switches to a different victim species in response to victim aggression, all look-alikes (con-specifics) would benefit while only the chasing individual incurs the cost of chasing. In this scenario, the chasing individual would produce a public good. If chasing does become costly in larger groups we predicted that victim aggression should be absent in large groups. In contrast, if chasing is inherently self-serving, we predicted an absence of or at best a weak negative correlation between local abundance of victims and chasing of the blenny.

Methods

Study Site

All original data presented here were collected in Sep. to Nov. 2002 at Ras Mohammed National Park in Sinai, Egypt. The study site was at Mersa Bareika (27°47'20.5"N, 34°13'28.7"E), a bay that is well protected against surge. In this area, incoming sand through wadis led to the formation of patch reefs that are separated from each other by sand. Observations took place at 12 different reef patches. All of these reef patches were small (estimated size between 3.5 and 30 m²) and located in shallow water (depth between 1.5 and 9 m).

Study Species

The two species of blennies studied, two *Plagiotremus rhinorhynchus* and 10 *P. tapeinosoma*, occur in the tropical Indo-West and Central Pacific and are found

on coral reefs and lagoons at depths from 1 to 40 m. At most reef patches, only one blenny was present while at the two largest blocks several blennies were present but we could focus on one individual because of their territoriality. Both blenny species are lepidophagous (scale eating) parasites that attack other fish to forage. Usually they sneak up on their victims from behind and bite off small chunks of skin, mucous and scales (Smith-Vaniz 1976; Johnson & Hull 2006). Normally they stop their biting attempts as soon as they are noticed (if their victims turn around, pers. obs). One of the common names of *P. tapeinosoma*, 'Hit and Run Blenny', describes the typical feeding behaviour of both species that comprises a rapid attack followed by a quick retreat to safety (Johnson & Hull 2006). Blennies follow this scheme independently of the reaction of the victim. Only in less than 1% of our observations was a victim bitten twice without any retreat of the blenny between bites.

With respect to victim species, we obtained data on 32 non-predatory resident species ('residents') and on 29 non-predatory visiting species ('visitors'), following the list of Bshary (2001). Resident species live permanently at the same reef patch, whereas visitors cross between reef patches and stay only for short periods at any one. The most abundant resident species *Pseudanthias squamipinnis* is sexually dimorphic. The data for males and females were used separately, increasing the n for residents to 33. We excluded predatory species because they have the additional option to try to eat a blenny rather than just chasing it, which makes their actions difficult to compare with non-predatory victims. In addition, we excluded non-predatory species that could not be classified clearly as either resident or visitor ('facultative visitors', see Bshary 2001) to avoid any confounding effects of this ambiguity.

Data Collection

Observations were carried out using scuba equipment and sitting on the surrounding sand 2–3 m in front of a reef patch with a blenny present. Observations lasting 60 min were evenly spread over the day and no blenny was observed more than once on the same day. Each of the three observers visited each reef patch twice at different times of day. Thus, a total of 6 h of observations are available for each blenny adding up to a total of 72 h of observations.

All interactions between the blenny and another fish were first observed over the entire duration, and

immediately afterwards, the following data was noted on a Plexiglas plate:

1. Victim species. Species were determined according to Randall (1983).
2. Length of victim. The total length of the individual was estimated to the nearest cm by comparison with a reference measuring stick.
3. Sex of victim species (in sexually dimorphic species).
4. Type of interaction:
 - unprovoked aggression by the ‘victim’;
 - biting attempt followed by a non-aggressive response of the victim’
 - biting attempt followed by aggressive response of the victim;
 - bite followed by a non-aggressive response of the victim;
 - bite followed by aggressive response of the victim.

Aggression by the victim was scored if it accelerated towards the blenny, usually evoking flight behaviour by the blenny. We scored ‘unprovoked aggression’ if a fish chased a blenny passing in front and hence not obviously intent on attacking the chaser. We scored a biting attempt if a blenny approached a fish from behind in a characteristic ‘stop and go’ manner, which also proceeds successful biting attempts (Smith-Vaniz 1976). We scored ‘aggressive response’ if the potential or real victim turned round and swam towards the blenny. A ‘non-aggressive response’ was scored if the potential or real victim swam away from the blenny or did not move at all.

