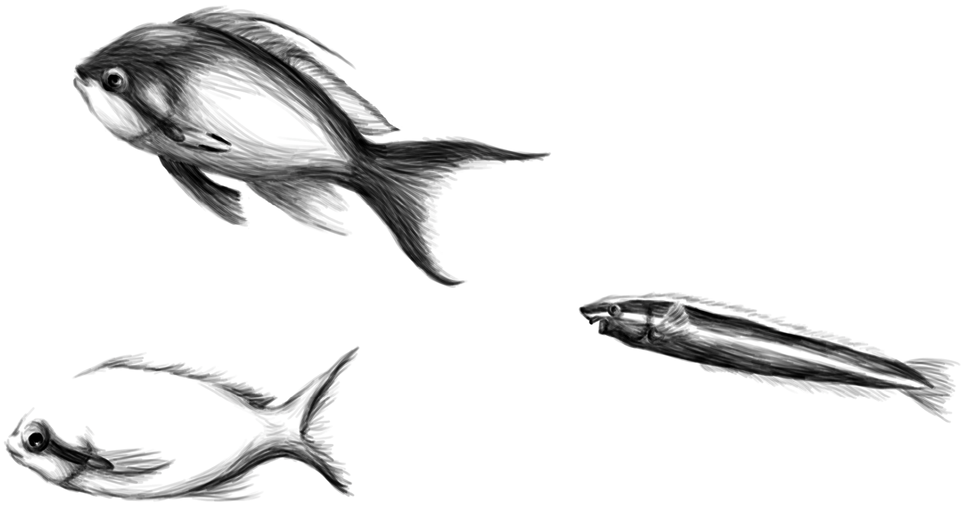
Punishment and the emergence of public goods in a marine host–parasite complex



Thèse présentée à la Faculté des Sciences
Institut de Biologie
Université de Neuchâtel
Pour l'obtention du grade de docteur ès sciences

Par

Andrea Bshary

Acceptée sur proposition du jury :
Prof. Martine Rahier, directrice de thèse
Prof. Théodoor Turlings, rapporteur
Prof. Michael Taborsky, rapporteur

Présenté et soutenue le 16. Mai 2011

Université de Neuchâtel
2011

Université
de Neuchâtel unine

FACULTE DES SCIENCES
Secrétariat-Décanat de la faculté
Rue Emile-Argand 11
CH-2000 Neuchâtel

IMPRIMATUR POUR LA THESE

Punishment and the emergence of public goods in a marine host-parasite complex

Mme Andrea BSHARY

UNIVERSITE DE NEUCHATEL

FACULTE DES SCIENCES

La Faculté des sciences de l'Université de Neuchâtel,
sur le rapport des membres du jury,

Prof. M. Rahier (directrice de thèse), Prof. Ted Turlings et Prof Michael Taborsky
(Faculty of biology, Berne)

autorise l'impression de la présente thèse.

Neuchâtel, le 5 septembre 2011

Le doyen

Prof. Peter Kropf

Mots clés : Coopération**,** bien public, interactions hôte-parasite, punition, différences individuelles, *Plagiotremus rhinorhynchus, P. tapeinosoma, Pseudanthias squamipinnis*

Key words : Cooperation, public good, host-parasite interactions, punishment, individual differences, *Plagiotremus rhinorhynchus, P. tapeinosoma, Pseudanthias squamipinnis*

Summary :

Cooperation in larger group is often more difficult to explain then cooperation in pairs. For humans it has been proposed that punishment plays a major role in stabilising individual contributions to group success ('public goods') but that claim remains contentious. The aim of this thesis was to gain understanding of a system in which both punishment and public goods may exist, and which can be studied both in nature and with an experimental setup in the laboratory. The interactions between victim reef fishes and parasitic sabre–tooth blennies that bite mucus and scales off other fishes provided a suitable study system.

In the first of three manuscripts I described the natural history of this peculiar host–parasite complex. The blennies occupy small territories. Resident victim species that are constantly under threat of being bitten reacted aggressively to blenny attacks, while visiting species used their potential to escape further interactions by swimming off. Among residents, the probability of aggressive reactions to blenny attacks was negatively correlated to group size without dropping to zero. The latter results fitted a public goods scenario where benefits of acting decrease with increasing group size. In the second manuscript I could demonstrate that aggression by victims functions as punishment as it

reduced the probability of future attacks by a blenny. Furthermore, field observations revealed that punishment creates a public good in locally abundant species as it increased the probability that blennies switched to a different victim species. Nevertheless, punishment appeared to be self–serving rather than altruistic because lab experiments suggested that blenny preferentially target non–punishing individuals. The third manuscript focussed more specifically on the blennies' foraging decision rules. Overall, I documented that blennies may attack at preferred locations, that they may prefer abundant hosts, and that they may focus on specific non–punishing individuals. However, there was huge variation between individuals with respect to the relative importance of these factors, including the probability of switching victim species between subsequent attacks irrespective of victim responses. This variation may locally undermine the effectiveness of punishment, and may also sometimes create competition between conspecifics instead of a public good.

In conclusion, the study demonstrates the existence of self–serving punishment in a parasite–host system. Public goods may emerge as a by–product of self–serving punishment due to the parasite's foraging decision rules, which typically select against non punishing 'free–riders'. How the observed variation in blenny decision rules may evolve and how victims should evolve their optimal responses in return would ideally be addressed in evolutionary game theoretic modelling, amenable to further empirical testing.

Content page

General Introduction

Helping behaviours have attracted the interest of evolutionary biologists ever since Darwin (1859) realised that such behaviours are not easy to reconcile with his theory of evolution through natural selection. In a world where all individuals should be competing for resources, any behaviour that increases the fitness of another should be selected against. Hamilton’s famous theory of kin selection explained how indirect fitness benefits can balance direct costs of helping (‘altruism’): if actor and recipient are related the benefit of helping to the recipient times the degree of relatedness to the helper has to be larger than the costs of helping (Hamilton 1964). However, there are many examples of helping between unrelated individuals or even between species. Altruistic individuals that help unrelated individuals without getting anything in return will always be under negative selection. Thus, the key problem in such interactions is how to ensure that helping will yield something in return, leading to mutual benefits (‘cooperation’).

The problem that may arise in potentially cooperative interactions is best illustrated in the prisoner’s dilemma game. In this game there are two players playing against each other. Each player can either cooperate or defect. The combined payoff is highest if both players cooperate but the individual payoff for defecting is always higher than for cooperating, independently of the partner’s action (see table 1). Thus, cooperation is no solution to the game if it is played only once. Cooperation can only emerge if the game is played repeatedly between the two players because under these conditions cooperating can be seen as an investment that yields future benefits due to the partner cooperating in response (‘positive reciprocity’; Trivers 1971, Axelrod & Hamilton 1981, Clutton–Brock & Parker 1995).

Table 1

	player 2 cooperates	player 2 defects
player 1 cooperates	**3**/3	**0**/5
player 1 defects	**5**/0	**1**/1

Payoff matrix of the prisoner’s dilemma, **bold**: payoff for **player 1**

Cooperation between two players

Today there are many models that can explain cooperation between two players (Sachs et al. 2004, West et al. 2007, Bshary & Bergmüller 2008). Bshary & Bergmüller identified nine basic concepts based on four parameters. A first key distinction to be made is whether helping is self–serving (by–product mutualism, Brown 1983) or an investment. In the latter case one has to ask whether the benefits are due to a self–serving response (‘pseudoreciprocity’, Connor 1986) or due to return investments (‘reciprocity’). Furthermore, the benefits may be due to the recipient’s behaviour (‘direct’) or due to the action of a third party (indirect’), and one can distinguish cases where investments yield benefits due to rewards (‘positive’) from cases in which investments yield benefits due to the absence of negative responses (‘negative’). Further parameters need to be introduced to distinguish between more specific concepts. For example, for indirect forms of reciprocity one has to distinguish whether or not interactions take place in a communication network in which bystanders eavesdrop and extract valuable information for own future interactions with the observed individuals (McGregor 1993). If a communication network exists, then bystanders can attribute an image score to observed individuals, which will increase with each helping act and decrease with each failure to help (Alexander 1987, Novak & Sigmund 1998). As long as individuals only help if the image score of the recipient is above a critical threshold then indirect reciprocity based on image scoring may evolve (Nowak & Sigmund 1998). In the absence of image scoring, a concept called generalised reciprocity (Hamilton & Taborsky 2005, Rutte & Taborsky 2007, Pfeiffer et al. 2005) may explain indirect reciprocity. The decision rule is that as long as an individual receives help it will help whoever is in need. Overall, the many existing concepts for two–player interactions appear to have their real–life counterparts (Bshary & Bronstein 2011), and the main challenge for empiricists seems to be to evaluate which concept may fit their study system best.

Cooperation between n players

In contrast to the larger body of both theoretical and empirical studies on cooperation between two individuals, cooperation between n>2 players is less well understood. It has been realised early on that cheating may be easier in n–player games. Most famously, Hardin (1968) introduced the concept of the ‘tragedy of the commons’. The tragedy typically arises if the benefits of individual contributions to a public good are shared equally by everyone. Under such conditions, so–called ‘free–riders do best as they don’t invest in the public good but benefit from the contributions of others.

Social dilemmas are typically studied with the classic public goods game: consider a situation where there are 10 players. Each one can pay between 0 and 20 € into a communal wallet in each round. After each round, the total amount of money in the wallet is doubled and given in equal proportions to all players. Under these conditions, the highest total payoff is achieved if everybody contributes the full 20 €. If all players pay 20 €, they all get 40 €. However, the highest individual payoff is achieved if the individual defects. This is because for the 20 € it can contribute it would only receive 40 €/10 players = 4 € back. Contributing is thus altruistic in the Hamilton sense (Hamilton 1964): it reduces an individual's lifetime success. As free–riders gain more than contributors, cooperation quickly breaks down whenever the game is played with humans, unless additional parameters are introduced (Fehr & Gächter 2002, Milinski et al. 2002).

While the standard public goods game predicts that contributions to a public good should break down there is plenty of empirical evidence that humans cooperate between unrelated individuals on a large scale, including in highly risky situations such as warfare. Therefore, many studies on humans aimed at finding the underlying mechanisms that allow the puzzling existence of public goods in our species. These studies typically use an experimental setup in the laboratory where humans are supposed to play cooperation games (mainly public good games) using computers. This allows controlling for many factors that are not under control in real life situations using detailed instructions and information for the participants. It is e.g. possible to make decisions completely anonymous and to control the information that each participant can use. The payoff is set by the experimenter and effects of different payoff matrices can be studied.

Experiments showed that humans behave in such games more cooperatively than was expected based on the payoff matrices (Ostrom 1998, Fehr & Fischbacher 2003). In particular two mechanisms appear to stabilise contributions to public goods, namely punishment and gain of reputation. Punishment as defined by Clutton–Brock & Parker (1995) is an action that reduces the payoffs of both the actor and a recipient who failed to cooperate, with the function to make the recipient behave more cooperatively in the future. Given the option, humans readily invest into punishment of non–cooperative individuals even if they will not interact with these individuals in the future (Fehr & Gächter 2002, Rockenbach & Milinski 2006, Egas & Riedl 2008, Gächter et al. 2008). This led to the development of the cultural group selection concept (Boyd et al. 2003, Gintis et al. 2003), which states that strong competition between groups of early humans selected for socially learned traits that help to stabilize cooperation within these groups to increase group survival. Colleagues interested in the inclusive fitness framework ‘translated’ the cultural group selection models and argued that these traits evolved when human groups consisted mainly of related individuals and that punishment of non–cooperators was under positive selection due to indirect fitness benefits (Gardner & West 2004, Lehmann et al. 2007). According to this view, punishment is a mechanism out of place in our globalized society. Clearly, if one accepts that people show their natural decision rules in the experiments and that the money they get in the experiments should translate into fitness correlates then punishment in one–off situations with all players being strangers is under negative selection. As punishment stimulates the punisher’s reward system in the brain (de Quervain et al. 2004) there is at least a proximate explanation why subjects cannot resist punishing even in one–off situations.

Nevertheless, it remains largely unclear why humans use punishment in public goods games, and more recent studies demonstrate that punishment works only in some cultures but not in all (Gächter et al. 2010).

In contrast to punishment, the gain of reputation through contributions to a public good seems to provide a straightforward functional explanation why people may benefit from contributions. A verbal argument by Alexander (1986) was formalised by various authors (Nowak & Sigmund 1998, Leimar & Hammerstein 2001, Lotem et al. 2003). Two main scenarios have emerged, namely indirect reciprocity (Nowak & Sigmund 1998, Leimar & Hammerstein 2001) and indirect pseudoreciprocity, also called ‘social prestige’ (Zahavi 1995, Roberts 1998, Lotem et al. 2003). In both cases, a basic condition is that interactions take place in a communication network in which bystanders eavesdrop on ongoing interactions (McGregor 1993). These bystanders evaluate the level of cooperation displayed by interacting partners and attribute a corresponding image score. The score is positive if help is given and negative if help is refused. In indirect reciprocity, it pays to help because third partners provide help in return (Nowak & Sigmund 1998, Leimar & Hammerstein 2001). Thus every single act is seen as a one–sided investment. In indirect pseudoreciprocity it pays to help because this increases the chance of being chosen for a mutually beneficial interaction (Zahavi 1995, Roberts 1998, Lotem et al. 2003). Thus, bystanders gain foreseeable benefits from observing interactions by identifying profitable partners. Currently, evidence that the gain of reputation provides a mechanism to stabilise contributions to a public good is restricted to humans (Milinski et al. 2002, Semmann et al 2005). Humans are indeed very sensitive even to subtle cues of being observed, as such cues significantly increase levels of cooperation in anonymous games (Haley & Fessler 2005, Bateson et al. 2006).

While humans are particularly able to cooperate on a large scale with unrelated individuals, there are some potential cases of n–player cooperation in other animals. One possible explanation is the concept of group augmentation (Kokko et al. 2001) that has been developed to explain unconditional contributions of helpers to offspring feeding and care in cooperatively breeding species. The logic behind group augmentation is that larger groups out–compete smaller groups and that therefore behaviours that promote an increase in group size can be self–serving even if it benefits all other group members as well. The group augmentation concept can be seen as by–product mutualism and/or pseudoreciprocity (where the benefits that get returned are a by–product of self–serving acts of the recipient) with more than one recipient at the same time. The concept of group augmentation has been best applied to cooperatively breeding meerkats. In meerkats, *Suricata suricatta,* sentinels look for predators in exposed locations while other group members are feeding. It could be shown that this behaviour is condition dependent and that individuals only act as sentinels if they are satiated (Clutton–Brock et al. 1999). Under these conditions it is the best option for an individual to look for a predator, which is not possible while digging for food, and thereby maximise the survival of all group members. Also the concept of generalised reciprocity (Pfeiffer et al 2005) may in principle apply to n–player interactions if helping is given to several recipients simultaneously. This idea has not yet been applied to non human animals.

Current problems with the empirical evidence on n–player concepts

The empirical problems differ between the studies on humans and non–human animals. In non–human animals, the key challenge is to properly measure payoffs. This is particularly true for species with a kin structured population as found in cooperatively breeding species. It is then difficult to distinguish between kin selection (indirect benefits) and group augmentation (direct benefits) as potential explanations for stable contributions to public goods. In the experiments on humans, high genetic relatedness can be excluded, while game structure and payoffs are determined by the experimenter. Despite these advantages, results are not always easy to interpret. Kümmerli et al (2010) criticize that often every deviation from the expected value of cooperation (zero cooperation in one–off interactions) in games on human cooperation is attributed to prosocial preferences without controlling for errors. Because of this they designed their experiment in a way that made 100 % cooperation the best option for every individual. The interesting part of this is that now both selfish interests and prosocial preferences should lead to 100 % cooperation. The experiment therefore can be seen as a control that was lacking in the experiments done before, where not contributing was the selfish option. Many of the subjects of this game did not fully cooperate even though their understanding of the setup was tested before. This demonstrates again that there is caution needed for the evolutionary interpretation of economic experiments on humans. The authors suggest that humans are reluctant to show extreme behaviour (100 % cooperation as well as 100 % defection) and this would also explain previous results of unexpectedly high cooperation without any need to assume highly developed prosocial preferences in humans. The authors also suggest that experimenters should analyze the relative effect of factors such as punishment or repeated interactions on human levels of cooperation rather than to interpret the absolute values of one single experiment.

Currently, the strongest disagreement in the literature on public goods is arguably the role of punishment in stabilizing contributions. Some studies found positive effects on cooperation (Rockenbach & Milinski 2006), others found that punishment can stabilize cooperation if it is effective and rather cheap (Egas & Riedl 2008) and others found negative effects of punishment: costly punishment can be negative not only for the punisher and the punished individual but even for the whole group (Dreber et al. 2008). Because these studies differ in many parameters such as group size, payoff structure and strategic options of the players it is difficult to draw general conclusions.

What is clearly lacking are studies in a natural setting and complementary experiments to identify ecological parameters that allow the existence of a public good and to study the role of punishment under natural conditions.

Given my interest in cooperation, public goods, punishment and the study of animal behaviour, an ideal study system should have the following features:

- n–player interactions between unrelated individuals
- the possibility to properly infer relative payoffs of possible behavioural actions
- the occurrence of a behaviour that might constitute punishment
- the possibility to study the animals in their natural environment
- the possibility to design laboratory experiments that are explicitly based on hypotheses developed during field observations

The system of parasitic blennies and their interactions with reef fish victims appeared to be a suitable system in that it fulfilled all the requirements listed above. I therefore decided to study this system in detail for my PhD thesis.

Short introduction to the study system

The two species of parasitic blennies:
Plagiotremus rhinorhynchus and P. tapeinosoma

Picture 1: ***P. tapeinosoma*** **in its hiding place**

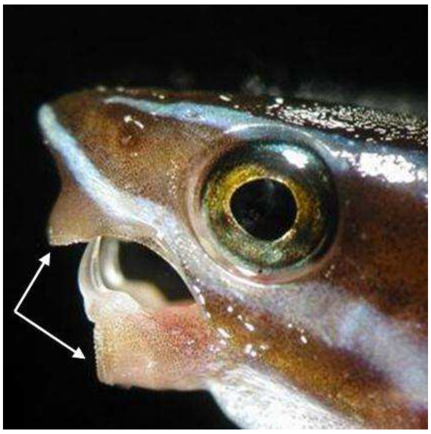


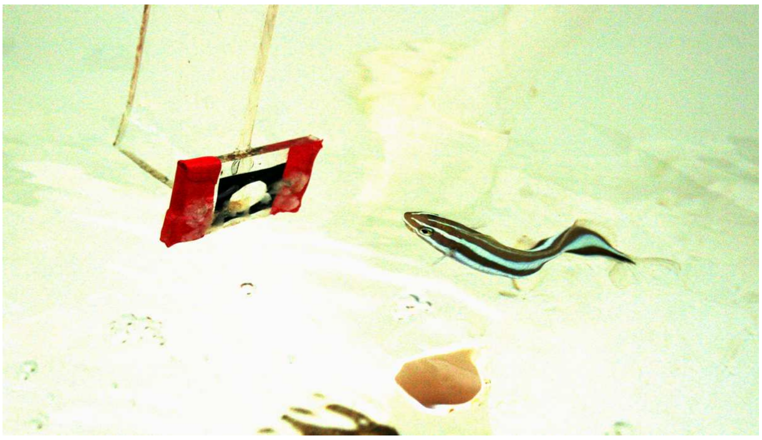
Figure 1:
Large canines of ***P. rhinorhynchus*** **and dense rows of incisors (white arrows).**

Scientific classification:

Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Infraphylum: Gnathostomata
Superclass: Osteichthyes
Class: Actinopterygii
Order: Perciformes
Family: Blenniidae
Tribe: Nemophini
Genus: Plagiotremus

The two species of blennies studied, *Plagiotremus rhinorhynchus* and *P. tapeinosoma*, occur in the tropical Indo–West and Central Pacific and are found on coral reefs and clear lagoons at depths from 1 m to 40 m. The two species are territorial and include into their territory a small hiding hole, normally an empty hole of a tube–worm (see picture1), perfectly fit for their elongated slim bodies. Members of the tribe “Nemophini” are also called “Fang–blennies” or “Sabre–tooth–blennies” because of their elongated canines (fig.1). These teeth are not used for foraging but for male–male fights and for defence (Smith–Vaniz 1976). Their dentary incisors are forming a dense row. The tips of these incisors are thin and wedge shaped, ideally suited to scrape off mucous and scales (Smith–Vanitz 1976).

