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Behaviour from an Evolutionary Point of View: Experimental Studies on Fish and Humans

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“…that’s where you realise that
humans are sort of close to fish.”

C. Eizaguirre, after observing male-male
competition in his colleagues

Table of Contents

Summary

Evolutionary theory based on natural selection states that individuals of a population vary in certain traits and pass these traits on to their offspring. Furthermore, individuals continuously compete with each other for limited resources, such as food items, mating partners, and territories. As a consequence, those individuals that feature traits enabling them to cope better with the current environmental conditions have an advantage in accessing and exploiting these resources and can, therefore, allocate more resources to reproduction. Thus, they will outcompete those individuals not having such advantageous traits and the respective traits will spread in the population. Disadvantageous traits will diminish. The result of evolution is ever better adapted organisms.

However, there are many traits that do not seem to be advantageous to the individual, but they still have evolved. The present work focuses on two such phenomena that are disadvantageous and costly at the first sight: sexual reproduction and human cooperation. Sexual reproduction is disadvantageous, because only one half of the population can bear offspring. Furthermore, it is costly to the individual, because, among other things, individuals have to search for mates. It has been suggested that sexually reproducing organisms have an advantage due to a higher genetic recombination rate. Thus, they are supposed to have an increased ability to adapt to environmental changes. A potential source of such changes are parasites: Organisms potentially need to continuously develop better adapted immune defence (e.g., genes of the major histocompatibility complex, MHC) to successfully fight parasites. This exerts selection pressure on the parasites which have to adapt subsequently. The result is an arms race between host and parasites in which it would be advantageous for the host to achieve a high genetic recombination rate and, hence, a high adaptability by sexual reproduction.

A crucial behaviour connected to sexual reproduction is mate choice, and the three-spined stickleback is a perfectly suited model organism to investigate this behaviour in more detail. It is known that female sticklebacks base their mating decision on various visual and olfactory male cues, such as red breeding colouration (visual cue) and MHC peptides (olfactory cue). Adding on to previous work, Chapter 1 deals with seasonal variation of male olfactory attractiveness to female sticklebacks. Our results document that, besides the MHC signal, a further cue conveys information about potential mates; male olfactory attractiveness to females peaked in summer while the males maintained a nest. This finding suggests that

males release special substances during nest maintenance that indicate male reproductive status to females. Evidently, female olfactory mate choice is not only based on the MHC signal, but on a combination of at least two cues.

A second experiment (Chapter 2) examined the evolutionary consequences of mate choice in sticklebacks under semi-natural conditions. Thereby, the focus was on MHC-based mate choice, and actual matings were analysed in six enclosure facilities in the lake Großer Plöner See. The obtained results are consistent with previous studies that linked MHC genetics with fitness related traits, and show that individuals with an intermediate number of MHC variants ultimately achieve the highest reproductive output. Consequently, choosing the right mate bearing the best MHC genotype might confer the individual advantage needed to cope with an ever changing environment of parasites. This finding is in line with the hypothesis that parasite pressure is a potential cause of the evolution and maintenance of sexual reproduction.

Another seemingly paradoxical phenomenon for evolutionary biologists is the evolution and maintenance of cooperation. Cooperation describes behaviour that is beneficial for another individual, but costly for the cooperator. Thus, a cooperator is someone who invests his own resources in order to help others. Evidently, a defector (i.e., someone who does not cooperate) does not bear the costs of cooperation and, therefore, has more resources to himself. But why is cooperative behaviour so abundant if it is costly? This is especially puzzling in the case of humans which tend to cooperate even with unrelated individuals in one-shot encounters.

In general, university students played computer-based games that served as experimental setup for the research presented in the second part of this thesis. Analysing the participants' behaviour provided further insight into the phenomenon of human cooperation.

A first study (Chapter 3) has elucidated whether the evolved strategies also enable humans to solve modern social dilemmas. Thereby, we focused in Chapter 3 on a global dilemma that we characterised as a collective-risk social dilemma: the prevention of dangerous climate change.