In separate dives, we counted the number of individuals per resident species on each reef patch. For up to 10 individuals, we counted exact numbers, while we used 5 unit categories for up to 50 individuals and 10 unit categories for estimations of local abundance above 50 individuals.

Data Analysis

We ran separate analyses for ‘unprovoked aggression’, aggression in response to biting attempts, and aggression in response to biting. For analyses of unprovoked aggression, we calculated the percentage of apparently unprovoked chasing relative to all observed chasing events. For the other two forms of aggression, we calculated the percentage of aggressive responses to biting attempts as n aggressive responses/biting attempts $\times 100$, and the percentage of aggressive responses to biting was calculated as n aggressive responses to biting/ all

bites $\times 100$. Species values were obtained by first calculating for every type of aggression one mean value per species per reef patch. These values were used to calculate one mean value per species. The species values were then used to compare aggression between residents and visitors, and to correlate aggression with our median values of group size. Not all species were observed both in the ‘attempting to bite’ and ‘successful bite’ situations, which explains the variation in sample sizes between the analyses.

For a within species correlation between group size and aggression, we focussed on the most abundant victim species, *Pseudanthias squamipinnis*. This species is sexually dimorphic so we had local abundance and aggression data for both males and females. For the analysis, we generated the category ‘general aggression’ as the percentage of aggressive behaviours by victims divided by all interactions in order to have a reasonable sample size.

Finally, we ran a series of control analyses to explore the effects of potentially confounding variables like body size and territoriality. Visiting species are on average larger than resident species (Bshary 2001), whereas resident species are more likely to be territorial. To control for size effects, we carried out one analysis in which we only considered species of 10–15 cm mean total length, and another analysis in which we calculated the correlation between body size and aggression in resident species only. To control for effects of territoriality, we identified the following ten resident species as non-territorial (typically shoaling) and asked how they would compare to visitor species with respect to aggression: *Adioryx diadema*, *Myripristis murdjan*, *Pseudanthias squamipinnis*, *P. taeniatus*, *Chromis ternatensis*, *C. dimidiata*, *C. caerulea*, *Cheilodipterus lineatus*, *Neopomacentrus miryae* and *Amblyglyphidodon leucogaster*. We did not run analyses that control for phylogeny. A phylogenetic tree that includes most victim species shows that while resident species and visitor species tend to group in clades, these clades are quite randomly distributed over the phylogeny and hence do not cause systematic errors (Bshary 2001).

All data were analysed using SPSS 17.0 applying only non-parametric statistics. All p-values are two tailed. When we tested whether the parameter ‘resident/visitor’ and or the parameter ‘local abundance’ had any effect on the probability of aggression, we had three behaviours (unprovoked aggression, aggression in response to biting attempt, and aggression in response to bites) that could potentially yield

significant results. We therefore had to adjust the alpha level with the sequential Bonferroni test (Rice 1989). In this method, the original α -level (0.05) is divided by n tests to be conducted to obtain the first α' . If one p-value is below the α' level, this result is accepted as significant and a new α'' is calculated by dividing 0.05 by n tests -1 . This procedure is repeated until all p-values fail to be below the corresponding critical α -level, and are hence considered to be non-significant.

Results

General Information

In total, 1932 interactions between blennies and their victims from the 12 reef blocks were used in the analysis. In 1200 cases (62.11%), the victim species showed aggressive behaviour. As victim behaviour towards the two *P. rhinorhynchus* individuals was within the range of values for *P. tapeinosoma* individuals we analysed the data without distinguishing between the blenny species.