Both blenny species are lepidophagous (scale eating) parasites that attack other fish to forage. Usually they sneak up on their victims from behind and try to catch them unaware (Smith–Vaniz 1976, Johnson & Hull 2006). Their attacks are very opportunistic; fish that are distracted, e.g. by fights or mating, get attacked immediately. Normally the blennies stop their biting attempts as soon as they are noticed (if their victims turn around and/or show threat displays). 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 my observations was a victim bitten twice without any retreat of the blenny between bites. This usually happens to large fish where the blennies hide underneath their bellies, repeatedly scraping off tissue in a zigzag movement and darting into safety before the fleeing victims are too far away from the secure reef.



Picture 2: ***P. tapeinosoma*** **in the laboratory**

The blennies feed on the mucus and scales of a large variety of fish species, including predatory species. We did not notice that they avoid any of the species that live in their territories. Only cave–living species or fish that hide during day were not attacked in their shelters. The size of their victims also varies greatly. The length of victims that were observed being attacked in this study ranges from 2–65 cm. That blennies also attack larger species is known by many divers. Divers often get attacked from behind (at their legs and fins) when they pass by a blenny (personal observations).

One of the two species, *P. rhinorhynchus*, has attracted attention because it shows variation in colour, with one morph closely resembling juvenile cleaner wrasses, *Labroides dimidiatus* (Kuwamura 1981; Côté & Cheney 2004, 2007; Moland & Jones 2004; Johnson & Hull 2006, picture 3). Both adult morphs show two brilliant pale blue stripes at the side of the body. The background colour of the non–mimetic form is orange or brownish; the mimetic form has a nearly black background colouration. In juvenile blennies the second blue stripe is not yet fully developed and this colour pattern is nearly identical to that of juvenile cleaner fish. The feeding efficiency of the blue and black (imitating the juvenile cleaner) morph seems to be higher in close proximity of juvenile cleaners (Côté & Cheney 2004, Moland & Jones 2004), but it is not clear yet if the main function of this mimicry is “aggressive” and helps to attack unaware fish or if it prevents attacks from predators (Côté & Cheney 2007) or even adult cleaners (Johnson & Hull 2006).

Also the “orange” form is said to be mimetic at some places. In New Britain and in New Guinea and the Solomon islands adult *P. rhinorhynchus* mingling with shoals of anthias (*Pseudanthias spec.*) were observed to be nearly uniformly orange, displaying only very narrow blue stripes (Smith–Vaniz 1976), blending into the shoal. In our study areas we could not find this extreme orange colour morph, though we found several blue and black individuals (imitating cleaners), adults as well as juveniles. These individuals were excluded from our observations as we were not interested in this potentially confounding aspect. Studying non–mimetic forms we never observed reef fishes that behaved in a way that suggested that they confounded the blennies with cleaner wrasses. No fish showed the typical displays (e.g. performing a head stand) that they normally show inviting a cleaner for inspection, though other studies found such behaviour (Johnson & Hull 2006).

Picture 3: ***P. rhinorhynchus,*** **left: non–mimetic morph;**
mimetic colouration: adult (middle, © Andy Lewis) and juvenile (right)

P. tapeinosoma also has two stripes at the side of the body, but they are nearly white. Between the two stripes there is an irregular pattern of vertical brownish stripes. This species does not mimic cleaner wrasses, but at the Great Barrier reef they are known to swim with schools of small wrasses (*Thalassoma amblycephalus*) that show a superficially similar pattern. The resemblance is not very good but confers according to Smith–Vaniz (1976) a real advantage because prey fishes are less likely to notice the predator. In the Red Sea, where we did our observations, there is no species that resembles *P. tapeinosoma* in a way that would allow such mimicry.

Picture 4: ***P. tapeinosoma*** **in the Red Sea**

The victims of sabre–tooth blennies

As mentioned above, the blennies are very opportunistic foragers and seem to avoid few species if any. In studying blennies we therefore studied many different victim species in the field. In fact, the diversity offered a great opportunity to investigate in a first step how differences in size, local abundance, or home range size may affect victim responses to blennies. The same species that are attacked by blennies also interact with the cleaner wrasse *Labroides dimidiatus* (Bshary 2001). In that mutualism, the cleaners are visited in their small territories (‘cleaning stations’) by so–called ‘clients’ from which they remove ectoparasites (Randall 1958, Grutter 1999). Conflict arises because cleaners actually prefer client mucus over ectoparasites, where eating mucus constitutes cheating (Grutter & Bshary 2003). Detailed studies have shown that three client categories need to be distinguished, namely predatory clients, resident clients with small territories/home ranges that include only one cleaning station, and visiting clients with large territories/home ranges that include several cleaning stations (Bshary 2001). The three categories of clients differ in the way they could respond to cheating by cleaners: predators could try to eat the cleaner, residents punish with aggressive chasing, and visitors switch to a different station for their next inspection (Bshary 2010). Thus, a logical question for the blenny–victim interactions was whether species also differ in how they respond to biting, i.e. aggressively or with flight. Predatory species were excluded from the study, 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.

The victim species that was studied in detail: *Pseudanthias squamipinnis*

Picture 5: Shoal of *P. squamipinnis* in the Red Sea

Scientific classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Infraphylum: Gnathostomata
Superclass: Osteichthyes
Class: Actinopterygii
Order: Perciformes
Family: Serranidae
Tribe: Anthiinae
Genus: Pseudanthias
Species: *P. squamipinnis*

Picture 6: *P. squamipinnis* females and *P. tapeinosoma* in the Red Sea

Apart from the initial general data collection we decided to focus on one victim species for more specific questions, with the aim to obtain sufficient sample sizes to properly answer the questions for one species. As it turned out, female scalefin anthias, *Pseudanthias squamipinnis,* appeared to be the most suitable option. *P. squamipinnis* is a sexual dimorphic, protogynous reef fish (individuals start as females and turn into males as soon as they are large enough to defend a harem) that occurs in the Indo Pacific in shoals of up to several thousand individuals. It is the most abundant species on our reef patches in the Red Sea. Females are more numerous than males and live in harems of about 5 females per male. Anthias feed in shoals on zooplankton that they find in the water column in front or above the corals, which provide them with hiding places. Anthias are residents on the reef patches (Bshary 2001) and turned out to be common victims of the two blenny species we observed.

Picture 7: *P. squamipinnis*, female (orange, left) and male (purple, right).

Due to pelagic eggs and larval stages, anthias individuals at one patch are not more closely related with each other than with individuals from neighbouring patches (Avise & Shapiro1986). This makes it possible to exclude kin selection as an explanation for any cooperative behaviour they might demonstrate among each other against the two blenny species.

Picture 8: Small reef patch with *P. squamipinnis* in the Red Sea

Basic observations as a starting point for the PhD project

Preliminary observations in the Red Sea made it obvious that the blennies are regularly aggressively chased by their victims. Several victim species were observed to turn towards the blenny and accelerate towards the parasite. This happened sometimes without obvious reasons, i.e. without the fish being bitten or approached by the parasite in a stealthy way from behind. Aggressive responses to bites were not ubiquitous, however. No response or fleeing were frequently observed alternatives. In addition, there seemed to be great variance between species with respect to the way they responded. Individuals of some species seemed to be invariably aggressive, while individuals of other species were sometimes aggressive, and for some yet other species we never observed any aggression towards a blenny. The preliminary observations hence suggested that several interesting questions can be addressed in this host–parasite community.

Specific research questions addressed in the thesis

The thesis consists of three result manuscripts where the sequence follows a logical process: results presented in the first manuscript led to questions addressed in the second manuscript, which raised questions addressed in the third one. The starting point was to collect sufficient field observations on blenny–victim interactions to be able to properly describe the system. More specifically, we wanted to determine any variation between victim species with respect to the probability of behaving aggressively towards the blenny. Given that we observe variation we wanted to find out which ecological variables might correlate with levels of aggression. We focussed on victim size, local abundance, discrimination between resident and visitor (the blennies are residents), and territoriality.

Key results from the field observations suggested that a) aggression towards the blenny may function as punishment by decreasing the probability of future attacks, and b) that willingness to behave aggressively may diminish with group size as would be predicted if aggression provides a public good (Bshary & Bshary 2010a). Therefore, we explicitly tested these possibilities in the second manuscript. We tested experimentally whether aggression increases the probability that the blenny attacks alternative victims, we observed in the field whether aggression may provide a public good in shoaling victim species by inducing blennies to switch to a different victim species, and we conducted more laboratory experiments to find a potential explanation why victims might obtain direct benefits from providing a public good (Bshary & Bshary 2010b).

The results from the second manuscript provided overall evidence that aggression towards blennies may constitute a self–serving punishment that provides a public good as a by–product. However, we noticed strong variation between individual blennies in how they responded to punishment. Therefore, we investigated individual variation systematically in the third manuscript, with a focus on the question how such variation may promote or hinder the occurrence of public goods in our system.

In the general discussion that follows the three data chapter I will try to bring together the results of the three manuscripts for a bigger picture. First, I will conclude what we have learned about the blenny–host system. I will then discuss several important open questions about our system. While all of these questions should be studied in the future, I have tried to address several of them in vain during my PhD project. I will mention preliminary results and explain the methodological reasons why these questions are difficult to study. Finally, I will discuss how my results may help to explain more generally the conditions for the existence of public goods based on punishment.

References general introduction

Alexander, R. D. 1987: The Biology of Moral Systems. New York: Aldine de Gruyter.

Avise, 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.

Bateson, M., Nettle, D. & Roberts, G. 2006: Cues of being watched enhance cooperation in a real–world setting. Biol. Lett. 2, 412–414.

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. 2010: Cooperation between unrelated individuals: A game theoretic approach. In Animal Behaviour: Evolution and Mechanisms, P. Kappeler, ed. (Heidelberg, Germany: Springer), pp. 213–240.

Bshary, R. & Bergmüller, R. 2008: Distinguishing four fundamental approaches to the evolution of helping. J. Evol. Biol. 21, 405–420.

Bshary R. & Bronstein J.S. 2011: A general scheme to predict partner control mechanisms in pairwise cooperative interactions between unrelated individuals. Ethology 17, 271–283.

Bshary, A., and Bshary, R. 2010a: Interactions between sabre–tooth blennies and their reef fish victims: Effects of enforced repeated game structure and local abundance on victim aggression. Ethology 116, 681–690.

Bshary, A., and Bshary, R. 2010b: Self–Serving Punishment of a Common Enemy Creates a Public Good in Reef Fishes, Current Biology, 20 (22) 2032–2035.

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.

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.

Darwin C. 1859: On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London 1859

de Quervain, D. J.-F., Fischbacher U., Treyer, V., Schellhammer M., Schnyder, U., Buck, A. & Fehr, E. 2004: The neural basis of altruistic punishment. Science, 305, 1254–1258.

Dreber, A., Rand, D. G., Fudenberg, D. & Nowak, M. A. 2008: Winners don't punish. Nature 452, 348–351.

Egas, M. & Riedl, A. 2008: The economics of altruistic punishment and the maintenance of cooperation. Proc. R. Soc. B 275, 871–878.

Fehr, E. & Gächter, S. 2002: Altruistic punishment in humans. Nature 415, 137–140.

Fehr, E. & Fischbacher, U. 2003: The nature of human altruism. Nature, 425, 785–791.

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.

Grutter, A. S. 1999 Cleaners really do clean. *Nature* 398, 672–673.

Grutter, A. S. & Bshary, R. 2003: Cleaner wrasses prefer client mucus: support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society Series B* 270, 242–244

Gächter, S., Renner, E. & Sefton, M. 2008: The long–run benefits of punishment. Science 322, 1510.

Gächter, S. Herrmann, B. and Thöni, C. 2010: Culture and cooperation. Philosophical Transactions of the Royal Society B 13, 2651–2661

Haley, K.J. & Fessler, D. M. T. 2005: Nobody’s watching? Subtle cues affect generosity in an anonymous economic game. Evolution and Human Behaviour 26, 245–256

Hamilton, W. D. 1964: The genetical evolution of social behaviour. Journal of Theoretical Biology, 7, 1–52.

Hamilton, I. M. & Taborsky, M. 2005: Contingent movement and cooperation evolve under generalized reciprocity. Proc. R. Soc. Lond. B, 272, 2259–2267.

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.

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.

Kümmerli, R., Burton, M. N., Ross–Gillespie, A., West, S. A. 2010: Resistance to extreme strategies, rather than prosocial preferences, can explain human cooperation in public goods games. Proceedings of the National Academy of Sciences of the United States of America 107: 10125–10130.

Kuwamura, T. 1981: Mimicry of the cleaner wrasse Labroides dimidiatus by the blennies Aspidontus taeniatus and Plagiotremus rhinorhynchus. Nanki Seibutu 23, 61–70.

Lehmann, L., Rousset, F., Roze, D., and Keller, L. 2007: Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. Am. Nat. 170, 21–36.

Leimar O. & Hammerstein, P. 2001: Evolution of cooperation through indirect reciprocity. Proceedings of the Royal Society of London, Series B, 268, 745–753.

Lotem, A., Fishman, M. A. & Stone, L. 2003: From reciprocity to unconditional altruism through signalling benefits. Proc. R. Soc. Lond. B. 270: 199–205.

McGregor, P. K. 1993: Signalling in Territorial Systems: A Context for Individual Identification, Ranging and Eavesdropping. Phil. Trans. R. Soc. Lond. B. 340: 237–244.

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. & Sigmund, K. 1998: Evolution of indirect reciprocity by image scoring. Nature, 393, 573–577.

Ostrom, E. A. 1998: Behavioral approach to the rational choice theory of collective action. American Political Science Review, 92, 1–22.

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. 2005: Evolution of cooperation by generalised reciprocity. Proc. R. Soc. Lond. B, 272, 1115–1120.

Randall, J. E. 1958: A review of the labrid fish genus Labroides, with descriptions of two new species and notes on ecology. Pacific Sci. 12, 327–347.

Roberts, G. 1998: Competitive altruism: from reciprocity to the handicap principle. Proc. R. Soc. Lond. B. 265: 427–431.

Roberts G., Sherratt T. N. 1998: Development of cooperative relationships through increasing investment. Nature 394:175–179

Rockenbach, B. & Milinski, M. 2006: The efficient interaction of indirect reciprocity and costly punishment. Nature 444: 718–23.

Rutte, C. & Taborsky, M. 2007: Generalized Reciprocity in Rats. PLoS Biology, 5, e196.

Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. 2004: The evolution of cooperation. Quarterly Review of Biology, 79, 135–160.

Semmann, D., Krambeck, H-J. & Milinski, M. 2005: Reputation is valuable within and outside one's own social group. Behav. Ecol. Sociobiol. 57: 611–616.

Smith–Vaniz, W.F. 1976: The Saber–Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae). Monograph 19 (Philadelphia: The Academy of Natural Sciences of Philadelphia).

Trivers, R. L. 1971: The evolution of reciprocal altruism. Quarterly Review of Biology, 46, 35–57.

Wedekind, C. & Milinski, M. 2000: Cooperation through image scoring in humans. Science, 288, 850–852.

West, S.A., Griffin, A.S., and Gardner, A. 2007: Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415–432.

Zahavi, A. 1995: Altruism as a handicap – the limitations of kin selection and reciprocity. J. Avian. Biol. 26, 1–3.

Interactions Between Sabre–Tooth Blennies and Reef Fishes A. Bshary & R. Bshary

10 Ethology 115 (2010) 1–10 ª 2010 Blackwell Verlag GmbH doi: 10.1111/j.1439–0310.2010.01781.

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

Bshary Andrea & Bshary Redouan

University of Neuchâtel, Institut de Biologie, Eco–Ethologie, Neuchâtel, Switzerland

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 (Kuwamura1981; 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 (conspecifics) 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 September to November 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 m3) 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 * 100, and the percentage of aggressive responses to biting was calculated as n aggressive responses to biting ⁄ all bites * 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 a–level (0.05) is divided by n tests to be conducted to obtain the first a'. If one p–value is below the a' level, this result is accepted as significant and a new a'' 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 a–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 a' = 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).

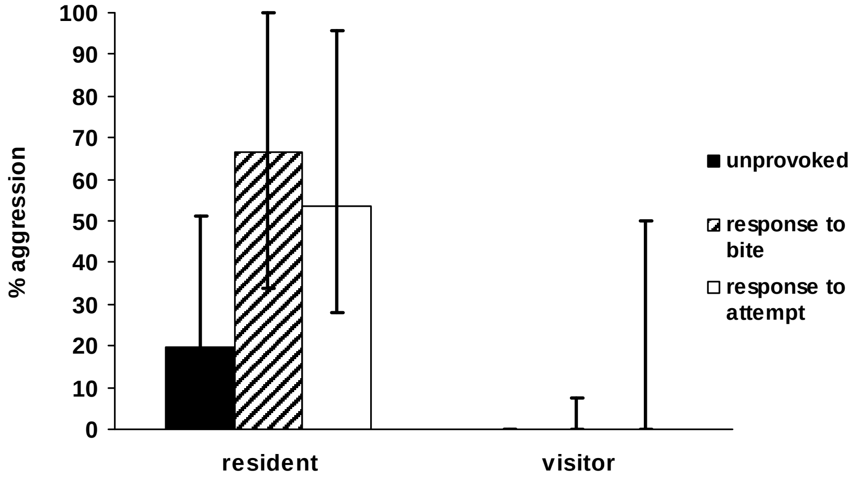


Figure. 1:
Comparison of occurrences of three types of aggressive behaviour (unprovoked aggression, aggression in response to biting attempts and aggression in response to bites) between resident and visiting victim species. Medians are represented with the 25 and 75 percentiles. Sample sizes per category 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.

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

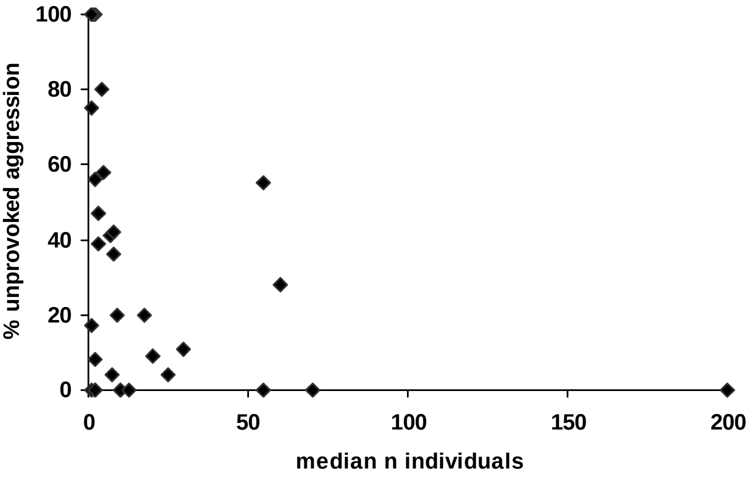
The differences between residents and visitors persisted when only the ten non–territorial resident species were considered for the comparisons (U–tests, initial a' = 0.017; unprovoked aggression: n residents = 10, n visitors = 29, z = '2.636, p = 0.008, aggression in response to biting attempts: n residents = 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 a' = 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).