To reduce the risk of dangerous climate change, greenhouse gas emissions need to be reduced to ~50% of the present level by 2050. Thus, states, companies, but also private individuals need to invest in environmentally friendly technologies and practices. In order to reduce greenhouse gas emissions down to a certain threshold, we need to invest in climate protection up to a certain threshold. Otherwise we will face substantial human, ecological, and economic losses. This scenario was simulated in an experimental game with 30 groups of six students each. The participants' investments in climate protection had to reach a known threshold to prevent dangerous climate change. Participants only reached this threshold if the risk of personal loss was high. Thus, we conclude that humans are able to solve the real climate dilemma if they are convinced about the extreme risk of losses.

Further experiments on cooperation (Chapters 4 and 5) are based on the finding that humans tend to direct their help towards people that have previously helped others. This so called indirect reciprocity can explain high levels of cooperation and is based on the reputation of the other person. But how do people get to know the reputation of others? Evidently, we cannot observe all the people we possibly interact with during our entire life, therefore various scientists proposed gossip as a possible means of spreading and gathering this information. In this thesis, this proposed function of gossip has been investigated experimentally. The first study in this context (Chapter 4) has shown that gossip indeed can serve as a vector for social, reputation-relevant information. Participants described the observed behaviour of others truthfully; this gossip was perceived as positive or negative in accordance with the author's intention; and, last, participants reacted on positive gossip with cooperative behaviour, and on negative gossip with defection towards the person who was described by that gossip. Yet, gossip also seems to have a strong manipulative potential; people's decisions were influenced by gossip designed by the experimenter even if they knew hard facts (i.e., past behaviour) about the other person.

In a follow-up study (Chapter 5), this effect was examined in more detail. The effect of multiple gossip statements was examined with respect to elicited cooperation from the people encountering them. The participants' response was compared to the same people's response based on a single gossip statement or direct observation. The results indicate that an increased number of gossip statements helps to reduce the risk of manipulation and to direct cooperative behaviour towards cooperators. Furthermore, this study suggests a strong connection between reputation, reciprocity, and trust: Participants who gained a high reputation through reciprocating were also perceived as more trustworthy. This connection might have fostered cooperative behaviour up to the present level in modern human societies. These findings support the hypothesis that gossip and, hence, the use of language, is connected to the high level of human cooperation.

Zusammenfassung

Die Theorie der Evolution durch natürliche Selektion basiert darauf, dass sich Individuen einer Population in verschiedenen Eigenschaften unterscheiden und diese an die Nachkommen weitergeben. Zudem stehen die Individuen in einem Konkurrenzkampf um begrenzte Ressourcen (zum Beispiel Nahrung, Paarungspartner und Territorien). Individuen, die diese Ressourcen effizienter verwerten oder sich besseren Zugang zu diesen verschaffen können, haben dabei einen Vorteil und können somit mehr in die Fortpflanzung investieren. Auf diese Weise werden sich vorteilhafte Eigenschaften in der Population ausbreiten. Zusammengefasst bedeutet das, Eigenschaften, die zu einer besseren Anpassung an die Umwelt und dadurch zu einem höheren Fortpflanzungserfolg führen, werden sich ausbreiten und etablieren.

Es gibt jedoch auch Eigenschaften, die sich entwickelt haben, obwohl sie unvorteilhaft zu sein scheinen. Die vorliegende Arbeit befasst sich mit zwei solcher Phänomene, die auf den ersten Blick hohe Kosten verursachen und damit vermeintlich einen Nachteil für das Individuum bringen: sexuelle Fortpflanzung und Kooperationsverhalten. Sich sexuell fortpflanzende Organismen haben einen auffälligen Nachteil gegenüber asexuellen Organismen: Nur die Hälfte der Population – die Weibchen – kann Nachwuchs hervorbringen. Zudem ist mit sexueller Fortpflanzung auch meist eine aufwendige Partnersuche verbunden. Ein Vorteil gegenüber asexuellen Linien wird jedoch in einer höheren genetischen Rekombinationsrate vermutet. Dadurch ist es theoretisch möglich, sich über Generationen schneller an wechselnde Umweltbedingungen anzupassen. Damit daraus wirklich ein Vorteil entsteht, müssen die Umweltbedingungen sich kontinuierlich ändern, und eine mögliche Ursache für solch starke Änderungen wird in Parasiten gesehen. Entsprechend dieser Theorie wird angenommen, dass Organismen ständig ihr Immunsystem anpassen müssen (zum Beispiel in Form der Immungene des Haupthistokompatibilitätskomplexes; engl. major histocompatibility complex, MHC), um sich gegen ebenfalls ständig evolvierende Parasiten zur Wehr setzen zu können. Diese Wechselbeziehung führt zu einem Wettrüsten zwischen Wirt und Parasit, bei dem es von Vorteil ist, eine hohe genetische Anpassungsfähigkeit zu besitzen. Unter diesen Umständen könnte sexuelle Fortpflanzung die erfolgreichere Strategie sein.