Comparison Between Residents and Visitors

Resident species showed significantly more aggressive behaviour in all categories of interaction when the sequential Bonferroni technique was applied (Mann–Whitney U-tests, initial $\alpha' = 0.017$; unprovoked aggression: n residents = 33, n visitors = 29, $z = -3.822$, $p < 0.001$; aggression in response to biting attempts: n residents = 24, n visitors = 15, $z = -3.408$, $p = 0.001$; aggression in response to bites: n residents = 27, n visitors = 27, $z = -4.686$, $p < 0.001$, Fig. 1).

Potentially Confounding Variables

The differences in aggressive behaviour towards blennies between residents and visitors largely persisted when only species of similar sizes (10–15 cm) were considered for the analysis (U-tests, unprovoked aggression: n residents = 10, n visitors = 9, $z = -1.870$, $p = 0.061$, aggression in response to biting attempts: n residents = 8, n visitors = 5, $z = -3.029$, $p = 0.002$; aggression in response to bites: n residents = 7, n visitors = 8, $z = -3.350$, $p = 0.001$). In addition, there are consistent positive correlations between resident body size and aggressive behaviour although the correlation is not significant for unprovoked aggression (Spearman correlations, unprovoked: $n = 33$, $rs = 0.234$, $p = 0.190$; biting attempts:

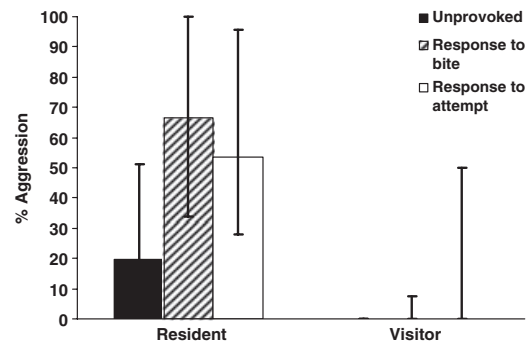


Fig. 1: Comparison of occurrences of three types of aggressive behaviour (unprovoked aggression, aggression in response to biting attempts and aggression in response to bites) between resident and visiting victim species. Medians are represented with the 25 and 75 percentiles. Sample sizes per category for residents: 33, 24 and 27, respectively. Sample sizes for visitors: 29, 15 and 27, respectively. Resident victims show significantly higher levels of aggression in all three comparisons.

$n = 24$, $rs = 0.595$, $p = 0.002$; bites: $n = 27$, $rs = 0.441$, $p = 0.021$).

The differences between residents and visitors persisted when only the ten non-territorial resident species were considered for the comparisons (U-tests, initial $\alpha' = 0.017$; unprovoked aggression: n residents = 10, n visitors = 29, $z = '2.636$, $p = 0.008$, aggression in response to biting attempts: n residents = 10, n visitors = 15, $z = '2.237$, $p = 0.025$ aggression in response to bites: n residents = 10, n visitors = 27, $z = -3.545$, $p < 0.001$).

Density Dependence of Aggression in Resident Species

In all three categories, the median abundance of species was negatively correlated with species aggression when the sequential Bonferroni technique was applied (Spearman correlations, initial $\alpha' = 0.017$; unprovoked aggression: $n = 33$, $rs = -0.397$, $p = 0.022$; response to attempt: $n = 24$, $rs = -0.491$, $p = 0.015$; response to bite: $n = 27$, $rs = -0.470$, $p = 0.013$, Fig. 2a–c).

Density Dependence of Aggression in *Pseudanthias squamipinnis*

There were marginally significant negative correlations between group size and 'general aggression' against blennies in both sexes (Spearman correlation, *P. squamipinnis*, $\alpha' = 0.025$; females: $n = 12$, $rs = -0.581$, $p = 0.047$; males: $n = 11$, $rs = -0.661$, $p = 0.027$, Fig. 3).