Figure 2

a)



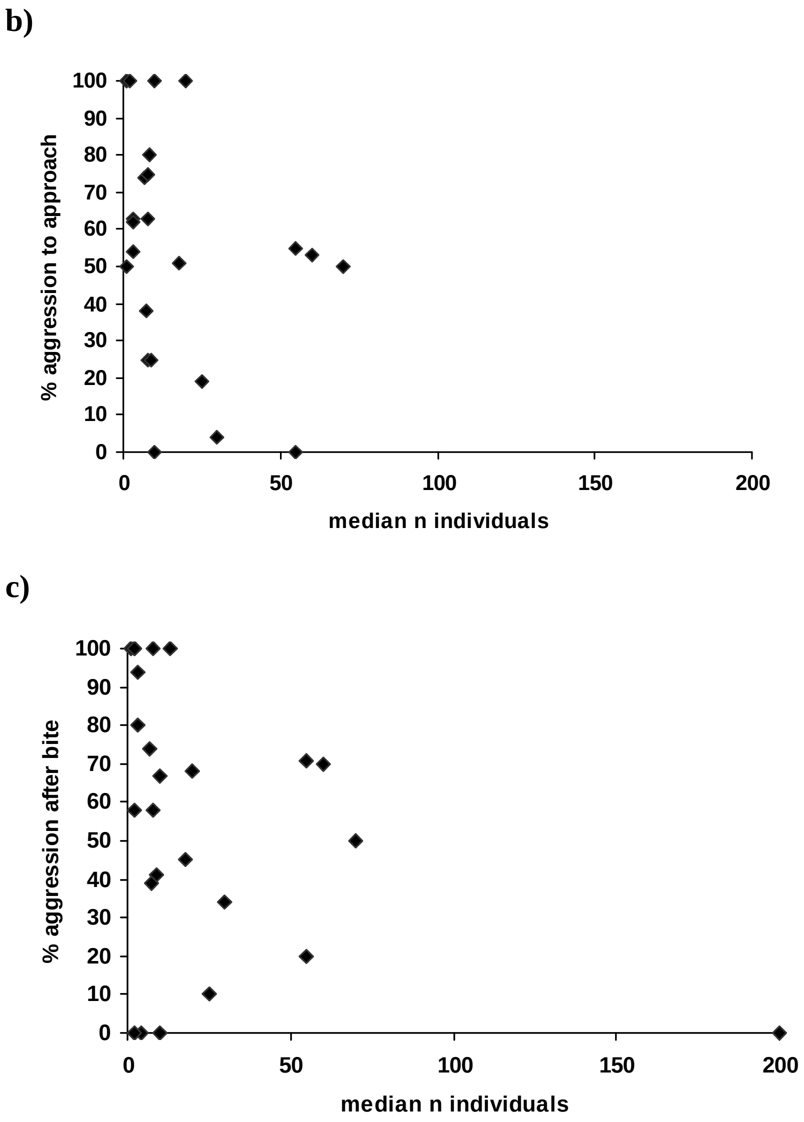


Figure. 2:
Correlations between the resident species' local abundance (median number of individuals at a patch) and aggression towards blennies. Each dot represents the mean value for one species.
(a) Spontaneous aggression relative to all aggressive acts towards blennies (n = 33 species);
(b) aggression 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.

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*, a' = 0.025; females: n = 12, rs = –0.581, p = 0.047; males: n = 11, rs = –0.661, p = 0.027, Fig. 3).

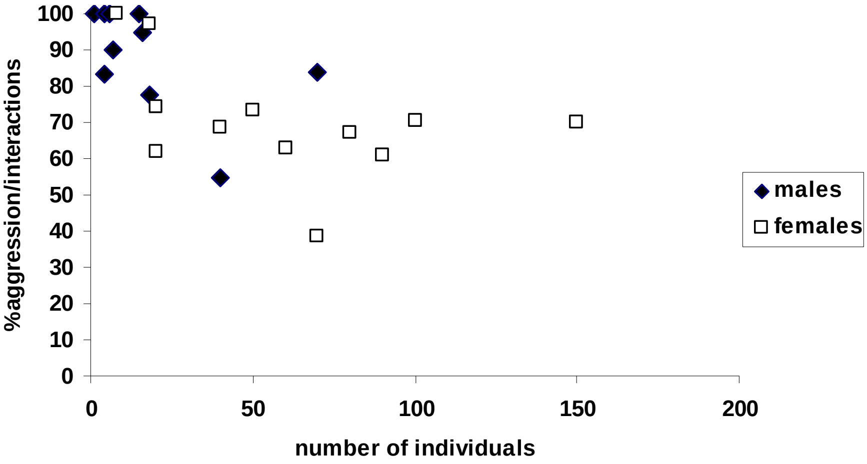


Figure. 3: Correlation between local abundance and aggressive behaviours towards blennies in 11 male and 12 female Pseudanthias squamipinnis shoals. Each shoal is represented by one dot. The correlations are marginally significant at the 0.025 level (because of Bonferroni correction).

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 to biting attempts (Spearman correlation, initial a) = 0.017, rs = 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: rs = 0.172, n = 24, p = 0.422; unprovoked aggression vs. aggression following bites: rs = 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, rs = 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: rs = –0.152, n = 8, p = 0.719; unprovoked aggression vs. aggression following bites: rs = –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: rs = 0.309, n = 11, p = 0.355, unprovoked aggression vs. aggression following attempts: rs = 0.273, n = 11, p = 0.417; unprovoked aggression vs. aggression following bites: rs = –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 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* (Avise & 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.

Acknowledgements

We thank the Egyptian Environmental Affairs Agency for the permission to conduct research in the Park and the Park rangers and Ingo Riepl for local support. We further thank Karin Bergmann for field assistance, Tom Sherratt for discussion and Jenny Oates for comments and correction of the English. The study was financed by a NERC fellowship and a grant by the Swiss Science Foundation to RB.

Literature Cited

Avilés, L. 2002: Solving the freeloaders paradox: genetic associations and frequency–dependent selection in the evolution of cooperation among nonrelatives. Proc. Natl Acad. Sci. USA 22, 14268–14273.

Avise, 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.

Bshary and Bshary, Self–Serving Punishment of a Common Enemy Creates a Public Good in Reef Fishes, Current Biology (2010), doi:10.1016/j.cub.2010.10.027

Self-Serving Punishment of a Common Enemy Creates a Public Good in Reef Fishes

Andrea Bshary 1, and Redouan Bshary 1
1 University of Neuchâtel, Institute of Biology,
Rue Emile-Argand 11, 2009 Neuchâtel, Switzerland

Summary

A key challenge for evolutionary biologists is to determine conditions under which individuals benefit from a contribution to public goods [1, 2]. For humans, it has been observed that punishment of free riders may promote contributions [3, 4], but the conditions that lead to stable cooperation based on punishment remain hotly debated [5–8]. Here we present empirical evidence that public goods may emerge as a by–product of self–serving punishment in interactions between coral reef fishes and parasitic saber–tooth blennies that stealthily attack their fish victims from behind to take a bite [9]. We first show that chasing the blenny functions as punishment [10], because it decreases the probability of future attacks. We then provide evidence that in female scalefin anthias, a shoaling species, punishment creates a public good because it increases the probability that the parasite switches to another species for the next attack. A final experiment suggests that punishment is nevertheless self–serving because blennies appear to be able to discriminate between look–alike punishers and nonpunishers. Thus, individuals that do (not*) contribute to the public good may risk being identified by the parasite as easy targets for future attacks.

*: is missing in the original publication

Results and Discussion

Cooperation in groups is difficult to explain because individual contributions are shared among group members, a condition that is often vulnerable to free riding [1, 2]. Free riders benefit from the contribution of others but do not contribute themselves, and they therefore gain higher payoffs than contributors do. Two main solutions have emerged in studies on humans. First, contributions to public goods can be stable if players may gain a positive reputation from contributing, which increases the probability of receiving help in other situations [11–13]. Second, humans may achieve stable cooperation in n–player games if players are allowed to punish cheaters [4]. Empirical evidence for the success of punishment even in one–off interactions has led to a heated theoretical discussion about which conditions such punishment may evolve from. Models of ‘‘cultural group selection’’ [5, 6] propose that fast social learning within groups stabilizes punishment against the problem of so–called second–order free riding (contributing to public goods but failing to pay for the punishment of free riders). Others have pointed out that punishment in one–shot games can only evolve as a result of indirect fitness benefits [7, 8]. For a better understanding of the conditions that lead to stable punishment, it seems to be of paramount importance to identify more natural conditions in which punishment occurs and to identify the consequences of punishment on an individual’s fitness. For example, under natural conditions it seems more likely that individuals interact repeatedly. Repeated interactions may create conditions in which, at least in theory, individuals may gain direct benefits from punishment, even if it creates a public good. The empirical evidence from experiments on humans is mixed in the sense that in some studies, punishing individuals gain more money than the average nonpunishing individual, whereas other studies find the opposite [14–19]. The cited studies differ from each other with respect to many parameters such as group size, information about the behavior of others, payoff structure, strategic options, and ethnic membership, making it difficult to draw general conclusions. Here we explore the possibility that punishment yields direct benefits in an animal system in which field observations suggest that the likelihood of punishment depends on both a repeated game structure and group size [9]. In our study system, saber–tooth blennies stealthily attack other reef fish species from behind to take a bite of mucus, scales, and/or tissue [20]. The blennies occupy small territories, and resident victim species that repeatedly interact with the same blenny often chase blennies in response to bites [9]. In contrast, visiting species that may simply swim beyond a blenny's range typically never chase blennies but swim off [9], suggesting that an enforced repeated game structure is essential for the emergence of residents chasing blennies. We tested first whether chasing a blenny functions as punishment sensu Clutton–Brock and Parker [10]: the immediate reduction in payoffs due to the costs of chasing the blenny might be offset by the blenny seeking alternative victims in the future. If that was the case, we asked what the consequences of punishment on the parasite's behavior might be if the punisher was a member of a shoaling species. Many resident victim species live in aggregations, raising the question of whether conspecifics may also benefit from the chasing done by a group member. This would be the case if punishment increases the probability that a blenny switches to a different victim species for its future attacks. We addressed this question on one particular shoaling resident species, scalefin anthias *Pseudanthias squamipinnis*. Individuals of this species frequently chase blennies [9], an observation that cannot be explained with kin selection as a potential mechanism because it has been demonstrated that anthias groups lack any kin structure [21]. Therefore, punishment has to increase the direct fitness of punishers even in this shoaling species. One possible explanation is that blennies select for stable punishment because they discriminate between lookalikes, where one individual punishes and another one does not. We tested this hypothesis experimentally.

Does Aggression Function as Punishment?

To test whether aggression reduces the probability of being selected again as a victim, we let 18 blennies feed off of two differently colored Plexiglas plates: one was invariably retrieved in response to the blenny taking a bite, whereas the other one invariably chased the blenny in response to taking a bite. After training, three naive persons presented independently of each other both plates simultaneously to the blenny at equal distance and scored what the blenny chose, without any further chasing. Blennies attacked the fleeing plate significantly more often than the chasing plate, no matter whether the chasing had been done by hand or in a more standardized way with a machine (sign test: handheld plate: $n = 8$ individuals, $x = 0$, $p = 0.008$; machine used to standardize chasing: $n = 10$ individuals, $x = 1$, $p = 0.02$). These data demonstrate that chasing may function as punishment: the apparent reduction in immediate payoffs of both actor (through energetic expenditure) and recipient (through energetic expenditure and risk of injury) yields future benefits to the actor, because the act alters future behavior of the recipient. In our case, the blenny will preferentially seek other victims. Clear demonstrations of punishment have hitherto been rare in animals (but see [22–24]) because it is often difficult to exclude the fact that immediate benefits drive the behavior. In our case, aggression does not yield immediate benefits because blennies almost always bite only once during an attack and retreat even without any reaction of their victim [9].

Does Punishment Create a Public Good in Locally Abundant Species?

To test whether chasing the blenny can create a public good in shoaling fishes, we observed 17 blennies in the field. We concentrated our observations on the females of a locally abundant species, scalefin anthias, *P. squamipinnis*, to get a sufficient amount of data of one species. We compared the percentage of the blennies switching to another species if they were aggressively chased with the percentage of switching without any aggressive response of the victim. Overall, chasing the blenny increased the probability that it switched to another species for its next attack both in a detailed sample on one blenny (X2 test, n = 256 interactions following a female anthias–blenny interaction, X2 = 9.2, df = 1, p = 0.0024, Figure 1) and when we compared mean switching probabilities of several blennies after being aggressed and after not being aggressed by a female anthias (Wilcoxon signed ranks test, n = 17 blennies, z = 22.059, p = 0.039, Figure 1).

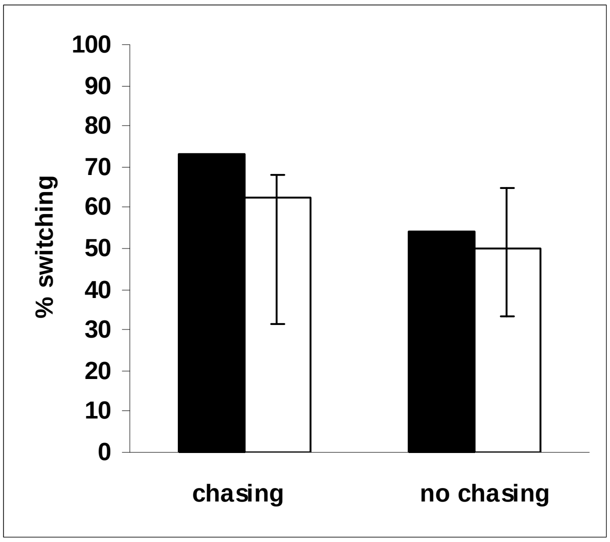


Figure 1. Punishment Creates a Public Good
The probabilities that blennies switch to another victim species for their next attack, depending on whether a female anthias chased or did not chase the blenny in the previous interaction.
Black: data on one blenny studied in detail for 16 hr.
White: data on 17 blennies, median and interquartiles of individual mean values.

These data suggest that all members of a shoal of lookalikes profit from the chasing done by an individual fish. Punishment by one individual thus appears to create a public good in shoaling species. In line with this assessment, a between–species comparison revealed a slightly negative correlation between local abundance and likelihood of chasing saber–tooth blennies [9]. Nevertheless, the creation of a public good does not lead to a breakdown of punishment, neither in scalefin anthias nor in other resident aggregating species [9]. Therefore, the question arises of what factors may cause that punishment to remain self–serving, even if it additionally creates a public good. One possibility is that the punisher gets a larger proportion of the benefits than other group members [25]. This logic has been proposed in the framework of ‘‘group augmentation’’ [26]. This concept proposes that individuals may benefit from helping other group members because their own reproductive success is linked to the survival of these group members. The concept was developed to explain apparently unconditional individual contributions to vigilance and pup feeding in meercats [27, 28]. Indeed, individuals contribute most to group benefitting activities when they are satiated, and they therefore benefit disproportionately from activities other than foraging. More generally, it has been noted that both by–product mutualism [29], in which an individual shows a self–serving behavior that benefits others as a by–product, and pseudoreciprocity [30], in which an individual’s investment causes self–serving responses that benefit the investor as a by–product, may explain cooperation in situations in which more than one individual benefits from helping [31, 32].

Could Blenny Foraging Decisions Select for Stable Punishment Even in Large Groups?

In a laboratory experiment, we tested whether blennies are able to identify free riders. We used four plates (see Figure S1A available online) to present look–alike pairs (mimicking conspecifics) and a different–looking individual (mimicking an allospecific) in a counterbalanced design across individual blennies. Each blenny was confronted with a 100 % punishing plate, a look–alike 0 % punishing ‘‘free riding’’ plate, and a different–looking plate that punished a foraging bite of the blenny with 50 % probability. In each trial, two plates were presented simultaneously, and the blenny was allowed to take a single bite. Depending on its choice, this would either lead to a punishment action followed by removal of both plates or to immediate removal of both plates. The three possible combinations in which two plates could be presented pairwise were counterbalanced across trials. Our construction, to which the lever of the plate was attached, allowed a standardized movement of the plate of fixed direction and distance to punish a blenny (Figure S1B). Under these conditions, blennies generally preferred the nonpunishing plate over its look–alike 100 % punishing plate (Wilcoxon signed rank test, $n = 8$, $Z = 22.38$, $p = 0.017$). Three out of eight blennies met our learning criteria for a significant preference to attack the nonpunishing plate when presented together with the 100 % punishing look–alike plate within a maximum of 80 joint presentations (Figure 2). In addition, we found that blennies generally preferred the two look–alike plates over the different–looking plate. They significantly preferred the nonpunishing plate over the 50 % punishing plate (Wilcoxon signed rank test, $n = 8$, $Z = 22.52$, $p = 0.012$, Figure 3), and there was a nonsignificant tendency that the blennies preferred the 100 % punishing plate over the 50 % punishing plate (Wilcoxon signed rank test, n = 8, Z = 21.82 p = 0.069, Figure 3).

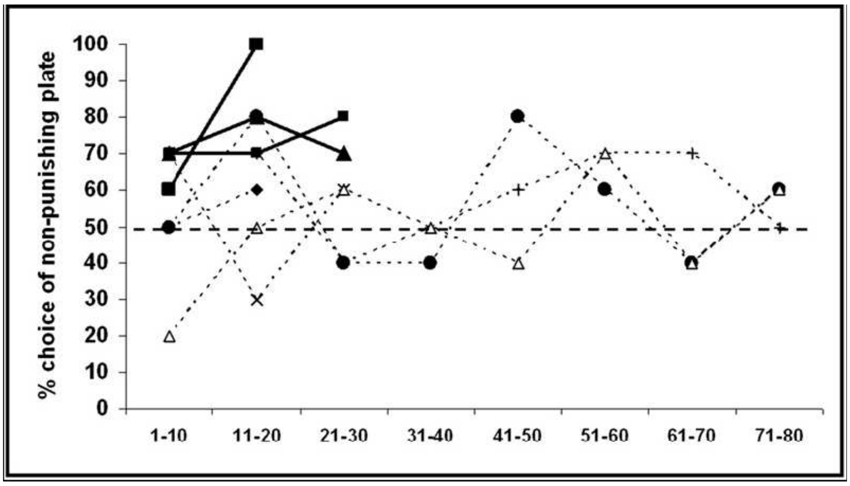


Figure 2. Blennies May Discriminate between Punishers and Free Riders
The probabilities for eight blennies to take a bite from the nonpunishing plate when paired with the look–alike 100 % punishing plate over a maximum of eight series of ten trials each.
Bold lines: individual blennies that fulfilled our criteria for significant preference for the nonpunishing plate.
Dashed line: expected value if blennies do not discriminate between plates.
For the experimental setup of experiment 2, see also Figure S1.

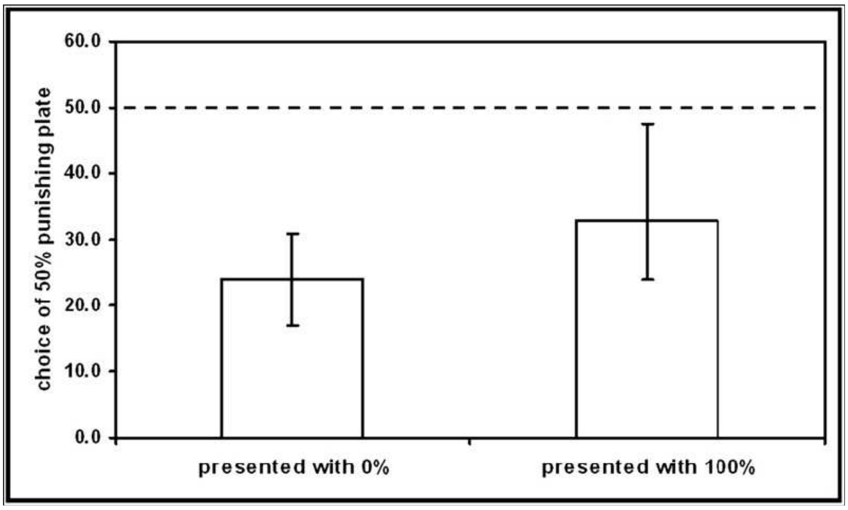


Figure 3. Blennies Prefer Abundant Victim Types
The percentages with which blennies took a bite from the plate that punished with 50 % probability when presented with a different–looking plate that either punished with 0 % probability or with 100 % probability.
Median and interquartiles of mean values for eight different blennies are presented.
Dashed line: expected value if blennies do not discriminate between plates.

The results demonstrate that at least some blennies may be able to learn to discriminate between punishers and nonpunishers and then selectively bite nonpunishers. Their foraging decision rules would then select against nonpunishing individuals and hence select against free riders. In addition, the results suggest that blennies generally prefer more–abundant victim types over rarer ones. In this respect, the blennies act like many predators: it is textbook knowledge that predators may select prey disproportionately to its abundance either because predators develop search images or because they prefer to frequent the habitat of abundant prey species [33]. The blennies' preference for abundant victim types could strongly interfere with their willingness to switch from frequently punishing but abundant species to rarely punishing species that occur at low densities. Nevertheless, we note that there are far more individual fish in the reef than the number of plates we used in our experiment. Thus, the challenge blennies face under natural conditions appears to be more cognitively demanding. On the other hand, it might still be easier for a blenny to distinguish between fish than between plates. In addition, in nature, blennies could simply stay close to a nonpunishing individual for repeated attacks and thereby select against free riders, whereas such a blenny strategy was excluded in our experiment because the plates were removed after each attack.