Eng verbunden mit sexueller Fortpflanzung ist die Partnerwahl. Welcher Partner ist der richtige, damit der Nachwuchs optimal mit den wechselnden Bedingungen umgehen kann?

Der dreistachlige Stichling ist für solche Untersuchungen ein ausgezeichneter Modellorganismus. Studien haben gezeigt, dass die Weibchen ihren Partner aufgrund verschiedener visueller (z.B. rote Balzfärbung) und olfaktorischer (z.B. MHC-Signal) Signale wählen. Das erste Kapitel dieser Arbeit ergänzt dieses Wissen und untersucht die zeitliche Komponente der Männchenattraktivität. Die Resultate zeigen, dass neben dem bekannten MHC-Signal ein weiteres olfaktorisches Signal eine wichtige Rolle im Partnerwahlverhalten der Stichlinge spielt. Am attraktivsten für Weibchen sind Männchen zum Zeitpunkt der Nestunterhaltung. Nach der Aufgabe des Nestes fällt die Attraktivität wieder ab. Scheinbar setzen die Männchen während des intensiven Nestbaus einen Geruchsstoff frei, der den Weibchen Paarungsbereitschaft signalisiert.

Eine zweite Studie (Kapitel 2) untersucht die evolutionären Folgen der Partnerwahl unter semi-natürlichen Bedingungen. Dazu wurden Stichlinge in sechs Außenanlagen im Großen Plöner See ausgesetzt und bezüglich ihrer MHC-abhängigen Partnerwahl untersucht. Die gefundenen Resultate sind im Einklang mit vorherigen Studien, die den Zusammenhang zwischen MHC und fitnessrelevanten Eigenschaften untersuchten, und zeigen, dass Fische, die eine mittlere Anzahl an MHC Varianten besitzen, den größten Gesamtreproduktionserfolg erzielten. Dies unterstützt zum einen die Annahme, dass eine MHC-abhängige Partnerwahl einen evolutionären Vorteil verschafft, der es ermöglicht mit einer sich ständig wandelnden Parasitenfauna umzugehen, und zum anderen die Hypothese, dass diese wechselnde Parasitenfauna eine mögliche Ursache für die Entstehung und die Aufrechterhaltung von sexueller Fortpflanzung ist.

Ein weiteres evolutionsbiologisches Phänomen ist die Evolution und Aufrechterhaltung von Kooperationsverhalten. Als Kooperation bezeichnet man Verhalten, bei dem ein Individuum Kosten auf sich nimmt, um einem anderen Individuum einen Vorteil zu verschaffen. Es ist dabei leicht ersichtlich, dass ein Individuum, das nicht kooperiert und somit diese Kosten nicht trägt, einen Vorteil hat, da es auf diese Weise Ressourcen spart. Wieso ist jedoch Kooperationsverhalten trotzdem so verbreitet? Diese Frage ist besonders im Hinblick auf den Menschen interessant. Menschen neigen dazu, auch nicht-verwandten Personen zu helfen, selbst wenn sie diese nicht kennen und auch nie wieder sehen werden. Kooperation ein wesentlicher Bestandteil von menschlichen Gesellschaften.

Die hier beschriebenen experimentellen Untersuchungen zu diesem Thema wurden mit Hilfe von computergestützten Spielen durchgeführt, an denen sich Studenten freiwillig beteiligten. Die Analyse derer Verhalten in speziell gestalteten Situationen gibt dabei einen hervorragenden Einblick in das Phänomen der Kooperation.