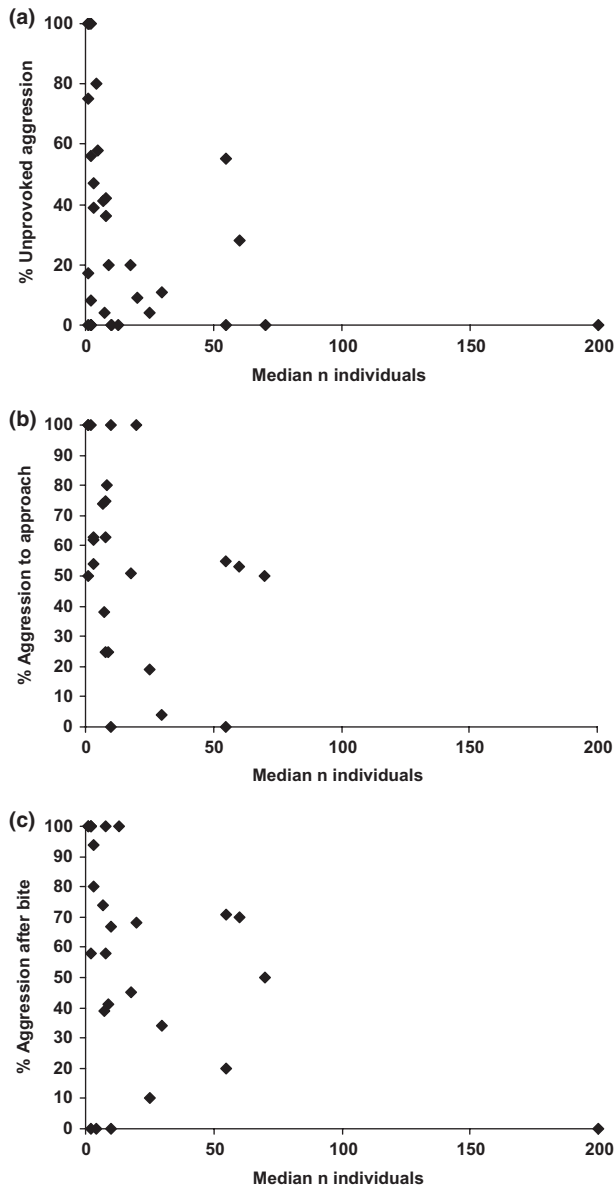


Fig. 2: Correlations between the resident species' local abundance (median number of individuals at a patch) and aggression towards blennies. Each dot represents the mean value for one species. (a) Spontaneous aggression relative to all aggressive acts towards blennies ($n = 33$ species); (b) aggression in response to a blenny's approach ($n = 24$ species); (c) aggression in response to a blenny's bite ($n = 27$ species). All correlations are significantly negative.

Correlations Between the Three Measures of Aggression

We only calculated correlations for resident species because of the absence of aggressive behaviour in visiting species. There was a significant positive correlation between the aggressive response to bites and

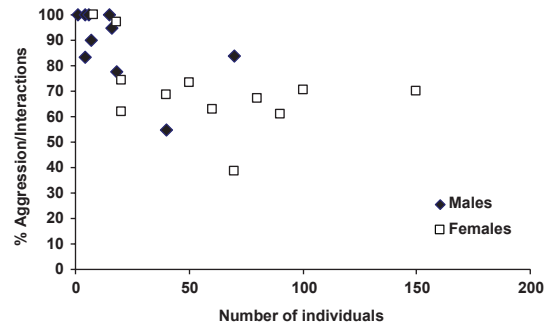


Fig. 3: Correlation between local abundance and aggressive behaviours towards blennies in 11 male and 12 female *Pseudanthias squamipinnis* shoals. Each shoal is represented by one dot. The correlations are marginally significant at the 0.025 level (because of Bonferroni correction).