In summary, our various results demonstrate that aggression by victims functions as punishment because it increases the probability that saber–tooth blennies select alternative victims during future attacks. In this respect, our experiments in which we used Plexiglas plates seem to corroborate well with our field observations. Punishment is likely to produce a public good in shoaling species because blennies are likely to switch to other victim species. In our victim study species, there is no kin structure [21] that could explain why individuals punish, though they provide a public good [7, 8]. More generally, kin structures will rarely exist in reef fish species, because the vast majority of them are open–water spawners with pelagic egg and larval stages, which creates a mixed population structure [34, 35]. Therefore, direct benefits of the observed punishment are needed to explain the persistence of the public good. The reason why contributions to the public good appear to be self–serving is that the common enemy selects for the contribution in our system. Free riders risk being identified as easy targets for future attacks by the blenny, and avoiding this risk may compensate for the costs of chasing, thereby selecting against free riding. Strictly speaking, contributions to the public good are therefore not a case of cooperation, because individuals are selected to punish completely independently of the positive effects their behavior might have on conspecifics [31]. Nevertheless, by–product effects may be important starting points for the evolution of more sophisticated helping behaviors [36]. Our study system differs in a key factor from standard game theoretic experiments on human groups: in each round, the blenny (the cheater) only interacts with a single individual of its own choice, whereas in many human experiments, all group members interact simultaneously [3, 4, 14, 16–18, 37]. As a consequence, it is always clear which individual of a shoal has to punish the blenny for its cheating. A victim cannot expect others to do the punishment, because they did not have a negative experience. We think that such conditions often apply to humans as well, in which punishment is a selfserving response to being cheated while benefiting the community as well. A person whose house gets broken into or who gets attacked by robbers will have to take action (call the police/fight back) even though all the neighbors may profit from this. This self–serving scenario might explain why humans ‘‘erroneously’’ punish free riders in a public goods game in which, in each round, a single individual is randomly selected to obtain the opportunity to punish other group members, even though punishment is costly, because group composition changes every round [38]

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and one figure and can be found with this article online at doi:10.1016/j.cub. 2010.10.027.

Acknowledgments

We thank the Egyptian Environmental Affairs Agency for the permission to conduct research in the park and the park rangers and Ingo Riepl for local support. We further thank the staff of the Lizard Island Research Station and Lexa Grutter for their support and friendship. We are grateful to Aurore Malapert for contributing to the field data collection and to Tom Sherratt and two anonymous referees for comments and corrections of the English. The study was financed by a Natural Environment Research Council fellowship and a grant by the Swiss Science Foundation to R.B.

References

1. Hardin, G. (1968). The tragedy of the commons. Science 162, 1243–1248.

2. Ostrom, E. (1990). Governing the Commons: The Evolution of Institutions for Collective Action (New York: Cambridge University Press).

3. Fehr, E., and Gächter, S. (2000). Cooperation and punishment in public goods experiments. Am. Econ. Rev. 90, 980–994.

4. Fehr, E., and Gächter, S. (2002). Altruistic punishment in humans. Nature 415, 137–140.

5. Boyd, R., Gintis, H., Bowles, S., and Richerson, P.J. (2003). The evolution of altruistic punishment. Proc. Natl. Acad. Sci. USA 100, 3531–3535.

6. Gintis, H., Bowles, S., Boyd, R., and Fehr, E. (2003). Explaining altruistic behavior in humans. Evol. Hum. Behav. 24, 153–172.

7. Gardner, A., and West, S.A. (2004). Cooperation and punishment, especially in humans. Am. Nat. 164, 753–764.

8. Lehmann, L., Rousset, F., Roze, D., and Keller, L. (2007). Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. Am. Nat. 170, 21–36.

9. Bshary, A., and Bshary, R. (2010). Interactions between sabre–tooth blennies and their reef fish victims: Effects of enforced repeated game structure and local abundance on victim aggression. Ethology 116, 681–690.

10. Clutton–Brock, T.H., and Parker, G.A. (1995). Punishment in animal societies. Nature 373, 209–216.

11. Alexander, R.D. (1987). The Biology of Moral Systems (New York: Aldine de Gruyter).

12. Nowak, M.A., and Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. Nature 393, 573–577.

13. Milinski, M., Semmann, D., and Krambeck, H.-J. (2002). Reputation helps solve the ‘tragedy of the commons’. Nature 415, 424–426.

14. Rockenbach, B., and Milinski,M. (2006). The efficient interaction of indirect reciprocity and costly punishment. Nature 444, 718–723.

15. Dreber, A., Rand, D.G., Fudenberg, D., and Nowak, M.A. (2008). Winners don’t punish. Nature 452, 348–351.

16. Gächter, S., Renner, E., and Sefton, M. (2008). The long–run benefits of punishment. Science 322, 1510–1510.

17. Gächter, S., Herrmann, B., and Thöni, C. (2010). Culture and cooperation. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365, 2651–2661.

18. Nikiforakis, N. (2008). Punishment and counter–punishment in public good games: Can we really govern ourselves? J. Public Econ. 92, 91–112.

19. Carpenter, J.P. (2007). Punishing free–riders: How group size effects mutual monitoring and the provision of public goods. Games Econ. Behav. 60, 31–51.

20. Smith–Vaniz, W.F. (1976). The Saber–Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae). Monograph 19 (Philadelphia: The Academy of Natural Sciences of Philadelphia).

21. Avise, J.C., and Shapiro, D.Y. (1986). Evaluating kinship of newly settled juveniles within social groups of the coral reef fish Anthias squamipinnis. Evolution 40, 1051–1059.

22. Bshary, R., and Grutter, A.S. (2005). Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. Biol. Lett. 1, 396–399.

23. Bshary, R., Grutter, A.S., Willener, A.S.T., and Leimar, O. (2008). Pairs of cooperating cleaner fish provide better service quality than singletons. Nature 455, 964–966.

24. Raihani, N.J., Grutter, A.S., and Bshary, R. (2010). Punishers benefit from third–party punishment in fish. Science 327, 171.

25. Sherratt, T.N., Roberts, G., and Kassen, R. (2009). Evolutionary stable investment in products that confer both an individual benefit and a public good. Front. Biosci. 1, 4557–4564.

26. Kokko, H., Johnstone, R.A., and Clutton–Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. Proc. Biol. Sci. 268, 187–196.

27. Clutton–Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S., and Manser, M. (1999). Selfish sentinels in cooperative mammals. Science 284, 1640–1644.

28. Clutton–Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Sharpe, L., Kansky, R., Manser, M.B., and McIlrath, G.M. (2000). Individual contributions to babysitting in a cooperative mongoose,Suricata suricatta. Proc. Biol. Sci. 267, 301–305.

29. Brown, J.L. (1983). Cooperation: A biologist's dilemma. In Advances in the Study of Behaviour, J.S. Rosenblatt, ed. (New York: Academic Press), pp. 1–37.

30. Connor, R.C. (1986). Pseudo–reciprocity: Investing in mutualism. Anim. Behav. 34, 1562–1566.

31. West, S.A., Griffin, A.S., and Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20, 415–432.

32. Bshary, R. (2010). Cooperation between unrelated individuals: A game theoretic approach. In Animal Behaviour: Evolution and Mechanisms, P. Kappeler, ed. (Heidelberg, Germany: Springer), pp. 213–240.

33. Krebs, J.R., and Davies, N.B. (1993). An Introduction to Behavioural Ecology, Third Edition (Oxford: Blackwell).

34. Cowen, R.K. (2002). Larval dispersal and retention and consequences for population connectivity. In Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem, P.F. Sale, ed. (London: Academic Press), pp. 149–170.

35. Leis, J.M., and McCormick, M.I. (2002). The biology, behaviour, and ecology of the pelagic, larval stage of coral reef fishes. In Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem, P.F. Sale, ed. (London: Academic Press), pp. 149–170.

36. Leimar, O., and Hammerstein, P. (2010). Cooperation for direct fitness benefits. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365, 2619–2626.

37. West, S.A., Gardner, A., Shuker, D.M., Reynolds, T., Burton–Chellow, M., Sykes, E.M., Guinnee, M.A., and Griffin, A.S. (2006). Cooperation and the scale of competition in humans. Curr. Biol. 16, 1103–1106.

38. O’Gorman, R., Henrich, J., and Van Vugt, M. (2009). Constraining free–riding in public goods games: Designated solitary punishers can sustain human cooperation. Proc. Biol. Sci. 276, 323–329.

Supplemental Data

Supplemental experimental procedures

A) Field data

Study site

Field data were collected in May 2005, May 2006 and June 2007 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). In this area, incoming sand through wadis led to the formation of patch reefs which are separated from each other by sand. Observations took place at 20 small reef patches (estimated size between 3.5 m^3 and 30 m^3) located in shallow water (bottom depth between 1.5 and 6 m).

Study species

The two blenny species studied, *Plagiotremus rhinorhynchus* and *P. tapeinosoma*, occur in the tropical Indo–West and Central Pacific and occupy small territories. 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, mucus and scales [1–3].

For the victims we focused on female scalefin anthias *Pseudanthias squamipinnis*. *P. squamipinnis* is a sexual dimorphic, protogynous reef fish that occurs in the Indo Pacific in shoals of up to several thousand individuals. It is one of the most abundant species on our reef patches. Females are more numerous than males and they are common victims of the two blenny species we observed. Anthias individuals at one patch are not more closely related with each other than with individuals from neighboring patches [4].

Data collection

Observations were carried out using scuba equipment and sitting on the surrounding sand 2-3 m in front of the reef patch. One observation session lasted 60 minutes. In 2005, we studied one blenny in detail for 16 hours. In 2006, we studied eleven blennies for 2–4 hours each, while in 2007 eight blennies were observed for 5–8 hours. Variation in observation duration was due to blennies disappearing and/or spending much time in their hiding holes during single sessions. A total of 95 hours of observations is available. We choose reef patches that showed a high abundance of *P. squamipinnis* females to get a large sample size of interactions with this species.

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. Category of victim species: *Pseudanthias squamipinnis* female or other
2. Type of interaction between blenny and female anthias victims:
   - – 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 behavior 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 [1,2]. 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.

Data analysis

From the sequence of interactions between the blennies and their victim species we extracted all interactions with female anthias and looked at follow-up interactions. We scored whether female anthias had been aggressive or not, and whether the next attack of a blenny was directed at a female anthias or not. As we could not recognize individual female anthias we could not determine if the blenny bit the same individual or a different one. Whenever the blenny spent time in its hole we ignored the previous interaction. We thus had for each blenny one probability of switching victim species after being aggressed by female anthias, and one probability of switching victim species without being aggressed by female anthias. These data were used to test the effect of aggression. At three reef patches we observed no non–aggressive interaction between the blenny and female anthias. These patches had to be excluded from the analysis. For the other blennies, the number of observations following an interaction with an aggressive female anthias varied between 8 and 171 (median: 29), and the number of observations following an interaction with a non aggressive female anthias varied between 2 and 85 (median: 5).

B) Experimental data in the laboratory

Experiments were conducted at the Lizard Island Research Station, Great Barrier Reef, Australia. Subjects were caught in the surrounding reefs and released at the site of capture after the experiments. We only used *Plagiotremus rhinorhynchus* as subjects because they are easier to catch than *P. tapeinosoma*. Individuals were caught by first harassing them to a point where they would hide in their little hole. Then, we placed a hand–net above the hole and sprayed a clove oil solution directly into the hole. The blennies then either fled directly into the hand–net or drifted anaesthetized into the net. Individuals were then put in sealed plastic bags and returned to the station.

The fish were kept individually in opaque aquaria sized 39x30x30 cm. Each aquarium contained a small tube (plastic or bamboo) attached to corral rubble that the fish used as hiding place. After one day of acclimatization we started holding tweezers with mashed prawn flesh in front of the entrance of the tube 3 times per day. All fish fed after a maximum of six days. In a second step the blennies learned to feed from a small plastic plate (3 x 2 cm) covered with mashed prawn, again held in front of their tube. Learning took 1 to 5 days of exposure. Once individuals fed reliably off the plate they were ready for the experiments.

Experiment 1: does victim aggression function as punishment?

Data were collected in July/August 2004, 2005 and 2006, testing in total 18 blennies. The blennies were confronted repeatedly with two new plates that differed in color and “behavior” from each other. One plate was removed from the tank (“fleeing”) after being attacked by the blenny while the other plate reacted with a short movement towards the blenny ("chasing"). The role of the two plates (fleeing or chasing) was counterbalanced across blennies. The plates were offered away from the hiding place to allow some movement of the plates and the blenny. In the first year (2004) the aggressive movement was performed manually using a hand–held lever, where the experimenter made the plate chase after the blenny over about 10 cm. In the following years the movement was standardized by using a machine that caused a fixed saltatory response by the plate, 5.5 cm towards the blenny. We analyzed the speed of the movement with a frame by frame evaluation of a video, using Ulead VideoStudio 8. The 5.5 cm were completed from one frame to the next, hence in ≤ 4/100s.

Initially, only one plate was offered at any given feeding event. Every feeding session consisted of several feeding events where the plates were offered in random order and was terminated when the fish was saturated and/or did not attack the plates any more. This phase lasted 6–7 days, after which the experiment followed. In the experiment, a naïve person offered both plates simultaneously at equal distance to the blenny and noted which plate was attacked. Every blenny was tested 3 times in total by 3 different persons.

We noted how often each blenny attacked the chasing/fleeing plate for matched pair comparisons. We conducted separate analyses for hand–held chasing and for standardized chasing.

Experiment 2: Do blenny foraging rules select against free–riding?

Data were collected in July 2009, testing 8 blennies. Each blenny was offered three plates in total, each 2 x 1.2 cm in size. Two plates looked very similar to each other and the other one showed a different color and pattern (Fig. S1a). Of the two look–alikes one plate always reacted to attacks with a chasing movement ("punishing") while the other one was always removed from the tank after being attacked ("fleeing"). The differently looking plate showed both reactions with a probability of 50 %, using sequences where the same response could maximally occur three times in a row and that were counterbalanced over units of 10 trials. The three plates were presented pair wise in all three possible combinations in a counterbalanced way across trials and blennies. All plates were attached to a wooden construction that allowed only a standardized 8 cm covering movement of the plate when pushed by hand (Figure S1b). The two plates were 5.5 cm apart. Both plate types were used four times for the look–alike plate type and four times for the differently looking single plate.

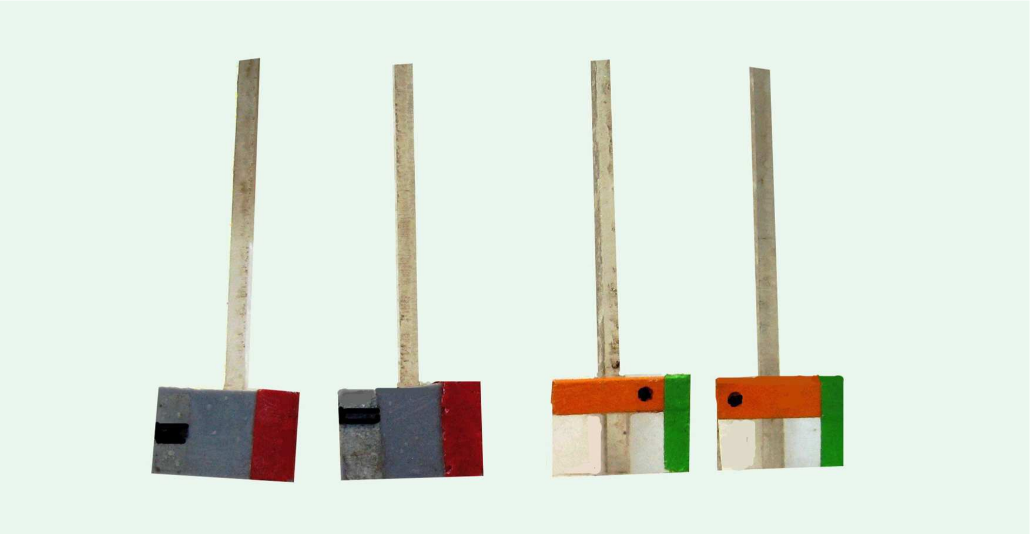
Blennies experienced two sessions per day. In each session, we tried to obtain 30 data points but this was rarely possible because the blennies often lost interest. Five blennies soon stopped entirely to feed off the plates. In our analyses we only consider the eight individuals that interacted at least 100 times with the plates. We stopped experiments after a maximum of 240 trials, which means that we had a maximum of 80 trials for each combination of two plates.

For the analyses we calculated for each plate combination and units of 10 trials the percentage of trials in which the blenny ate from the less aggressive plate (0 % aggression versus 50 % aggression, 0 % versus 100 %, and 50 % versus 100 %). We tested whether blennies showed significant discrimination between each combination of plates. Our criteria for discrimination were either once 9 or 10 out of 10 trials, or twice 8 out of 10 trials, or three times at least 7 out of 10 trials. If an individual reached the criterion for the discrimination between the 0 % aggression and the look–alike 100 % aggression plate we stopped the experiment.

Most statistical tests were calculated using SPSS version 17.0. X^2 tests were performed using the free internet service of Preacher [5].

Figure S1

a



b

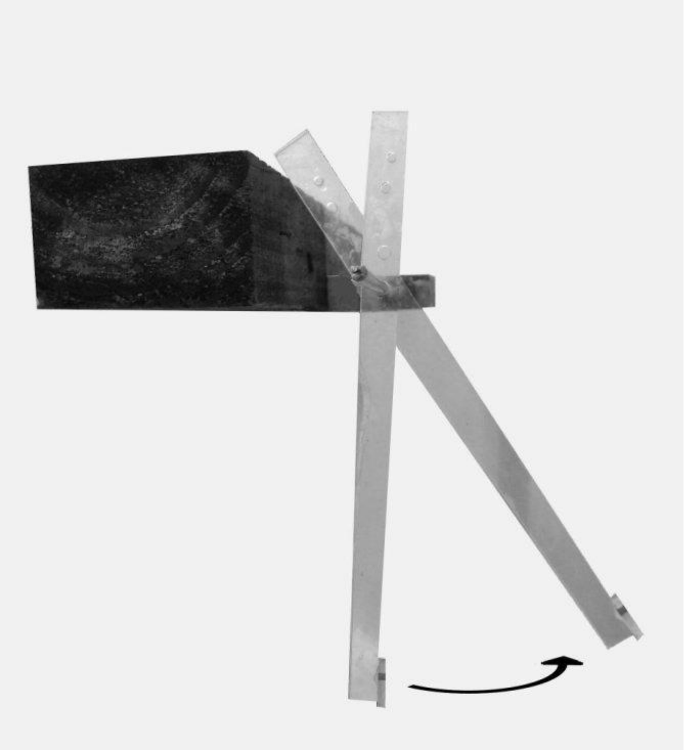


Figure S1: **Experimental setup for experiment 2**.
S1a: a picture of the plates, each 2 x 1.2 cm in size. Each blenny was tested with one pair of look–alikes and one plate with the alternative colors and design.
The combinations were counterbalanced between blennies. S1b: Lateral view of the construction used for standardized punishment. Lever duplicated to show the amplitude of movement.

Supplemental References

1. Smith–Vaniz, W. F. (1976). The Saber–Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae). Monograph 19 (The Academy of Natural Sciences of Philadelphia, Pennsylvania).

2. Johnson, M. L. and 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.

3. Bshary, A. and Bshary, R. (2010). Interactions Between Sabre–Tooth Blennies and Their Reef Fish Victims: Effects Of Enforced Repeated Game Structure and Local Abundance on Victim Aggression. Ethology 116, 681–690.

4. Avise, J. C. and Shapiro, D. Y. (1986). Evaluating kinship of newly settled juveniles within social groups of the coral reef fish *Anthias squamipinnis*. Evolution 40, 1051–1059.

5. Preacher, K. J. (2001). Calculation for the chi–square test: An interactive calculation tool for chi–square tests of goodness of fit and independence [Computer software]. Available from http://quantpsy.org.

Individual differences in foraging strategies of a parasite and their implication for the maintenance of a public good in reef fishes (unpublished manuscript)

Bshary Andrea & Bshary Redouan

Université de Neuchâtel, Institut de Biologie, Eco-Ethologie, Neuchâtel, Switzerland

Abstract

In its beginnings evolutionary game theory typically predicted that optimal behaviour in a given situation is uniform or bimodal. However, the growing evidence that animals behave more variably while individuals may differ consistently in their behaviour, has led to the development of models that predict a distribution of strategies. Here we support the importance of such models by providing evidence that punishment may have variable effects on targets in a coral reef fish host–parasite system. Parasitic blennies (*Plagiotremus spec*.) regularly attack other fishes to bite off scales and mucus. Individuals of some species react to being bitten with punishing the parasite through aggressive chasing. Such punishment can create a public good in shoaling species as it typically increases the probability that the parasite attacks other species. However, our field observations and laboratory experiments show that individual blennies differ markedly in how they incorporate being punished into their foraging decisions. Differences like this may have profound effects on the payoff structure and hence on the maintenance of the public good in this system.

Introduction

Cooperation in groups that consist of more than two unrelated individuals has attracted considerable research interest. A major reason for this interest is that humans seem to be much more able to cooperate in large groups of unrelated individuals than other species (Fehr & Fischbacher 2003, Gintis et al. 2003, Boyd et al. 2003), raising questions about potentially unique selective pressures and/or cognitive or psychological mechanisms present in humans.

A key problem for achieving cooperation in larger groups is typically illustrated with the standard public goods game. In this game each group member may contribute to a communal wallet. Contributions create additional value, which in the game is achieved by the experimenter matching contributions. After each round the group’s gains are equally split between group members, irrespective of how much each individual contributed. These rules typically lead to a situation where it is in the group interest that everybody contributes while for individuals contributions are altruistic. As a consequence, it has been repeatedly demonstrated that humans fail to cooperate in this game.

However, variants of the public goods game may allow cooperative solutions. For example, individuals may benefit from contributing to a public good if this raises their image score and hence increases the probability of receiving help in other contexts (Milinski et al. 2002). Also, if human players have the option to punish free–riders (non contributing individuals) then stable cooperation may be achieved (Fehr & Gächter 2002), even though large cultural differences exist (Henrich et al. 2006, Gächter et al 2008, 2010). Most importantly, it has been argued that cooperative behaviour in n–player interactions may readily emerge if some assumptions of the standard public goods game are relaxed. For example, the assumption of a linear relationship between the amount of contribution and the size of the public good is rarely fulfilled in reality (Archetti 2009a). If one assumes a sigmoid or step function, contributions are no longer altruistic but contributions and free–riding are under negative frequency dependent selection (Archetti 2009 a, b, 2001; Archetti & Scheuring 2010). Stable contributions to a public good may also emerge if individuals gain disproportionally from their own contributions (Sherratt et al. 2009). For example, bacteria gain disproportionally from their own extra–cellular compounds due to their spatial proximity (examples in West et al. 2007).

Recently, the idea that individuals gaining disproportionate benefits from own contributions leads to stable contributions to public goods has been applied to a host–parasite system involving reef fishes and parasitic scale eating blennies of the genus *Plagiotremus*. Reef fish regularly get attacked by parasitic blennies (*Plagiotremus spec.*) and many species react to this with chasing the parasite (Bshary &Bshary 2010a). This chasing functions as punishment sensu Clutton–Brock & Parker (1995) as the momentary costs yield future benefits: chasing decreases the probability that the chasing individual gets attacked in the future (Bshary & Bshary 2010b). In shoaling species this self–serving punishment can additionally create a public good, as the parasites are more likely to avoid members of the group for the next attack if they were chased by one individual (Bshary & Bshary 2010b). As the probability of punishment correlates slightly negatively with group size (Bshary & Bshary 2010a) the relation between group size and public good seems to follow a non linear benefit function (Archetti 2009a,b; Raihani & Bshary 2011).

The emergence of a public good due to self–serving contributions depends critically on the foraging decision rules of the blenny. While Bshary & Bshary (2010b) found a significantly increased probability that blennies switch victim species in response to individual punishment, there appeared to be quite some variance in the field data. In the past such variance was often ignored as game theoretic models typically predicted uniform or bimodal evolutionarily stable strategies (Maynard Smith 1982). However, there is a growing literature that demonstrates considerable and often persistent variation between individuals (Sih et al. 2004, Bergmüller et al. 2010), and theoretical models demonstrate that such variation may be adaptive (McNamara et al. 2004, Wolf et al. 2007, Wolf et al. 2011). Most examples are on animal personality but of particular interest to our study are observations that individual predators or ectoparasites of one species may specialize on different victim species and/or hunting strategies. For example, individual leopards may specialise on either antelopes or monkeys (Hoppe–Dominique 1984), and individual scale eating cichlids specialize on attacking their victims from either the left or the right side (Hori 1993, Nshombo 1994).

The aim of the current paper was to study the foraging decision rules of sabre–tooth blennies with a special emphasis on the question whether there is individual variation in blenny foraging strategies and if so how that would affect the effectiveness of punishment and the emergence of a public good. We were particularly interested in two parameters: the importance of location for an attack and the probability of switching between victim species as a function of victim response. In a first step we reanalyzed the data of Bshary & Bshary (2010b) to test whether individual blennies differ significantly with respect to the probability that they switch victim species after being aggressed in interactions with a highly abundant victim species, the females of scalefin anthias, *Pseudanthias squamipinnis*. We further analysed whether the probability of switching after punishment correlates with the importance female anthias have in the blenny's diet and/or with the probability that female anthias punish. As a second step we performed experiments in the laboratory to investigate the foraging decision rules of individual blennies. We offered blennies simultaneously two small plates covered with mashed prawn. The plates could look quite similar or very different. In the first three experiments neither plate would respond to a blenny taking a bite with aggression ('no punishment') which allows us to explore spontaneous preferences. With the following questions we explored preferences for a location and/or an individual in attacks and if the blennies need to keep an individual in sight in order to be able to attack it repeatedly: a) If each plate remains in the same spot and in sight, will blennies bite at random or will they focus on one particular victim? b) If plate positions are counterbalanced and plates are out of sight between trials, will blennies bite at random or will they focus on one particular victim or will they focus on one location?

In a third experiment we confronted blennies with three plates that were presented pair–wise in all possible combinations and in randomized positions. Two plates looked very similar to each other while the third plate looked very different. All three plates punished with 50 % probability. In such a set–up there is nothing to learn for a blenny. We asked whether blennies would nevertheless show spontaneous adjustment in current choices based on their experience in the previous trial. More specifically we asked whether punishment would affect the likelihood to switch to another location, to another individual/plate or to take a bite. Our observations in the field suggested that punishment can have different effects in different individuals.

In all experiments we asked whether blennies show general decision rules or whether individuals differed significantly in their decisions. Finally we will discuss how our findings relate to the idea that punishment of blennies by victims constitutes a self–serving contribution to a public good in a shoaling reef fish species.

Methods

A) Field data

Study site

Field data were collected in May 2005, May 2006 and June 2007 in the Red Sea, 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). In this area, incoming sand through wadis led to the formation of patch reefs which are separated from each other by sand. Observations took place at 20 small reef patches (estimated size between 3.5 m^3 and 30 m^3) located in shallow water (bottom depth between 1.5 and 6 m).

Study species

The two blenny species studied, *Plagiotremus rhinorhynchus* and *P. tapeinosoma*, occur in the tropical Indo–West and Central Pacific and occupy small territories. 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, mucus and scales (Smith–Vaniz 1976, Johnson & Hull 2006, Bshary & Bshary 2010a).

For the victims we focussed on female scalefin anthias, *Pseudanthias squamipinnis*, which is a sexually dimorphic, protogynous reef fish occurring in the Indo Pacific in groups of up to several thousand individuals. It is one of the most abundant species on our study reef patches. Females are more numerous than males and they are common victims of the two blenny species we observed. Anthias individuals at one patch are not more closely related with each other than with individuals from neighbouring patches (Avise & Shapiro 1986). This excludes the possibility that any cooperation we observed is due to kin selection.

Data collection

Observations were carried out using scuba equipment and sitting on the surrounding sand 2–3 m in front of the reef patch. One observation session lasted 60 minutes. In total 20 blennies were observed. In 2005, we studied one blenny in detail for 16 hours. In 2006, we studied eleven blennies for 2–4 hours each, while in 2007 eight blennies were observed for 5–8 hours each. Variation in observation duration was due to blennies disappearing and/or spending much time in their hiding holes during single sessions. A total of 95 hours of observations were recorded. We choose reef patches that showed a high abundance of *P. squamipinnis* females (between 50 and 150 individuals) to get a large sample size of interactions with this species.

All interactions between the blenny and another fish were continuously observed over the entire observation period, and, immediately after the observation, the following data was noted on a Plexiglas plate:

1. Category of victim species: *Pseudanthias squamipinnis* female or other
2. Type of interaction between blenny and female anthias victims:
   - – 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 intending to attack the chaser. We scored a biting attempt if a blenny approached a fish from behind in a characteristic 'stop and go' manner, which usually proceeds successful biting attempts (Smith–Vaniz 1976, Johnson & Hull 2006). 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.

Data analysis

Effect of punishment

From the sequence of interactions between the blennies and their victim species we extracted all interactions with female anthias and scored the follow–up interactions. We scored whether female anthias had been aggressive or not, and whether the next attack of a blenny was directed at a female anthias or not. Because a time delay could degrade the effectiveness of aggression we ignored the previous interaction if the blenny had spent time in its hole. We thus had for each blenny one probability of switching victim species after being aggressed by female anthias, and one probability of switching victim species without being aggressed by female anthias. These data had been used previously to demonstrate that aggression increases the probability that a blenny switches to a different victim species for its next attack. Here we asked how important female anthias were for the diet of our blennies and whether or not individual blennies responded with similar switching probability to aggression.

More specifically we calculated for every blenny the percentage of anthias chosen as victims in two ways: as percentage of anthias approached for attack and bitten of all approaches and bites observed in all species (approaches and bites of anthias/all approaches and bites x 100) as well as in a more restrictive way as percentage of bites on anthias in relation to all bites on all species observed (bites of anthias/all bites x 100). The effect of punishment was calculated only for the six blennies where we observed at least 50 aggressive responses by female anthias as the percentage of switching after aggression minus the percentage of switching after no aggression. 50 data points were selected as criterion on the basis that we wanted to avoid a) low expected values in our chi square test, b) low power of finding a significant difference if it exists due to small sample size, and c) overall high variance in the data (probability of the blenny switching to another victim species) due to small sample size. Note that be reducing the number of blennies included in our test we reduced the probability of finding significant differences between any two individuals. Thus, any significant result would be robust while in case of a lack of significant results our omission of individuals would have to be discussed.

B) Experimental data in the laboratory

Experiments were conducted in August 2006 and July 2009 in the Indo Pacific, at the Lizard Island Research Station, Great Barrier Reef, Australia. Subjects were caught in the surrounding reefs and released at the site of capture after the experiments. We only used *Plagiotremus rhinorhynchus* as subjects because they are easier to catch than *P. tapeinosoma*. Individuals were caught by first harassing them to a point where they would hide in their little hole. Then, we placed a hand–net above the hole and sprayed a clove oil solution directly into the hole. The blennies then either fled directly into the hand–net or drifted anaesthetised into the net. Individuals were then put in sealed plastic bags and returned to the station.

The fish were kept individually in opaque aquaria sized 39x30x30 cm. Each aquarium contained a small tube (plastic or bamboo) attached to corral rubble that the fish used as hiding place. After one day of acclimatisation we started holding tweezers with mashed prawn flesh in front of the entrance of the tube 3 times per day. All fish fed after a maximum of six days. In a second step the blennies learned to feed from a small plastic plate (3 x 2 cm) covered with mashed prawn, again held in front of their tube. Learning took 1 to 5 days of exposure. Once individuals fed reliably off the plate they were ready for the experiments.

We performed three experiments in the laboratory. Data of the first two experiments were collected in July 2009, testing 8 blennies, all in the same order. Data of the 3rd experiment were collected in August 2006, testing 3 blennies. For all experiments we used Plexiglas plates (Size: 2.0 x 1.2 cm) that were attached to a lever and could be attached to a wooden construction that allowed a movement of a standardized amplitude when pushed by hand. The two plates were 5.5 cm apart (figure1). The plates varied in their coloration and patterns. For every experiment each blenny was presented a different sub–set of plates and no plate was presented to the same blenny in more than one experiment.

Figure 1

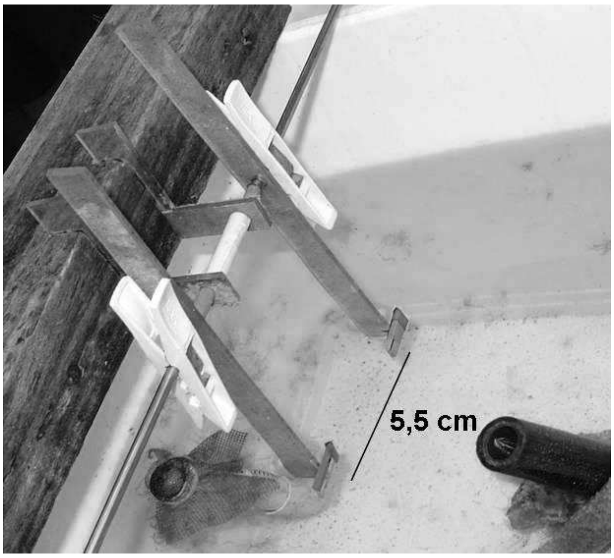


Figure 1: Tank with the construction that was used in the experiments in the laboratory. By pulling a lever towards self until it hit the wooden block the experimenter could cause a standardised punishment action of the attached food–containing plates.

Experiment 1:

Choice of target in a setup without punishment: Targets in fixed positions and always in sight.

We presented the free swimming blenny two similar looking plates in fixed positions that did not react to the feeding of the blennies. The experiment was terminated after 20 bites or after10 minutes if the fish did not feed any more. The experiment consisted of 2 rounds. In the second round the positions of the two plates were reversed.

Experiment 2:

Choice of target in a setup without punishment. Targets in alternating positions and out of sight between trials.

We presented two similar looking plates in alternating positions that were removed after each bite. The feeding round was terminated after maximally 20 bites or after10 minutes if the fish did not feed any more. There was only one round per feeding session.

Experiment 3:

Effects of location and behaviour in a randomized setup including punishment.

Each blenny was offered three plates in total. Two plates looked very similar to each other and the other one showed a different colour and pattern. All plates reacted in tow ways to attacks and showed each reaction with a probability of 50 %. They could perform a standardized movement toward the blenny (“chasing/punishment”) or they could be removed from the tank after being attacked (“fleeing”). The three plates were presented pair–wise in all three possible combinations in a counterbalanced way across trials and blennies.

Blennies experienced two sessions per day. In each session, we tried to obtain 18 data points but this was rarely possible because the blennies often stopped foraging before the completion of a session. We stopped experiments after a maximum of 328 bites (243, 248, 328).

For the analyses we tested in each of the blennies:

1. if there was a general side preference. For this we tested if the observed choice of side differed from the expected 50 % chance value.
2. if there was a preference for one of the three plates. We tested if the observed choice differed from the expected value. We calculated the expected value by multiplying the total number of observed bites by the percentage of the presence of the given plate. Ideally this would be 33.33 % for all the 3 plates, but because the blennies often stopped feeding or refused to bite, the actual values varied between 32.1 % and 35.4 %.
3. if the chasing movement (punishment) led the blennies to switch to the other side for the next bite. To test this we compared the percentage of switching with and without punishment.
4. if the chasing movement (punishment) led the blennies to stop biting of the plates altogether. To test this we compared the percentage of refusals to bite with and without punishment.
5. if the chasing movement (punishment) influenced the choice of plate at the next bite. For this we compared the choices of plates with and without punishment.

For the laboratory experiments X^2 tests were performed using the free internet service of Preacher (2001). For the analysis of field data we used SPSS 17. For the sign tests we used the table of Darlington (2008) provided by the Psychology department of Cornell University.

Results

A) Field

Choice of victims

The percentage of anthias attacked varied significantly between individuals, i.e. between 10 % and 83 % (approached and bitten) or 9 % and 85 % (only bitten) respectively (X^2 test, $n = 20$ individuals, approached and bitten: N interactions: 3248, $X^2 = 503.404$, $p < 0.001$, only bitten: N interactions: 2173, $X^2 = 392.844$, $p < 0.001$, fig. 2). The two different ways of measuring the choice of victims did not provide different results.

Reaction to punishment/effect of punishment

Six blennies were observed being punished more than 50 times by anthias and hence analysed in more detail (see methods). The probability of a blenny switching to another species after being punished varied between 14.1 % – 71.4 %, yielding overall highly significant differences between individuals (X^2 test, $n = 560$ observations on 6 blennies, $X^2 = 227.82$, $df = 5$, $p < 0.001$, fig. 2).

Figure 2

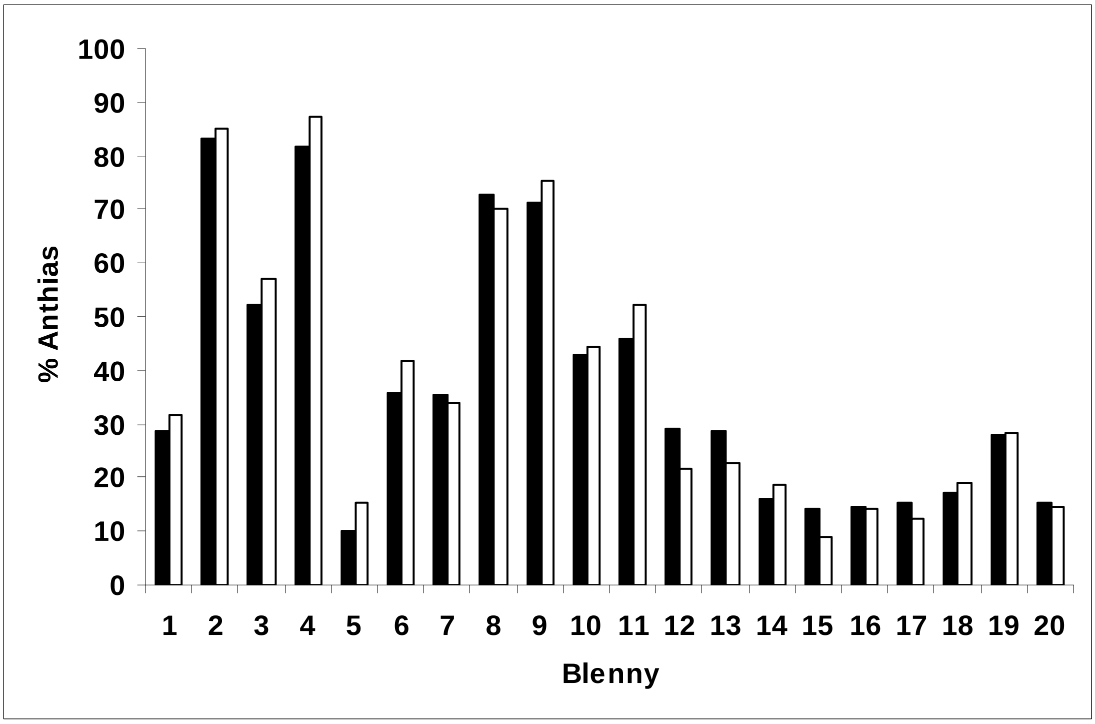


Figure 2: **Specialisation on anthias**
The proportion of scalefin anthias, *Pseudanthias squamipinnis*, in all the attacks of 20 different blennies observed in the field. Black: Percentage of anthias bitten. White: percentage of anthias approached or bitten

The effect of punishment (switching to another species following punishment – switching without punishment) was not correlated to the probability of aggressive reactions (punishment) of anthias (percentage of aggressive reactions of all reactions) though the correlation coefficient was quite positive (Spearman correlation, N = 6 correlation coefficient = 0.714, p = 0.111). The percentage of aggression was high in all observed groups of anthias, (> 66 %).

The relative effect of punishment on switching to a different victim species for the next attack was negatively correlated to the probability of switching without punishment (Spearman correlation, Correlation Coefficient = – 0.941, p = 0.005). In other words, the positive effect of punishment was strongest if blennies were generally unlikely to switch to another victim species (blennies 2, 3 and 4 in figure 3).