to biting attempts (Spearman correlation, initial $\alpha = 0.017$, $r_s = 0.788$, $n = 22$, $p < 0.001$). In contrast, unprovoked aggression showed no correlation with the other two types of aggression (Spearman correlations, unprovoked aggression vs. aggression following attempts: $r_s = 0.172$, $n = 24$, $p = 0.422$; unprovoked aggression vs. aggression following bites: $r_s = 0.186$, $n = 27$, $p = 0.352$). A similar pattern emerged in the within species correlations for male *Pseudanthias squamipinnis*. There was a non-significant but very positive correlation between the aggressive response to bites and to biting attempts (Spearman correlation, $r_s = 0.731$, $n = 7$, $p = 0.062$), while unprovoked aggression yielded non-significant but negative correlations with the other two types of aggression (Spearman correlations, unprovoked aggression vs. aggression following attempts: $r_s = -0.152$, $n = 8$, $p = 0.719$; unprovoked aggression vs. aggression following bites: $r_s = -0.317$, $n = 8$, $p = 0.444$). In female *P. squamipinnis* all correlations between the three types of aggressive responses were far from being significant (Spearman correlations, aggression following biting attempts vs. aggressive response to bites: $r_s = 0.309$, $n = 11$, $p = 0.355$, unprovoked aggression vs. aggression following attempts: $r_s = 0.273$, $n = 11$, $p = 0.417$; unprovoked aggression vs. aggression following bites: $r_s = -0.118$, $n = 11$, $p = 0.729$).

Discussion

We asked two principal questions about the interactions between blennies and their victims. First, whether any variation between species' probability to chase blennies can be explained by the distinction

between resident victims that experience an enforced repeated game structure, and visiting victims that can in principle avoid repeated interactions with a blenny. Second, whether the probability of victim aggression is linked to variation in the local abundance of species, where high abundance may cause aggression to become costly. Our results show that both parameters are important.

Enforced Repeated Game Structure

Resident species were consistently more likely than visitors to aggress blennies after being bitten, in response to an approach and without provocation. The differences between residents and visitors largely persisted when we controlled for size and territoriality. Visitors not only fled after an attack but typically left the reef patch (Bshary, A. & Bshary, R., pers. obs.). Thus, they effectively excluded the possibility of another interaction in the near future, an option that resident species lack. The results thus correspond very well to the behaviour of the same species during cleaning interactions with the cleaner wrasse *Labroides dimidiatus*, where residents are likely to punish cleaners for taking bites of mucus [which Bshary (2001) defined as cheating behaviour] while visiting clients are likely to swim off instead (Bshary & Grutter 2002; Bshary & Schäffer 2002). It could therefore be that the responses to cleaners and sabre-tooth blennies co-evolved or that the reactions to one are because of selection on the reaction to the other. This could be tested by exposing Caribbean fishes to sabre-tooth blennies. Caribbean fishes are not exposed to such parasites and they do not punish or switch cleaning station in interactions with cleaning gobies of the genus *Elacatinus* (Soares et al. 2008a) even although these gobies sometimes cheat as well (Soares et al. 2008b). With respect to the current study, we propose that an enforced repeated game structure caused the evolution of aggression towards blennies in resident species. This hypothesis should be tested in the future by testing whether aggression functions as punishment by reducing the probability of future attacks. Currently, it is clear that victim aggression does not yield immediate benefits as blennies very rarely bite twice in one attack (observed only 10 times in this study) but instead retreat immediately after one bite. Therefore, aggression is not necessary to make the blenny swim away. While there are currently few examples of punishment in animals other than humans, it has already been shown that the very same victim fish species use punishment successfully to increase service

quality by cleaner wrasse (Bshary 2002; Bshary & Grutter 2005).

Alternative explanations for the aggressive behaviour of residents seem to be unlikely: aggression cannot be a direct response to pain because if this was the case then both resident and visitor species should show aggressive behaviour after painful attacks. While smaller fish might find attacks more painful than large fish, we found that the difference between residents and visitors in reaction to bites persisted when we controlled for size. We also found that larger residents tended to be more aggressive to blennies than small residents, while we would expect the opposite if aggression was a direct response to pain, since bites should be more painful to smaller fish. Also, aggression does not seem to be a by-product of territoriality as non-territorial resident species were still more aggressive towards blennies than visitors were.

Despite the fact that visitors can avoid repeated interactions with blennies, it seems unlikely that they will never return again to a reef patch where they have been bitten. Thus, it appears that visitors as well as residents may experience several interactions with any blenny within their home ranges. Nevertheless, encounter rates with visitors for any particular blenny will be much lower than for the blenny's resident victims. Long time intervals between subsequent interactions may impose cognitive constraints on both blenny and victim, turning their repeated interactions into functionally one-off interactions. Models of reciprocity and punishment demonstrate that remembering the partner's last behaviour is essential for punishment to work (Clutton-Brock & Parker 1995). In contrast, punishment in one-off interactions or functionally one-off interactions may only work if kin selection between the victim and other potential victims is invoked (Gardner & West 2004). In the blenny-visitor case, relatives of the chasing victim would have to benefit from a temporarily reduced attack probability. However, such a scenario is unlikely to apply to reef fishes because pelagic egg and/or larval stages should prevent any kin structure in shoals, as demonstrated in *Pseudanthias squamipinnis* (Avisé & Shapiro 1986).

Local Abundance/Density Dependence

The negative correlations of aggression with group size both on the inter-specific and the intra-specific level can be interpreted in two ways. First, with increasing group size each individual experiences

less pressure from the blenny and hence the potential benefits of chasing diminish with increasing group size. In this scenario, the decision to chase or not is unaffected by its consequences on the fitness of conspecifics. Second, it could be that aggression by victims causes blennies to switch to other victim species for future attacks. In that case, chasing would produce a public good to all look-alikes. As group size increases, the personal benefits for the chasing individual would be reduced while the costs remain constant, and chasing would hence become less likely in larger groups. To distinguish between the two potential explanations, future studies that focus on the foraging strategies of the blennies are necessary.

An interesting result was that high levels of aggression were maintained in species that occurred in high densities of around 40–60 individuals per reef patch. This result provides evidence against the possibility that reef fish face a basic tragedy of the commons problem (Hardin 1968) when chasing a blenny. In the basic tragedy of the commons scenario, contributions to a public good are invariably under negative selection for such large group sizes unless additional parameters are included, such as strong between-group competition (Boyd et al. 2003; Gintis et al. 2003) or the possibility of gaining social prestige which is useful in other situations (Nowak & Sigmund 1998; Milinski et al. 2002). Our results fit with a scenario where a contributor gets a higher share of the benefits it generates than other group members (Sherratt et al. 2009). Indeed, individuals may gain an extra personal benefit from chasing a blenny in two possible and not mutually exclusive ways. First, aggression leads to the blenny attacking elsewhere in the future. This potential benefit would require a degree of site fidelity of the victim at least over short time periods. Second, aggression makes the blenny focus on other individuals. This would require individual recognition of potential victims by the blenny. Evidence for individual recognition is widespread for fishes (Griffiths & Ward 2006) and includes individual recognition of members of other species (Tebbich et al. 2002), but individual recognition in blennies has yet to be tested.

Correlation Between the Three Forms of Aggression

Unprovoked aggression is not correlated to the other two types of aggression, with some of the correlation coefficients even yielding negative tendencies. We explored some potentially confounding factors such as territoriality and hiding in crevices and found no

influence of these (results not shown). We do not know in what way unprovoked aggressive behaviour is different from aggression towards a stalking or biting blenny. As all three forms of aggression are similarly correlated with an enforced repeated game structure and with local abundance one would expect a common cause. In the absence of indications explaining why unprovoked aggression is different, future studies should keep the separation between the various situations of aggression towards blennies.

Conclusions and Outlook

Our results provide evidence that enforced repeated game structure is necessary for the evolution of aggression towards a cheater, although the benefits of such aggression remain to be evaluated. In addition, blenny–victim interactions provide a setting in which the effect of the number of partners on the level of aggression towards a shared enemy can be studied. The observation that even members of large groups chase blennies with about 50% probability is interesting because the result suggests that the putative benefits of punishment are not dissolved in large groups, while public goods may potentially emerge in this setting. As a next step, two important hypotheses have to be tested: that aggression towards a blenny functions as punishment and that punishment in larger groups constitutes a public good.