Figure 3

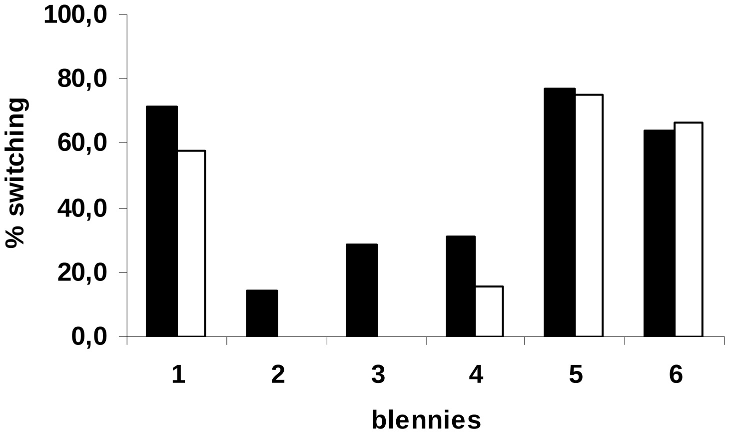


Figure 3: The effect of punishment
Black: the probability of six blennies switching to another species following aggression by a female anthias. White: the percentage of switching to another species without previous aggression. Data shown for the six blennies that were observed being aggressed by female scalefin anthias more than 50 times.

B) Laboratory

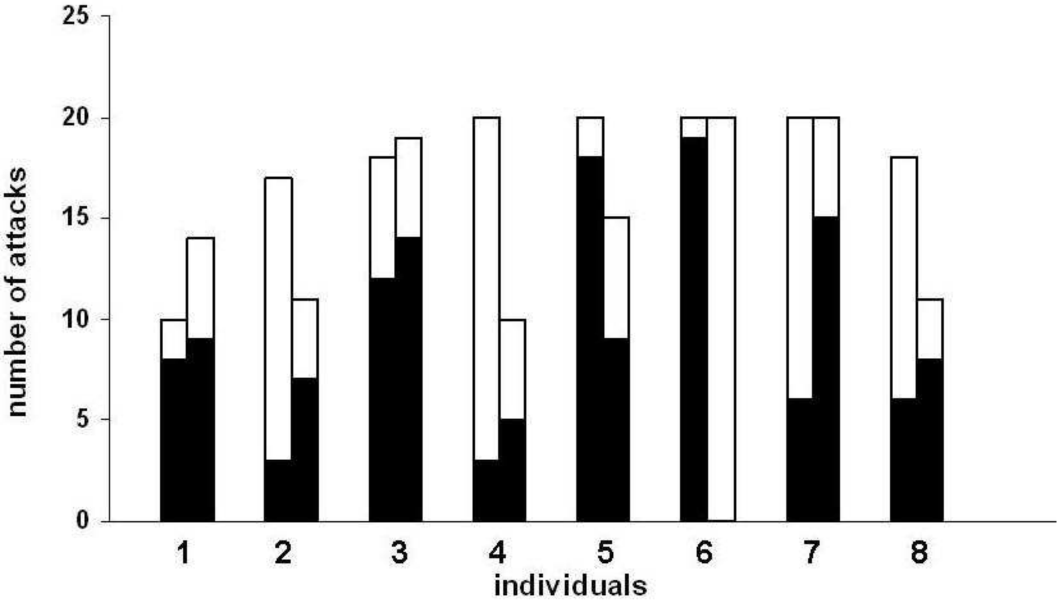
Experiment 1: Do blennies focus on a location or on a particular victim in the absence of punishment (plate remains in the same spot and in sight between trials)?

Combining the data of the two sessions, 3 blennies (3, 4 and 5) showed a significant side preference (Sign tests: all $n > 24$, all $p \leq 0.02$), while blenny 1 showed a tendency to prefer one side (Sign test: $n = 24$, $p = 0.06$). 5 blennies (2, 4, 5, 6 and 7) showed a significant preference for one of the two plates (Sign tests: all $n > 24$, all $p \leq 0.04$, fig.

4) while blenny 8 showed a tendency to prefer one plate (Sign test: n = 29, p = 0.06).

Figure 4

Figure. 4 Choices of side in the first experiment



black: left side chosen, white: right side chosen.
A similar, asymmetric distribution of black and white indicates a side preference;
a dissimilar, asymmetric distribution of black and white indicates a plate preference;
a similar, symmetric distribution of black and white indicates random choice.

Experiment 2: Do blennies focus on a location or on a particular victim in the absence of punishment (plate moves and is out of sight between trials)?

Plates differed in colour and pattern from experiment 1. Only blenny 3 developed a side preference (Sign test: n = 12, p = 0.038, fig. 5). Four blennies (4, 5, 6 and 7) developed a preference for one of the two plates (Sign tests: all n > 18, all p ≤ 0.002, fig. 5). Note that the five individuals with significant preferences (3, 4, 5, 6 and 7) kept their preferences from experiment 1 under the new conditions. Three blennies yielded non significant results, where two of them (blennies 1 and 2) showed a tendency to prefer one plate (Sign test: n1 = 8, p1 = 0.07, n2 = 18, p2 = 0.09, fig. 5).

Figure 5

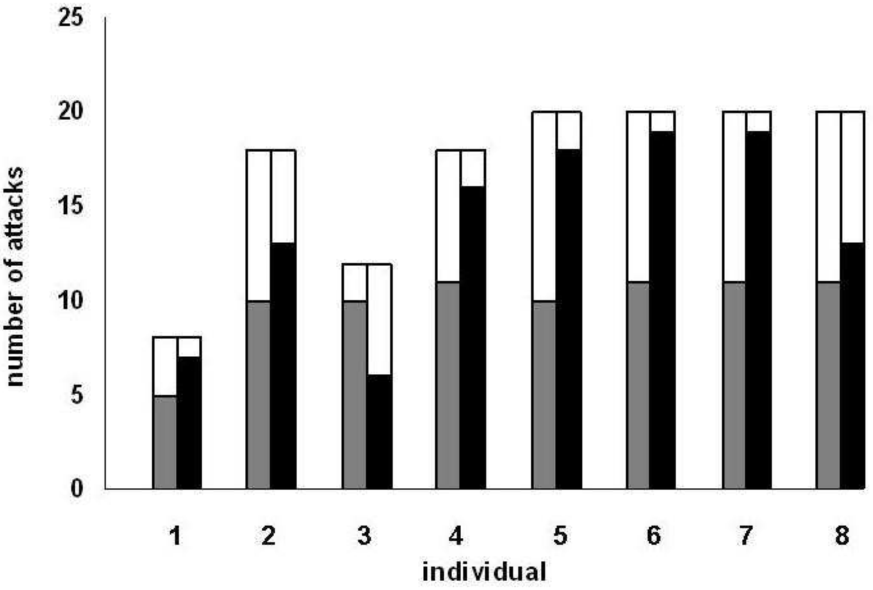


Figure 5: Choice of side and plate in experiment 2
First column:
Grey: side chosen more often; white: side chosen less often
Second column:
Black: plate chosen more often; white: plate chosen less often

Experiment 3: Does punishment influence the likelihood of attacking and the choice of target and location?

Spontaneous preferences

All three blennies developed a clear side preference (X^2 tests, all $X^2 > 16$, all $p < 0.001$). In addition, all blennies showed a significant preference for specific plates. However, which plate was preferred actually differed between them: One blenny preferred the two look–alike plates over the differently looking plate, one blenny preferred one of the look–alike plates over the other two plates, and the third blenny preferred the different looking plate over the two look–alike plates (X^2 tests, all $X^2 > 9$, all $p < 0.01$).

Influence of punishment:

Likelihood of attack

Two of the blennies were significantly more likely to stop biting after being punished, one blenny showed a tendency in the same direction (X^2 test, $p1 = 0.0035$, $p2 = 0.036$, $p3 = 0.091$).

Choice of target

Punishment influenced the choice of the plate in two of the blennies. One was significantly less likely to bite the same plate after being punished and another showed a tendency in the same direction (X^2 tests, $X^{2}1 = 3.9$, $p1 = 0.05$, $X^{2}2 = 3.05$, $p2 = 0.081$). The latter was also significantly more likely to switch from a look–alike plate to the different looking plate after being punished (X^2 test, $X^2 = 9.66$, $p = 0.002$). The switching from the differently looking plate to one of the look–alikes was in none of the three blennies influenced by punishment (X^2 tests, all $X^2 < 1.4$, all $p > 0.2$).

Choice of location

Punishment did not make it more likely that the blennies switched to the other side for the next attack (X^2 tests, all $p > 0.2$).

Discussion

In previous studies on parasitic blenny–victim interactions we had found evidence for a public good that is maintained through blenny–foraging decisions in two ways

(Bshary & Bshary 2010 a, b). First, the punishment of the parasite is stable because it is self–serving: blennies avoid punishing individuals. Second, a public good emerges because the parasites also are more likely to avoid the whole group after being punished. Individual differences in the foraging decisions of blennies could change the effect of punishment in a way that makes punishment useless and/or does not create a public good. Therefore we were interested if there is variation in blenny feeding preferences that could affect both the self–serving aspect of punishment of the parasite and the emergence of a public good in shoals of fish. We found variation in the behaviour of individual blennies both in the field as well as in the laboratory. Moreover, the first two laboratory experiments indicate that individuals are rather consistent with respect to a key initial decision: to focus on a suitable location or to focus on suitable victims. We will first discuss the potential causes of this variation and then discuss the consequences of such variation for the establishment of public goods through self–serving punishment.

Potential causes for individual differences between blennies

Local victim species composition

One possibility could be that small–scale ecological differences between the territories of the parasites, like differences in the local victim composition, lead to different hunting strategies. But even at the reef blocks we observed that all show a high abundance of anthias the percentage of anthias bitten by blennies varied greatly. Abundance alone seems not to be enough to explain the observed differences. Different victim species react differently to attacks of blennies. The largest differences exist between species that are resident in the territory of the blenny and species that occupy larger territories and are only shortly visiting the territory of the blennies. Generally, visiting species do not chase the parasites after attacks while resident species regularly show this punishing behaviour (Bshary and Bshary 2010a). Blennies that occupy territories that are frequently visited by non–punishing fish might preferably bite these victims. But this still has to be confirmed and does not explain the whole range of differences between individual blennies. Other differences between victim species like differences in mobility or size could also lead to preferences in the blennies in dependence of local species composition.

Specialisation on few victim species

Generally, predators seem to prefer abundant prey types (Murdoch et al 1975, Cook & Miller 1977) and the abundance of a given species varies between the territories observed. In the field we observed that some blennies specialized on only few victim species and were not very likely to switch to other species. Such specialisation has been described for many predators and also pollinators (Hoppe–Dominique 1984, Waser 1986, Chittka et al 1999, Rana et al. 2002, Bolnick et al. 2003). Feeding efficiency may be improved because the predators can focus on one search image at a time though they may switch between several search images (Dukas & Kamil 2001).

It is possible that the different specialisations found in our study species are based on individual learning. Blennies could learn which victim species to attack to optimize the energy gain (Waser 1986, Hamblin & Giraldeau 2009; Isii & Shimada 2009, Schindler et al. 1997). This would be comparable to optimal foraging rules observed in other predators and pollinators (Krebs et al. 1978, Ollason 1980, Waser 1986).

Specialisation on location

In the laboratory we observed that some blennies show a strong preference for the location of attacks. At reef patches where victims show a high probability of aggressive reactions blennies might prefer to attack close to their hiding place to be able to quickly retreat into safety.

Some of the observed differences between blennies could also be due to cognitive limitations due to the costs of learning. For the blennies it may not be optimal to aim at a perfect knowledge of the system they live in. Instead of trying to get a complete understanding of the reactions of all individual fish in their territory they therefore might rely on simple rules of thumb like: “after being chased avoid this area for the next attack” or “if you could get a bite without being aggressed keep the victim in view for a possible additional bite”. Such rules of thumb could vary between blennies due to differences in victim species composition and other differences between the territories. In a complex environment, simple rules may maximise the balance between benefits of performing well and the costs of information while individuals forego the possibility to achieve maximal rewards in each specific situation (“bounded rationality”, Gigerenzer & Selten 2002).

Personality traits

Much of the literature about individual differences is about personality traits (Sih et al. 2004a, b, Bergmüller et al. 2010). It is possible that some differences in blenny decision rules might be due to differences in personalities. For example, bold individuals may be less flexible and hence rather unresponsive to victim behaviour while shy individuals incorporate environmental feedback more readily in their foraging decisions. As we did not score any personality traits in our blennies yet we won't discuss this possibility any further.

Consequences of blenny foraging decisions for the evolution of punishment and the emergence of public goods

The victim species we studied in detail, *Pseudanthias squamipinnis*, seems to be rather inflexible in its response to blenny–attacks. Apart from the slightly negative correlation between local abundance and probability of punishment we found in our previous study (Bshary & Bshary 2010a), there is apparently not much variation in the probability of aggressive responses, which was always above 60 %. Thus, we can focus on the question how variation in blenny strategies may affect a) the self–serving effect of punishment, and b) the emergence of public goods as a side effect.

There are three main scenarios illustrating the importance of variation in blenny feeding strategies:

a) In locations where the blenny is very likely to switch anyway between species no matter if it was punished before or not, punishment is not functional. If switching was the blennies' standard strategy, then individual victims would be under selection not to punish. There would be no public good but also no competition between look–alikes because the behaviour of the blenny is not influenced by the behaviour of the victims.

b) If the blenny switches to another individual if punished but not to another species then punishment pays for the individual. But this blenny strategy will lead to competition between look–alikes rather than to a public good, because for conspecifics punishment increases rather than decreases the risk of being attacked.

c) Only if punishment causes the blenny to switch to another species does punishment pay for the individual while providing a public good by decreasing the risk of future attacks for both the individual and its conspecifics.

Here we make some predictions how variation in a blenny's preference for certain locations and a focus on individual recognition and book–keeping of victim responses may lead to punishment being self–serving or not, and providing a public good or not. These predictions are amenable for future testing. First, blennies with a strong preference for a location are highly likely to cause repeated interactions within short time periods. This is the situation where punishment may be effective if the victim lives in the core area. Outside the core area interactions will be infrequent and punishment won't pay because the blenny is very likely to switch to another victim anyway. Alternatively, a blenny roves within its territory and hence is likely to switch automatically between victims because of the roving. In such circumstances punishment does not provide benefits to the punisher.
Second, blennies that mainly pay attention to individual identity select for punishment but such punishment could cause either increased competition or a public good. An increase in competition would be more likely if the blennies remember an experience with a specific individual rather than with a species. If blennies mainly avoid location in response to punishment then they may shift microhabitat, which should increase the likelihood that they switch to another species, and hence punishment would pay for the individual and create a public good. The predictions are summarised in Table 1.

	Aspects of blenny foraging rules		
	Roving	Preference for location/species	Preference for non-punishing individuals
Blenny reaction to punishment:	none; switches anyway between individual/species	switches to another individual/species	switches to another individual/species
Punishment provides:	no benefit	benefit for individual	benefit for individual
Without punishment	no difference	blenny is likely to return to same location	blenny is likely to return to same individual
Effect of punishment on conspecifics	no effect	decreases risk	increases risk
Public good	no public good	public good	no public good

Table 1: predictions how aspects of blenny foraging rules affect the efficiency of punishment and the emergence of a public good in shoaling victim species *with a spatial structure*.

On the stability of punishment and public goods

Our field observations and laboratory experiments demonstrate that individual blennies are indeed variable with respect to the importance of location and victim identity for their foraging decisions. Thus, the major open question at this stage is whether the observed variation in blenny decision rules, which sometimes renders punishment ineffective or merely self–serving, and which may affect look–alikes in either positive or negative ways, overall helps to stabilise the emergence of a public good due to self–serving punishment (Bshary & Bshary 2010b). Several models of cooperation yield stable cooperation because variation is maintained by ontogenetic effects (‘phenotypic defectors’ in Sherratt & Roberts 2001) or mutation rates (McNamara et al. 2004). Thus, the observed variation may indeed help to stabilise contributions to the public good in our system. On the other hand, one has to explain why anthias seem to be rather inflexible in their decision rules and always show high levels of aggressive responses. At this stage we cannot exclude that there is variation between individuals but the observations suggest that individuals confronted with a blenny that switches anyway are on average as aggressive as individuals that face a blenny specialising on anthias. A game theoretic exploration of the observations may help to generate more specific predictions amenable for future testing.

Acknowledgements

We thank the Egyptian Environmental Affairs Agency for the permission to conduct research in the park and the park rangers and Ingo Riepl for local support. We further thank the staff of the Lizard Island Research Station and Lexa Grutter for their support and friendship. We are grateful to Aurore Malapert for contributing to the field data collection, Laetitia Brun for contribution to the experiments and to Tom Sherratt for comments. The study was financed by a Natural Environment Research Council fellowship and a grant by the Swiss Science Foundation to R.B.

References

Archetti, M. 2009a: Cooperation as a volunteer's dilemma and the strategy of conflict in public goods games. J. Evol. Biol. 22: 2192–2200.

Archetti, M. 2009b: The volunteer's dilemma and the optimal size of a social group. J. Theor. Biol. 261: 475–480.

Archetti, M. 2011: A strategy to increase cooperation in the volunteer's dilemma: reducing vigilance improves alarm calls. Evolution 65: 885–892.

Archetti, M. and Scheuring, I. 2010: Coexistence of cooperation and defection in public goods games. Evolution 65: 1140–1148.

Avise, 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.

Bergmüller, R., Schürch, R. & Hamilton, I. M. 2010: Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. Philosophical Transactions of the Royal Society B 365, 2751–2764.

Bolnick, D. I, Svanbäck, R., Fordyce, J.A, Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M. L. 2003: The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist, 161 (1), 1–28

Boyd, R., Gintis, H., Bowles, S. & Richerson, P. J. 2003: The evolution of altruistic punishment. Proc. Natl Acad. Sci. 100, 3531–3535.

Bshary, A., and Bshary, R. 2010a: Interactions between sabre–tooth blennies and their reef fish victims: Effects of enforced repeated game structure and local abundance on victim aggression. Ethology 116, 681–690.

Bshary, A., and Bshary, R. 2010b: Self–Serving Punishment of a Common Enemy Creates a Public Good in Reef Fishes, Current Biology, 20 (22) 2032–2035.

Chittka, L., Thomson, J.D, Waser, N.M., 1999: Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86: 361–377.

Clutton–Brock, T. H. & Parker, G. A. 1995: Punishment in animal societies. Nature 373, 209–216.

Cook, L. M. & Miller, P. 1977: Density–dependent selection on polymorphic prey - some data. Am. Nat. 111, 594–598.

Darlington, R. B. 2008: Sign test table, http://www.psych.cornell.edu/darlington/signtest/signtst1.htm

Dawes R. M., 1980: Social dilemmas. Annu Rev Psychol 31:169–193.

Dukas, R. & Kamil, A. C. 2001: Limited attention: the constraint underlying search image. Behav. Ecol. 12, 192–199.

Fehr, E. & Fischbacher, U. 2003: The nature of human altruism. Nature, 425, 785–791.

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.

Gächter, S. Herrmann, B. and Thöni, C. 2010: Culture and cooperation. Philosophical Transactions of the Royal Society B 13, 2651–2661

Gigerenzer & Selten 2002: Gigerenzer, G. & Selten, R. (Eds.) (2002). Bounded Rationality: The Adaptive Toolbox. Cambridge, MA: MIT Press

Gintis, H., Bowles, S., Boyd, R. & Fehr, E. 2003: Explaining altruistic behaviour in humans. Evol. Hum. Behav. 24, 153–172.

Hamblin, S. & Giraldeau, L.A., 2009: Finding the evolutionarily stable learning rule for frequency–dependent foraging. Animal Behaviour 78 (6), 1343–1350.

Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, A., Cardenas, J.C., Gurven, M., Gwako, E., Henrich, N., Lesorogol, C., Marlow, F., Tracer, D., Ziker, J., 2006: Costly punishment across human societies. Science 312, 1767–1770.

Hoppedominik, B. 1984: Prey Frequency Of The Leopard, *Panthera–Pardus*, In The Tai–National–Park Of The Ivory–Coast. MAMMALIA, 48 (4): 477–487

Hori, M., 1993: Frequency–Dependent Natural–Selection In The Handedness Of Scale–Eating Cichlid Fish. Science 260 (5105), 216–219.

Isii, Y & Shimada, M., 2009: The effect of learning and search images on predator–prey interactions. Population Ecology 52 (1), 27–35.

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.

Krebs J-R., Kacelnik, A., Taylor, P. 1978: Test of optimal sampling by foraging great tits. Nature, 275 (5675): 27–31.

Maynard Smith, J. 1982: Evolution and the Theory of Games. Cambridge University Press, Cambridge.

McNamara, J. M., Barta, Z. & Houston, A. I. 2004: Variation in behaviour promotes cooperation in the Prisoner's Dilemma game. Nature 428: 745–748.

Milinski, M., Semmann, D. & Krambeck, H.-J. 2002: Reputation helps solve the ‘tragedy of the commons’. Nature 415, 424–426.

Murdoch, W.W., Avery, S., Smyth, M.E.B., 1975: Switching in predatory fish. Ecology 56 (5), 1094–1105.

Nshombo, M., 1994: Foraging Behavior Of The Scale–Eater Plecodus–Straeleni (Cichlidae, Teleostei) In Lake Tanganyika, Africa. Environmental Biology Of Fishes, 39 (1), 59–72.

Ollason, L.G. 1980: Learning to forage optimally. Theoretical Population Biology, 18 (1): 44–56.

Preacher, K. J. (2001, April): Calculation for the chi–square test: An interactive calculation tool for chi–square tests of goodness of fit and independence [Computer software]. Available from http://quantpsy.org.

Raihani N. J. & Bshary, R. 2011: Evolution of punishment in n–player public goods games: a volunteer's dilemma. Evolution

Rana, J.S., Dixon, A. F. G., Jaro, V., 2002: Costs and benefits of prey specialization in a generalist insect predator. Journal of Animal Ecology 71, 15–22.

Schindler, D.E., Hodgson, J.R.& Kitchell, J.F. 1997: Density–dependent changes in individual foraging specialization of largemouth bass. Oecologia 110, 592–600.

Sherratt T.N. & Roberts, G. 2001: The importance of phenotypic defectors in stabilising reciprocal altruism. Behav. Ecol. 12: 313–317.

Sherratt, T.N., Roberts, G., and Kassen, R. 2009: Evolutionary stable investment in products that confer both an individual benefit and a public good. Front. Biosci. 1, 4557–4564.

Sih, A., Bell, A. & Johnson, J. C. 2004a: Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. 19, 372–378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b: Behavioral syndromes: an integrative overview. Q. Rev. Biol. 79, 241–277

Smith–Vaniz 1976: The Saber–Toothed Blennies, Tribe Nemophini (Pisces: Blenniidae). Monograph 19 (Philadelphia: The Academy of Natural Sciences of Philadelphia).

Waser, N.M., 1986: Flower Constancy: Definition, Cause, and Measurement. The American Naturalist, 127, 5, pp. 593–603.

West, S. A., Diggle, S. P., Buckling, A., Gardner, A. and Griffin, S. P. 2007: The social lives of microbes. *Annual Review of Ecology, Evolution and Systematics* 38, 53–77

Wolf, M., van Doorn, G.S., Leimar, O., Weissing, F. J., 2007: Life–history trade–offs favour the evolution of animal personalities. Nature, 447 (7144), 581–584.

Wolf, M., van Doorn, G.S., Weissing, F. J. 2011: On the coevolution of social responsiveness and behavioural consistency. Proc. R. Soc. B, 278 (1704), 440–448.

General Discussion

The aim of this thesis was to study in detail the interactions between parasitic sabre–tooth blennies and their victim reef fishes. The perspective was to gain understanding of a system in which both punishment and public goods may exist, and which can be studied both in nature and with an experimental setup in the laboratory. Overall, I was lucky enough to be able to answer some of the questions I intended to address. In this general discussion, I will first summarise the key results of the three data chapters in order to discuss what we have learned about the blenny–host system. I will then propose several ideas for future research. While not developed in detail in this thesis, I had tried to answer several additional questions during my PhD, and I will introduce preliminary results and the methodological problems I encountered as inspiration and help for future students working on the system. Finally, I will discuss what we may have learned more generally about punishment and contributions to public goods.

Discussion of all papers combined

The three manuscripts build naturally upon each other. The first paper contains the basic field observations on blenny–host interactions with the aim of describing the system and generating predictions amenable for future testing. The second paper explicitly tests hypotheses about punishment and emerging public goods, while the third paper documents individual variation in behaviour and decision rules of the blennies.

The key results of the field observations were first that not all fish respond in the same way to blenny attacks. Only resident species that share their territory with a blenny and repeatedly interact with the same parasite react aggressively to its attacks, while visiting species use their potential to escape further interactions by swimming off. Second, we found that the probability of aggressive reactions to blenny attacks is negatively correlated to group size, but even in large groups of victim species the aggressive chasing does not disappear. The first result matches observations on the cleaner wrasse – client mutualism, where the same resident clients but not visiting clients respond to occasional cheating by cleaners with chasing, for which it was demonstrated that it functions as punishment (Bshary & Grutter 2002; 2005). Visiting clients swam off in response to cleaner cheating and avoided the cleaning station in the future (Bshary & Schäffer 2002). It seemed likely that the function of the observed behaviours is the same in reef fish – blenny interactions. For punishment to be effective repeated interactions are important (Clutton–Brock & Parker 1995). This could explain the difference between resident and visiting species: as resident species do not have the option to avoid repeated interactions with the parasite, it could be beneficial for them to invest in punishment. Visiting victim species, on the other hand, could in principle avoid close proximity to a blenny by staying away from its reef patch. Thus, they are most likely to meet the very same blenny again once they have forgotten the negative experience and hence revisit the patch. In any case, time intervals between subsequent close encounters with a blenny will be much longer for visitors than for residents, which should undermine the ability of both visitors and blenny to remember the last interaction. Thus, the benefits of punishment are unlikely to apply to visitor–blenny interactions due to cognitive constraints. Along this line of argument, Oates et al. (2010 a, b) found that roving cleaner wrasses *Labroides bicolor* cheated clients more frequently than *L. dimidiatus* individuals did, and proposed that prolonged time intervals between successive interactions played a key role for this difference.

The result that chasing was negatively correlated to group size suggested that the benefits of chasing decrease with increasing group size. There were two possible explanations for this: a) in large groups there are fewer interactions between an individual fish and the parasite and therefore the individual incentive to chase decreases with group size. b) the effect of the chasing is that the parasite switches to another victim species. This would create a public good in large shoals of look–alikes. In this case the benefit gets diluted because all members gain from the chasing while the costs stay the same for a chasing individual. As aggressive chasing did not stop completely in large groups the results suggested that there is no classic “tragedy of the commons” involved in this system. On the other hand it seemed unlikely that the most promoted explanations for stable contributions to public goods in humans, namely ‘altruistic punishment’ stabilised by strong between–group competition (Fehr & Gächter 2002; Boyd et al. 2003; Gintis et al. 2003) or reputation (Nowak & Sigmund 1998; Milinski et al. 2002). In particular altruistic punishment seemed unlikely because of the lack of kin structure (Avise & Shapiro 1986).

Nevertheless, as the aggression by victims towards blennies suggested the existence of punishment in the system, we had to consider ways in which individuals gain direct fitness benefits from chasing blennies. At some point during my thesis, Sherratt et al (2009) provided a potentially fitting explanation. The authors tried to understand why bacteria produce and release a variety of substances like enzymes into their environment, which benefits neighbouring bacteria as well (West et al. 2007). Sherratt et al. (2009) found that contributions to a public good can be self–serving as long as each individual benefits disproportionately from its own contribution. This condition fits the bacteria examples as due to limited diffusion each individual gains most from its own contributions while cells that are far away will not gain anything. In the blenny–host system two non–exclusive mechanisms could lead to individuals benefiting disproportionately from their own punishment of blennies. First, if shoals have a spatial structure and hence individuals have preferred locations punishment may benefit the actor if the blenny subsequently avoids the location where it was chased. Second, if blennies have the ability to recognize individual victims then aggression may lead to the blennies avoiding punishing individuals. Both scenarios seemed to be possible in the blenny–host system. Individual recognition has been demonstrated repeatedly in fishes, including recognition of members of other species (Griffiths & Ward 2006, Tebbich et al. 2002). The issue of spatial structures within shoals was mainly addressed within the framework of a Master thesis by Gabriel Cisarovsky, who documented that at least female scalefin anthias have indeed a spatial structure in their shoals (Cisarovsky et al., unpublished manuscript).

The most urgent open questions from the first manuscript that I addressed in the second manuscript were to test whether aggression functions as punishment, whether punishment creates a public good in locally abundant species, and what factors cause the aggression by victims to be self–serving. To test if the chasing of the parasite acts as punishment we performed experiments in the laboratory to be able to control the behaviour of the “victims” using Plexiglas plates as substitutes for real victims. If the blennies were allowed to choose between a plate that always chases and another that always “flees” they showed a significant preference for the fleeing plate and avoided the chaser. This showed that the investment of chasing the parasite changes its behaviour in a way that benefits the chasing individual in future interactions. The chasing observed in victims of parasitic blennies completely fulfils the definition of “punishment” provided in Clutton–Brock & Parker (1995). Until now there are only few examples of punishment in non–human animals that not only show that individuals inflict costs on individuals that harm them but also that the punished individuals change their behaviour in future interactions in a way that is beneficial to the punisher (Bshary & Grutter 2005, Bshary et al. 2008, Raihani et al. 2010).

Field observations focussing on female anthias documented that punishment can create a public good in large groups of fish. In this species individual punishment makes it more likely that the blenny switches to another species for its next attack. Hence all members of a shoal of anthias benefit from the chasing done by one member of the group while only the punishing individual has to bear the costs. While the results resembled very much a solution to the tragedy of the commons we also tested Sherratt et al.’s (2009) prediction that individuals gain disproportionately from their own contribution. Unfortunately we could not collect enough field data to analyse whether punishing fish face a reduced risk of future attacks in comparison to non–punishing individuals. In any case such data would have been only correlational, while we could test the hypothesis explicitly in the laboratory. To test how the blennies react to a mix of punishing individuals and free–riders in a group of look–alikes we performed an experiment using three Plexiglas plates, two of which looked alike but differed with respect to the probability of punishing the blennies. The differently looking plate punished with intermediate probability. Under these conditions the blennies generally preferred the non–punishing plate over the punishing plate. Our studies in the laboratory suggest that blennies avoid punishing individuals and that these can profit from the chasing while non–punishing individuals are at risk to be identified as easy targets. Free–riding under these conditions is therefore no option, because the blennies' foraging strategies select against it. This is in accordance with our observations in the field that the chasing persists even in large groups of fish. In conclusion, punishment turned out to be self–serving while providing a public good as a by–product. The benefits of punishment are not so much due to the punisher gaining disproportionate benefits but to the free–rider facing disproportionate costs due to blenny foraging decision rules.

The results from the second manuscript made it clear that we should study the foraging decision rules of blennies in more detail in a third data manuscript. Do blennies specialize on one or several victim species or are they fully opportunistic? How important are spatial and individual victim cues for their decision to attack? Is there variation between individuals with respect to the importance of these variables? We had actually already noticed (without exploring them in detail) in the field data presented in Bshary & Bshary (2010b) that there were individual differences in the foraging decisions of the blennies. The laboratory experiments demonstrated that the blennies generally prefer to attack abundant species. Given that many variables may affect blenny foraging decisions and lead to individual differences between blennies, how would such variation affect the effectiveness of punishment and the emergence of public goods?

A detailed re–analysis of the field observation revealed indeed strong variation between individual blennies with respect to the foraging decision rules. Some would switch with high probability between victim species regardless of victim responses while others focussed on anthias as victim species and would only switch victim species if punished. The laboratory experiments demonstrated that some blennies have preferred locations for their attacks while others focus on preferred individuals. Punishment affects most blennies but not all respond in a way that benefits the punishing individual. All this variation implies that while punishment is on average effective and public goods may typically arise in locally abundant species, the precise outcome will vary from blenny to blenny. How the variation in blenny decision rules may evolve and how victims should evolve their optimal responses in return has to be addressed in proper evolutionary game theoretic modelling and is indeed underway (Sherratt et al. unpublished model). Finally, it is important to note that the variation we documented may be novel within the particular context and the detail (‘responsiveness to punishment’) but it fits the conclusions from a variety of other studies that found that individual predators and individual parasites may develop prey/host specialisations during their ontogeny (Hoppedominik 1984, Bolnick 2003, Schindler 1997).

In summary, we found a) that victim species that cannot escape from frequent exposure to sabre–tooth blenny attacks behave aggressively towards the blennies, b) that aggression serves as punishment, c) that punishment may provide a public good in locally abundant species, d) that free–riding is not a good option because blennies prefer to attack free–riders (non–punishers), and e) that individual blennies differ strongly in their foraging decision rules, which may affect both the efficiency of punishment and the emergence of public goods.

Open questions

While I was lucky enough to be able to answer some of the key questions I had initially hoped to address during my thesis, there are several remaining questions, and inevitably new ones emerged based on the results I obtained. There is thus still a lot of research to be done on blenny–host interactions. The following part may help to inspire specific research projects, without any particular order of relevance or feasibility.

Function of and differences between the different types of aggressive chasing

In our observations in the reef we noticed that the victims of blennies not only react to attacks but also show aggressive chasing when they are approached by the parasite in a biting attempt (the blenny approaches from behind in a typical stop and go manner) and sometimes without obvious reasons (pre–emptive). Most strikingly, aggression in the three circumstances – after being bitten, in response to approach and spontaneously – were not all significantly correlated with each other. This lack of correlation suggests different functions but what these are remains unclear. In all three circumstances a deterrent effect on the blenny seems to be plausible. But we noticed that in response to an approach by a blenny it was generally enough for the prospective victim to turn into the direction of the parasite to stop the attack. So why do some individuals invest into aggressive chasing under these circumstances?

Laboratory observations on anthias–blenny interactions suggest that ‘spontaneous aggression’ may not be spontaneous after all. Originally aimed at studying individual variation in punishment and the effects of group size on the probability of punishment, the blennies hardly ever attacked unless the anthias were fed. But while they were fed the anthias rarely responded aggressively to bites. However, we noticed that individual anthias that had been bitten during feeding sessions were more likely to chase the blennies ‘spontaneously’ during the five minutes following the feeding session than individuals that had not been bitten (A. Bshary, unpublished data). Maybe the ‘spontaneous aggression’ we observed in the reef is something similar, but this has to be tested. What the laboratory data show is that anthias hold grudges: while they typically respond to an immediate attack failure to do so increases chances to chase the parasite later on. Furthermore, it is possible that there is general variation between individuals with respect to their aggressiveness, and that aggressiveness in intra– and inter–specific contexts correlate with each other. We found in our laboratory studies on anthias that intra–and inter–specific (against blennies) aggression were positively correlated in all five study tanks (A. Bshary, unpublished data). We also tried to measure hormonal concentrations of Testosterone and 11–K Testosterone in our study animals but the samples appeared to be contaminated as the controls yielded similar values as the experimental samples. Despite the failure with the hormonal analyses, the results indicate that proximate causes may partly help to explain aggression/punishment in our system. Nevertheless, holding grudges may be functional if the delayed chasing alters the blenny’s perception of its victim from ‘free–rider’ to ‘punisher’ and hence decreases the risk of future attacks.

Is there individual variation in aggressive responses of victims to blenny attacks?

We observed differences in the level of aggressive responses on species level. Until now it is not completely clear if the observed differences are due to a mix of (mainly) punishing and (mainly) non–punishing individuals or due to strong variability in the response of single individuals. It is possible that the probability of aggressive reactions is condition dependent and individual fish only invest into punishment if they can afford to do so at any given moment. This would lead to variability in every given individual (intra–individual differences). It is also possible that there are individual fish that are more aggressive than others and therefore always more likely to react aggressively to attacks by blennies, as suggested by the positive correlation between intra– and inter–specific aggression in male anthias observed in the laboratory. While the correlation does not demonstrate individual differences there is plenty of evidence in the animal personality literature that animals differ with respect to aggressiveness (Sih et al. 2004, Bergmüller et al. 2010). Larger sample sizes in the laboratory where all fish can be individually marked would allow answering several of the questions raised in the current and in the previous section. These data should be complemented by field observations. Below are some specific methodological suggestions for such experiments and field observations based on my largely failed attempts.

Laboratory experiment considerations

For the blennies I would chose *Plagiotremus rhinorhynchus*, because it seems to be easier to catch then *P. tapeinosoma* and we know how to keep this species under laboratory conditions (Bshary &Bshary 2010b). As victim species I would chose again the species *Pseudanthias squamipinnis*. They are a common species in the Red Sea, easy to catch and frequently attacked by the two blenny species. We also know already how to keep them under laboratory conditions. As they are rather susceptible to infections under laboratory conditions they should be bathed in a Praziquantel solution (an anthelmintic effective against different parasites) before they are released into the tanks.

The number of individuals should not be too small because anthias are shoaling fish and do not behave naturally in small numbers. I would consider 20 individuals the minimum. The tanks have to include shelters for every individual anthias (plastic tubes, bricks) and a tube (plastic or bamboo, see figure 1 and 2) as hiding place for the blenny. The anthias need additional structures surrounding the shelters to behave normally (figure 1). Anthias are plankton feeders and normally feed in front or above the reef structures where they have their hiding places. The tanks have to be high enough to allow the anthias to move in a natural way. If they are too shallow the anthias stay most of the time in their hiding places and do not show much activity except during feeding sessions and the parasitic blennies will not interact normally with the anthias. The diameter of the tanks should be large enough to allow for enough space between the shelters of the anthias to reduce intra–specific aggression. The tanks we used in my experiments had a diameter of 1m which was just enough to fit 20 shelters inside (figure 1). Larger tanks may be preferable in future experiments.

Figure 1
Experimental setup at Lizard Island research station, 2004; left tanks; right structures and hiding places, anthias males (violet) and females (orange) and blenny.

A major challenge will be to create conditions in which blennies will produce natural foraging behaviour, which would mean about 20 bites per hour. I predict that a high water column will make them behave more active. Strong influx and outlet could produce a current in the tank which may promote attacks as well. A key feature of a successful setup will be continuous provisioning of small amounts of food, mimicking plankton floating by in nature. Distracted individuals are most likely to be bitten by blennies but our previous experiments showed that if feeding is restricted to few sessions per day the victims will focus on foraging and will not respond immediately to bites by the blenny.

Figure 2

Female *P. squamipinnis*, tagged beneath the dorsal fin.

***P. rhinorhynchus* in its hiding place in the laboratory.**

Field observation considerations

For some of my questions observing anthias in the field yielded good quality data sets. Additional data sets will rely on the ability to observe repeated interactions between blennies and marked individuals. The blennies could be of either species, while anthias still appear to be the most appropriate victim species as they are abundant, frequently in the open water column and regularly attacked by blennies. Nevertheless, the problem with these data is that we did not manage to get them yet despite repeated attempts. In the field there are too many potential victims on a patch (typically 60–150) so that they cannot be all individually marked: the method is to inject coloured elastomer (VIE, visible implant elastomer tag provided by NMT) into scale pouches (see figure 2). Two easily visible colours (blue and white/yellow) and six different locations help rapid identification of up to 24 individuals. In addition to this reduced data set there are on average few interactions per individual and day. Cisarovsky (unpublished manuscript) estimated that there is about 1 interaction per individual anthias per 12 hour day. This implies that a person who would dive four hours per day would have to spend two month at one reef patch in order get on average 20 interactions per marked individual. Therefore, the laboratory setup seems to offer more promising conditions.

Is punishment of cleaners and blennies something that co–evolved?

As the same species that punish blennies also punish cleaners for cheating it appears to be possible that the behaviour in the two situations did co–evolve or that evolution in one context promoted the use in the other one. Maybe punishment evolved in the cleaner – client context and is a reaction to “cheating” by cleaners that led to the same reaction to “cheating” in another context. A possibility to test this hypothesis would be to look at how fish in the Caribbean that coevolved with cleaning gobies instead of cleaning wrasses react to blennies. These clients do not punish the gobies (Soares et al. 2008), which seems to be understandable because cleaning gobies prefer ectoparasites over client mucus and hence prefer to cooperate (Soares et al. 2010). In the Caribbean there are no biting blennies present, so they are not adapted to interact with the parasites. But it would be possible to let them interact with cleaner wrasses that occasionally cheat and test their behaviour after being bitten by a cleaner. If Caribbean resident fish that are for some time confronted with cleaner wrasses in the laboratory show aggressive chasing of the biting cleaners even though they do not do this to cleaning gobies then this inter–specific aggression is present in their behavioural repertoire and they are flexible enough to use it if necessary. In this case it is not necessary to evolve punishment in the cleaner context to be able to punish blennies. If they do not show any aggressive chasing if they are confronted with biting cleaners then this suggests that the aggression against the two different cheaters may be linked in some way.