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Literature Cited

- Avilés, L. 2002: Solving the freeloader paradox: genetic associations and frequency-dependent selection in the evolution of cooperation among nonrelatives. *Proc. Natl Acad. Sci. USA* **22**, 14268–14273.
- Awise, J. C. & Shapiro, D. Y. 1986: Evaluating kinship of newly settled juveniles within social groups of the coral reef fish *Anthias squamipinnis*. *Evolution* **40**, 1051–1059.

- Axelrod, R. & Hamilton, W. D. 1981: The evolution of cooperation. *Science* **211**, 1390—1396.
- Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. 2003: The evolution of altruistic punishment. *Proc. Natl Acad. Sci.* **100**, 3531—3535.
- Brown, J. L. 1983: Cooperation: a biologist's dilemma. *Adv. Stud. Behav.* **13**, 1—37.
- Bshary, R. 2001: The cleanerfish market. In: *Economics in Nature* (Noe, R., Van Hoof, J. A. R. A. M. & Hammerstein, P., eds). Cambridge Univ. Press, Cambridge, pp. 147—172.
- Bshary, R. 2002: Building up relationships in asymmetric co-operation games between the cleaner wrasse *Labroides dimidiatus* and client cleaner fish. *Behav. Ecol. Sociobiol.* **52**, 365—371.
- Bshary, R. & Bergmüller, R. 2008: Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* **21**, 405—420.
- Bshary, R. & Côté, I. M. 2008: New perspectives on marine cleaning mutualism. In: *Fish Behaviour* (Magnhagen, C., Braithwaite, V. A., Forsgren, E. & Kapoor, B. G., eds). Science Publishers, Enfield, pp. 563—592.
- Bshary, R. & Grutter, A. S. 2002: Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* **63**, 547—555.
- Bshary, R. & Grutter, A. S. 2005: Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biol. Lett.* **1**, 396—399.
- Bshary, R. & Schäffer, D. 2002: Choosy reef fish select cleaner fish that provide high service quality. *Anim. Behav.* **63**, 557—564.
- Clutton-Brock, T. H. & Parker, G. A. 1995: Punishment in animal societies. *Nature* **373**, 209—216.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. & Manser, M. 1999: Selfish sentinels in cooperative mammals. *Science* **284**, 1640—1644.
- Clutton-Brock, T. H., Brotherton, P. N. M. & O'Riain, M. J. 2000: Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proc. R. Soc. Lond. B* **267**, 301—305.
- Clutton-Brock, T. H. 2002: Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69—72.
- Connor, R. C. 1986: Pseudo-reciprocity: investing in mutualism. *Anim. Behav.* **34**, 1562—1566.
- Côté, I. M. & Cheney, K. L. 2004: Distance-dependent costs and benefits of aggressive mimicry in a cleaning symbiosis. *Proc. R. Soc. B*, **271**, 2627—2630.
- Côté, I. M. & Cheney, K. L. 2007: A protective function for aggressive mimicry? *Proc. R. Soc. B* **274**, 2445—2448.
- Dreber, A., Rand, D. G., Fudenberg, D. & Nowak, M. A. 2008: Winners don't punish. *Nature* **452**, 348—351.
- Dugatkin, L. A., Perlin, M., Lucas, J. S. & Atlas, R. 2005: Group beneficial traits, frequency-dependent selection and genotypic diversity: an antibiotic resistance paradigm. *Proc. R. Soc. B* **272**, 79—83.
- Egas, M. & Riedl, A. 2008: The economics of altruistic punishment and the maintenance of cooperation. *Proc. R. Soc. B* **275**, 871—878.
- Fehr, E. & Fischbacher, U. 2004: Third-party punishment and social norms. *Evol. Hum. Behav.* **25**, 63—87.
- Fehr, E. & Gächter, S. 2002: Altruistic punishment in humans. *Nature* **415**, 137—140.
- Gächter, S., Renner, E. & Sefton, M. 2008: The long-run benefits of punishment. *Science* **322**, 1510.
- Gardner, A. & West, S. A. 2004: Cooperation and punishment, especially in humans. *Am. Nat.* **164**, 753—764.
- Gintis, H., Bowles, S., Boyd, R. & Fehr, E. 2003: Explaining altruistic behaviour in humans. *Evol. Hum. Behav.* **24**, 153—172.
- Griffin, A. S., West, S. A. & Buckling, A. 2004: Cooperation and competition in pathogenic bacteria. *Nature* **430**, 1024—1027.
- Griffiths, S. W. & Ward, A. 2006: Learned recognition of conspecifics. In: *Fish Cognition and Behavior* (Brown, C., Laland, K. N. & Krause, J., eds). Blackwell, Oxford, pp. 139—165.
- Hardin, G. 1968: The tragedy of the commons. *Science* **162**, 1243—1248.
- Johnson, M. L. & Hull, S. L. 2006: Interactions between fangblennies (*Plagiotremus rhinorhynchus*) and their potential victims: fooling the model rather than the client? *Mar. Biol.* **148**, 889—897.
- Killingback, T., Doebeli, M. & Knowlton, N. 1999: Variable investment, the continuous prisoner's dilemma, and the origin of cooperation. *Proc. R. Soc. Lond. B* **266**, 1723—1728.
- Kokko, H. & Johnstone, R. A. 1999: Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. Lond. B* **266**, 571—578.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001: The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187—196.
- Kuwamura, T. 1981: Mimicry of the cleaner wrasse *Labroides dimidiatus* by the blennies *Aspidontus taeniatus* and *Plagiotremus rhinorhynchus*. *Nanki Seibutu* **23**, 61—70.
- Milinski, M., Semmann, D. & Krambeck, H.-J. 2002: Reputation helps solve the 'tragedy of the commons'. *Nature* **415**, 424—426.
- Moland, E. & Jones, G. P. 2004: Experimental confirmation of aggressive mimicry by a coral reef fish. *Oecologia* **140**, 676—683.
- Nowak, M. A. & May, R. M. 1992: Evolutionary games and spatial chaos. *Nature* **359**, 826—829.