Is there an additional public good effect of delayed attacks after punishment?

We observed in our laboratory studies on the effect of punishment on blennies that the parasites sometimes refuse to attack the next set of plates if they were punished in the previous round (page 98). It would be interesting to see if there is a similar effect under natural conditions. If the parasites delay the next attack after being punished this could add to the public good that we observed, because ALL other victims in the territory of the blenny, not only the punisher and its group members, would benefit from a period of repose. It would be rather easy to test this in the field. Until now there are no measurements of time intervals between attacks. Using this information it would be possible to compare the time intervals between attacks with and without previous punishment. The hypothesis would be that after punishment the next attack is delayed. This could have several reasons. First, the chasing itself will use up some time. Second, the blennies are sometimes hiding in their hiding place if they were chased intensely. This could delay the search for a new victim. And third, as observed in the laboratory experiments, the punishment itself could deter the blennies for some time from attacking. To exclude the two first possibilities it would be necessary to ignore the time spent chasing and hiding.

Are there personality differences between blennies and are they linked to differences in feeding strategies?

While I documented individual differences in behaviour in my thesis it remains unclear what factors cause this variation. Individual experience and operant conditioning (successful actions are more likely to be repeated than unsuccessful actions) could cause much of the variation we observed. Nevertheless, personality differences seem to be widespread in animals (Bergmüller et al. 2010, Sih et al. 2004 a, b, Gosling & John 1999). It could be interesting to test the blennies for personality differences and more importantly to test if these differences, if there are any, are linked to some of the observed differences in feeding strategies. One could imagine that individuals that are risk averse might stay closer to their hiding place and avoid predatory species as well as highly mobile species. Those individuals might also respond more strongly to being chased by their victims. Personality therefore could lead to differences in victim species composition as well as to differences in the effectiveness of punishment in this system. There are standard tests for individual differences in boldness and aggressiveness (Wechsler 1995, Gosling 2001, Reale et al. 2007) like the “novel object” test that compares individual differences in factors like the time delay to approach a novel object. These tests could be combined with the kind of experiments conducted in my thesis.

Is there a preference for visiting species?

The field observations allowed us to document a major difference between resident victim species and victim species that are only visiting the territories of blennies: visiting species nearly never react aggressively to blenny attacks but rather swim off to avoid future attacks. When we observed the blennies in the field it looked like the parasites started to attack visiting species as soon as they arrived. Until now there is no data that allows us to test if blennies exploit this difference and prefer to attack visiting species over resident species. To test this we would need quantitative data about resident and visiting species present at any given time. Because the numbers for resident species are constant over time it would only be necessary to keep track of visitors that are entering and leaving the territory. It would also be interesting if there is a difference between blennies in territories that are regularly visited and in territories that are only rarely visited. This could give us an idea about how beneficial – or costly – it is to "specialize" on "easy prey" like visiting species.

Do blennies that experience a more complex victim composition have different feeding strategies than blennies with a simpler victim composition?

One possible explanation for the different feeding strategies observed could be small scale differences in victim composition and in its complexity. In the cleaner – client context it could be shown that cleaners that live in a more complex environment (on the continuous reef) including more client species perform better in learning tasks than cleaners that live at small reef blocks that are less complex in respect to client composition (Sharon Wismer unpublished Master thesis). This suggests that for cleaners in a simpler environment it is enough to use some "rules of thumb" to be able to interact with all clients while cleaner in a more complex environment have to stay flexible and to be able to learn more fine–tuned behavioural rules. Though it is not clear if the interactions of blennies and their victims are complex enough to produce a similar pattern it is still possible that the complexity of victim composition has an important effect on the foraging rules of the parasites. At reef blocks with high numbers of individuals it might pay to specialize on the most abundant species instead of learning how to interact with all the different species while at some small reef patches there might simply not be enough individuals of any one species in total to allow for specialization.

The importance of location for blenny attacks

An important issue for a thorough understanding of the blenny–host system is to determine how both parasite and victims use space. Do blennies have preferred locations for attack? Do they tend to avoid a location where they have been chased recently? Do individual victims of the various victim species use preferential locations and could hence benefit from keeping a blenny away from their favourite sites? Gabriel Cisarovsky could demonstrate that female anthias shoals indeed have a spatial structure (Cisarovsky et al., unpublished manuscript). I tried do answer if the blennies indeed avoid a location where they have been chased recently, and more specifically if the distance between the parasite and the victims is larger after punishment than after no reaction or victim flight. The data were largely inconclusive due to small sample sizes in the 'non–punishment' condition and a low resolution of the grid system we established (1x1x1m cells). Regarding the distance between blennies and their victims I observed the blennies and their victims and after each attack I followed the victim for 20 seconds (the shortest time interval that allowed the blenny and the victim to be "back to normal") and then estimated with the help of a reference stick a) the distance between victim and blenny, b) the distance between victim and location of attack, and c) the distance between blenny and location of attack. Because there was always only one blenny present this was rather straightforward. For the two blennies for which I had enough data to perform statistics there was no difference in the distances between aggression/no aggression if I looked at the distance between the victim and the location and between the victim and the blenny. But the distance between the blenny and the location of attack was larger following aggression in one of the two blocks (Mann–Whitney U test, N = 144, Z = –2.5, p= 0.012). This indicated that this blenny might indeed avoid the location of attack rather than the aggressive individual. For the other blenny there was no significant effect. It is thus interesting to note that we find individual differences in space use decisions in the two blennies of this study.

General conclusions

The starting point of my PhD was to study punishment and public goods. The literature on laboratory studies on humans based on simple but rather artificial games provided mixed results. Some studies found positive effects of punishment on cooperation (Rockenbach & Milinski 2006), others found that punishment can stabilize cooperation if it is effective and rather cheap (Egas & Riedl 2008) and others found negative effects of punishment (Dreber et al. 2008). Therefore it seemed promising to study a system in which punishment occurred under natural conditions to evaluate its effects on the potential emergence of a public good.

The most important result of my study on parasitic blennies and their host reef fishes is that punishment is not necessarily altruistic if it creates a public good. Moreover, the amelioration of a public good does not need to be the goal of the punishing action. Instead, a public good may arise as a by–product of self–serving punishment. Stable contributions to public goods were not due to any controlling actions between group members. Instead, the problem of free–riding was solved by the common enemy: the parasitic blennies would self–servingly ‘punish’ free–riders by focussing their attacks on such individuals.

Overall, the study system seemed to fit the assumptions of a volunteer’s dilemma better than the assumptions of a classic public goods game. In the latter game group gains are proportional to overall contributions while in the former game a contribution by few or even just one individual is enough to create the public good (Diekmann 1985, Archetti 2011). Theoretical analyses of the volunteer’s dilemma focus on how individuals should adapt the probability of contributing to factors like group size, the number of acting individuals necessary to produce the public good, or relative payoffs (Diekmann 1985, Archetti 2011). My study system provides a new solution to the general problem: the individual that has been bitten was ‘chosen’ by the parasite to make a decision and cannot expect any conspecifics to act instead. These asymmetries remove uncertainties over who could/should take action and at the same time cause a situation where the acting individual gains a disproportionate benefit compared to other group members, which greatly stabilises contributions to public goods (Sherratt et al. 2009).

For future studies on humans, I propose that we need more observations on real–life interactions that involve punishment and/or public goods. Such observations would give first indications whether punishment in humans may also often be primarily self–serving and whether the emergence of public goods may often be a by–product rather than the goal. One hitherto rather unexplored potential individual benefit of punishing for the benefit of a public good could be the gain of a reputation. If the reputation of being a punisher increases the probability of receiving help in future interactions or if it deters competitors (Johnstone & Bshary 2004) it might be worth to invest into such a reputation.

Another important line of future research concerns the potential existence of asymmetric benefits, more specifically cases in which individuals benefit disproportionately from their own contributions to the public good. Reputation provides one mechanism in humans how individuals may benefit disproportionately from their own contribution. Spatial structures in which benefits get diluted with increasing distance is another way (Sherratt et al 2009), e.g. if humans care about their neighbourhood. Asymmetries in strength can be yet another. If stronger individuals can get more than the average share of the benefits they might be willing to undertake actions that benefit the group as whole. For example, Nunn & Lewis (2001) suggested that dominant males may evict floating males from the territory to their own benefit but also to the benefit of lower ranking (and hence weaker) male group members that remain passive. In humans, an experiment showed that if only one individual has the possibility to punish for the whole group this leads to more effective cooperation in a public goods game (O'Gorman et al. 2009). Asymmetries may be important for the evolution of punishment in general, also outside the public goods context. The best example of punishment outside humans involves marine cleaning mutualism (Bshary & Grutter 2005). In this mutualism, interactions between cleaner wrasses and resident non–predatory clients are asymmetric and it is clear who is always the good (the client) and who is potentially the bad who then needs to be punished (the cleaner). Maybe such asymmetries that are normally not present in the design of human studies are essential for punishment to function.

What is still needed are more systems in which public goods could be studied in nature. There are some explicit studies on bacteria (West et al. 2007) and on cooperatively breeding species (Clutton–Brock et al.2000, 2009, Kingma er al. 2011, Bergmüller et al. 2005, Sparkman et al. 2011). Both bacteria and cooperatively breeding species have the methodological problem that kin selection may play a role. But there may be other examples of public goods that do not necessarily include related individuals. It would be worthwhile to think in more detail about shared vigilance, cooperative hunting or mobbing that often include several species (Sridar et al. 2009, Nolen & Lucas 2009, Stojan–Dolar & Heymann 2010, Bshary et al. 2006). In these systems it seems likely that the public goods are typically due to self–serving actions of individuals. Hence, established concepts like by–product mutualism (Brown 1983), pseudoreciprocity (Connor 1986) and Group augmentation (Kokko et al. 2001) may be applied. These concepts may not excite game theoreticians because cheating is not an issue because of the self–serving nature of contributions. However, it will be interesting to use an ecological approach in order to understand what ecological factors promote self–serving behaviours that lead to the emergence of public goods. Given that modern humans face major public goods problems like overuse of resources, pollution, or global warming, two possible solutions emerge. The first is to find ways to convince humans to behave altruistically. The second is to use laws and/or financial incentives to create ‘ecological conditions’ under which contributions to public goods become self–serving. The latter option appears to provide a more realistic way.

Acknowledgements

First of all I have to thank my family that supported me during the years of my studies. Without the help of my parents and my parents in law that supported me and cared for my daughters whenever needed it would not have been possible to do field trips and experiments and much less finishing this manuscript.

My husband Redouan Bshary not only had the initial idea of studying the system I introduced in this thesis, but also was very helpful in conducting observations and experiments, babysitting and, most important for the success of this thesis, discussing the subject and inspiring new ideas.

Although Martine Rahier was not familiar with the subject and the study system she generously accepted me as her PhD student in Neuchâtel and supported me during my studies.

The staff of the Lizard Island Research Station and Lexa Grutter supported my work in every possible way and I am grateful for their friendship.

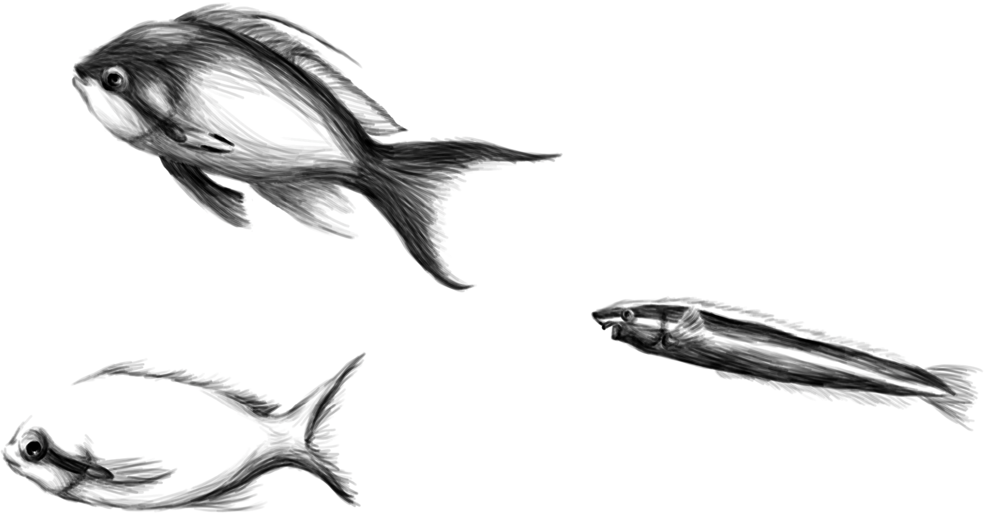
I also thank the park rangers and our friend Ingo Riepl and his team for local support in the Ras Mohammed National Park, Egypt.

The Eco–Ethology team at Neuchâtel provided a friendly and supporting atmosphere in the lab that definitely improved my studies and made it a pleasure to work in Neuchâtel. Especially it was great to share my office with Ralph Bergmüller who provided us all with a cup of coffee whenever needed.

Tom Sherratt inspired much of the third manuscript and it was a pleasure to have him in Bern for lively discussions.

I thank all the people that helped collecting data for the thesis, especially Aurore Malapert, Karin Bergmann, Gabriel Cisarovsky and Laetitia Brun.

Last but not least I want to thank my daughter Johanna Hohner for the beautiful illustrations that she created for the cover of this manuscript.



Refrences general discussion

Avise, 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.

Archetti M. 2011: A strategy to increase cooperation in the volutnteer’s dilemma: Reducing vigilance improves alarm calls. Evolution 65, 885–892.

Bergmüller, R; Heg, D; Taborsky, M., 2005: Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. Proc. R. Soc. Lond. B, 272 (1560): 325–331.

Bergmüller, R., Schürch, R. & Hamilton, I. M. 2010 Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. Philosophical Transactions of the Royal Society B 365, 2751–2764.

Bolnick, D.I, Svanbäck, R., Fordyce,J.A, Yang,L.H., Davis, J.M., Hulsey, C.D., Forister, M.L. 2003: The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist, 161 (1), 1–28

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, A., and Bshary, R. 2010a: Interactions between sabre–tooth blennies and their reef fish victims: Effects of enforced repeated game structure and local abundance on victim aggression. Ethology 116, 681–690.

Bshary, A., and Bshary, R. 2010b: Self–Serving Punishment of a Common Enemy Creates a Public Good in Reef Fishes, Current Biology, 20 (22) 2032–2035.

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.

Bshary R, Grutter AS, Willener AST & Leimar O (2008) Pairs of cooperating cleaner fish provide better service quality than singletons. Nature 455, 964–967.

Bshary R, Hohner A, Ait–el–Djoudi K, Fricke H 2006: Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. PLoS Biol 4(12): e431.

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. et al. 1999. Selfish sentinels in cooperative mammals. Science 284: 1640–1644.

Clutton–Brock, T. H., Brotherton, P. N. M., O'Riain, M. J. et al. 2000. Individual contributions to babysitting in a cooperative mongoose, Suricata suricatta. Proc. R. Soc. Lond. B 267: 301–305

Connor, R. C. 1986: Pseudo–reciprocity: investing in mutualism. Anim. Behav. 34, 1562–1566.

Diekmann A 1985: Volunteer's Dilemma. Journal of Conflict Resolution 29:605–610

Dreber, A., Rand, D. G., Fudenberg, D. & Nowak, M. A. 2008: Winners don't punish. Nature 452, 348–351.

Egas, M. & Riedl, A. 2008: The economics of altruistic punishment and the maintenance of cooperation. Proc. R. Soc. B 275, 871–878.

Fehr, E. & Gächter, S. 2002: Altruistic punishment in humans. Nature 415, 137–140.

Gigerenzer & Selten 2002: Gigerenzer, G. & Selten, R. (Eds.) (2002). *Bounded Rationality: The Adaptive Toolbox*. Cambridge, MA: MIT Press

Gintis, H., Bowles, S., Boyd, R. & Fehr, E. 2003: Explaining altruistic behaviour in humans. Evol. Hum. Behav. 24, 153–172.

Gosling, S. D. & John, O. P. 1999 Personality dimensions in nonhuman animals: a cross–species review. Curr. Direct. Psychol. Sci. 8, 69–75.

Gosling, S. D. 2001: From mice to men: what can we learn about personality from animal research? Psychol. Bull. 127, 45–86.

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.

Hoppedominik, B. 1984: Prey Frequency of the Leopard, Panthera – pardus, in the Tai–National–Park of the Ivoy–Coast. Mammalia 48 (4): 477–487

Johnstone R. A. & Bshary R. 2004: The evolution of spiteful behaviour. Proc. R. Soc. Lond. B 271, 1917–1922.

Kingma, S.A.; Hall, M.L.; Peters, A., 2011: Multiple Benefits Drive Helping Behavior in a Cooperatively Breeding Bird: An Integrated Analysis. Am. Nat., 177 (4): 486–495.

Kokko, H., Johnstone, R. A. & Clutton–Brock, T. H. 2001: The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society of London, Series B, 268, 187–196.

Milinski, M., Semmann, D. & Krambeck, H.-J. 2002: Reputation helps solve the ‘tragedy of the commons’. Nature 415, 424–426.

Nolen, M.T.; Lucas, J.R., 2009: Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice. Animal Behaviour, 77 (5): 1137–1146.

Nowak, M. A. & Sigmund, K. 1998: Evolution of indirect reciprocity by image scoring. Nature, 393, 573–577.

Nunn, C. L. & Lewis, R. J. 2001: Cooperation and collective action in animal behaviour. In: Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 42–66. Cambridge: Cambridge University Press.

O’Gorman, R., Henrich, J., and Van Vugt, M. 2009: Constraining free–riding in public goods games: Designated solitary punishers can sustain human cooperation. Proc. Biol. Sci. 276, 323–329

Oates J, Manica A & Bshary R 2010: The Shadow of the Future affects cooperation in cleaner fish. Cur. Biol. 20, R472–R473.

Oates J, Manica A & Bshary R 2010: Roving decreases service quality in the cleaner wrasse Labroides bicolor. Ethology 116, 309–315.

Raihani NJ, Grutter AS & Bshary R 2010: Punishers benefit from third–party punishment in fish. Science 327, 171.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007: Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291–318.

Rockenbach, B. & Milinski, M. 2006: The efficient interaction of indirect reciprocity and costly punishment. Nature 444: 718–23.

Schindler, D.E., Hodgson, J.R. & Kitchell, J.F. 1997: Density–dependent changes in individual foraging specialization of largemouth bass. Oecologia 110, 592–600.

Sherratt, T.N., Roberts, G., and Kassen, R. 2009: Evolutionary stable investment in products that confer both an individual benefit and a public good. Front. Biosci. 1, 4557–4564.

Sih, A., Bell, A. & Johnson, J. C. 2004a: Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. 19, 372–378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b: Behavioral syndromes: an integrative overview. Q. Rev. Biol. 79, 241–277.

Soares MC, Côté IM, Cardoso SC & Bshary R 2008: On the absence of punishment, partner switching and tactile stimulation in the cleaning goby – client mutualism. Journal of Zoology 276, 306–312.

Soares, M.C., Côté, I.M., Cardoso, S.C., 2010: Caribbean Cleaning Gobies Prefer Client Ectoparasites Over Mucus. Ethology, 116, 12, 1244–1248.

Sparkman, AM; Adams, JR; Steury, TD; Waits L.P., Murray D.L., 2011: Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (Canis rufus). Behav. Ecol., 22 (1): 199–205.

Sridhar, H; Beauchamp, G; Shanker, K., 2009: Why do birds participate in mixed–species foraging flocks? A large–scale synthesis. Animal Behaviour, 78 (2): 337–347.

Stojan–Dolar, M; Heymann, EW., 2010: Vigilance of mustached tamarins in single–species and mixed–species groups–the influence of group composition. Behav. Ecol. Sociobiol., 64 (3): 325–335.

Tebbich, S., Bshary, R. & Grutter, A. S. 2002: Cleaner fish Labroides dimidiatus recognise familiar clients. Anim. Cogn. 5, 139–145.

Wechsler, B. 1995 Coping and coping strategies: a behavioural view. Appl. Anim. Behav. Sci. 43, 123–134.

S. A. West, S. P. Diggle, A. Buckling, A. Gardner, and A. S. Griffin 2007: The social lives of microbes. *Annual Review of Ecology, Evolution and Systematics* 38, 53–77.