- Nowak, M. A. & Sigmund, K. 1998: Evolution of indirect reciprocity by image scoring. *Nature*, **393**, 573—577.
- Randall, J. E. 1983: *Red Sea Reef Fishes*. Immel Publishing, London.
- Rice, W. R. 1989: Analyzing tables of statistical tests. *Evolution* **43**, 223—225.
- Roberts, G. 2005: Cooperation through interdependence. *Anim. Behav.* **70**, 901—908.
- Rockenbach, B. & Milinski, M. 2006: The efficient interaction of indirect reciprocity and costly punishment. *Nature* **444**, 718—723.
- Sherratt, T. N. & Roberts, G. 2001: The role of phenotypic defectors in stabilizing reciprocal altruism. *Behav. Ecol.* **12**, 313—317.
- Sherratt, T. N., Roberts, G., L & Kassen, R. 2009: Evolutionary stable investment in products that confer both an individual benefit and a public good. *Front. Biosci.* **44**, 4557—4564.
- Smith-Vaniz, W. F. 1976: *The Saber-Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae)*. Monograph 19, The Academy of Natural Sciences Of Philadelphia, Pennsylvania.
- Soares, M. C., Côté, I. M., Cardoso, S. C. & Bshary, R. 2008a: On the absence of punishment, partner switching and tactile stimulation in the cleaning goby client mutualism. *J. Zool.* **276**, 306—312.
- Soares, M. C., Bshary, R., Cardoso, S. C. & Côté, I. M. 2008b: The meaning of jolts by fish clients of cleaning gobies. *Ethology* **114**, 209—214.
- Taylor, P. D. & Irwin, A. J. 2000: Overlapping generations can promote altruistic behavior. *Evolution* **54**, 1135—1141.
- Tebbich, S., Bshary, R. & Grutter, A. S. 2002: Cleaner fish *Labroides dimidiatus* recognise familiar clients. *Anim. Cogn.* **5**, 139—145.
- Van Baalen, M. & Rand, D. A. 1998: The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* **193**, 631—648.
- Wilson, D. S. 1990: Weak altruism, strong group selection. *Oikos* **59**, 135—140.