Kapitel 3 befasst sich mit der Frage, ob es die im Laufe der Evolution entstandenen Verhaltensstrategien den Menschen auch ermöglichen, auf moderne soziale Dilemmata erfolgreich zu reagieren. Dabei konzentriert sich diese Studie auf ein globales Problem, das wir als eine „Dilemma des gemeinsamen Risikos“ (engl. collective-risk social dilemma) charakterisieren: die Bekämpfung gefährlichen Klimawandels. Um das Risiko, dass gefährlicher Klimawandel eintritt, zu verringern, müssen die weltweiten Emissionen von Treibhausgasen bis 2050 auf ~50% des heutigen Niveaus gesenkt werden. Damit wir diese Schwelle erreichen, müssen Staaten, Konzerne und Privatpersonen gemeinschaftlich in den Klimaschutz investieren. Können die Treibhausgasemissionen nicht genug gesenkt werden, wird dies extreme menschliche, ökologische und wirtschaftliche Verluste zur Folge haben. Dieses Szenario wurde in einem Experiment mit 30 Gruppen à sechs Studenten simuliert, in welchem die Teilnehmer mit ihren Investitionen in den Klimaschutz eine bestimmte Schwelle erreichen mussten, um gefährlichen Klimawandel zu verhindern. Die Teilnehmer haben die erforderliche Schwelle nur dann erreicht, wenn sie sich einer hohen Verlustwahrscheinlichkeit bewusst waren.

Weitere Studien zum Thema Kooperation (Kapitel 4 und 5) stützen sich auf experimentelle Untersuchungen, die gezeigt haben, dass Menschen besonders solchen Personen helfen, die selbst schon anderen geholfen haben. Diese indirekte Reziprozität basiert auf der Reputation der Beteiligten und kann das hohe Kooperationsniveau bei Menschen erklären. Jedoch ist die Frage, wie die Menschen zu dem nötigen Wissen über die Reputation anderer kommen, noch ungeklärt. Es ist offensichtlich, dass wir nicht alle Menschen, mit denen wir möglicherweise in der Zukunft zusammentreffen, ständig beobachten können. Daher vermuten Wissenschaftler, dass die entsprechende Information über Klatsch und Tratsch (im Folgenden Klatsch genannt; engl. gossip) erlangt und verbreitet werden könnte. Ob Klatsch diese Funktion erfüllen kann wird in den letzten zwei Kapiteln dieser Arbeit untersucht. Die erste Studie (Kapitel 4) zu diesem Thema zeigt, dass Klatsch einige der dafür nötigen Grundvoraussetzungen erfüllt: Teilnehmer beschrieben das Verhalten von anderen wahrheitsgetreu, und vom Verfasser als positiv gemeinter Klatsch wurde auch von anderen Teilnehmern als positiv erachtet und negativ gemeinter Klatsch als negativ. Zudem haben die Teilnehmer entsprechend dem Klatsch auf andere Personen reagiert; sie haben Personen, über die sie etwas Positives gelesen hatten, geholfen und solchen, über die sie etwas Negatives gelesen hatten, nicht. Nichtsdestotrotz zeigte diese Studie auch, dass Klatsch ein großes Manipulationspotential besitzt: Die Teilnehmer haben sich von experimentell manipuliertem Klatsch über den Spielpartner auch dann beeinflussen lassen, wenn sie dessen Verhalten selbst genau beobachten konnten.

Dieser Effekt wurde in einer Folgestudie genauer untersucht (Kapitel 5). Geben mehrere Aussagen (Klatsch) von verschiedenen Teilnehmern ein besseres Bild über eine Person als einzelne Aussagen? Das Verhalten der Studenten basierend auf einer einzigen Aussage, bzw. auf mehreren Aussagen, wurde mit dem Verhalten verglichen, dass sie in einer Situation zeigten, in der sie den Partner direkt beobachten konnten. Die Ergebnisse zeigen, dass mehrere Aussagen es den Teilnehmern erleichtern, solche Personen zu unterstützen, die selbst auch anderen helfen. Des Weiteren sind die Resultate im Einklang mit der Hypothese, dass Reputation, Reziprozität und Vertrauen eng miteinander verbunden sind. Teilnehmer, die sich einen guten Ruf durch Reziprozität erarbeitet hatten, wurden als vertrauenswürdiger angesehen, als solche, die einen schlechten Ruf hatten. Dieser Zusammenhang könnte dazu beigetragen haben, dass moderne Gesellschaften ein so hohes Kooperationsniveau aufweisen. Außerdem unterstützen die Ergebnisse die Hypothese, dass Klatsch und Tratsch, und daher auch Sprache, eng mit der Evolution des Kooperationsverhaltens beim Menschen verbunden ist.

Introduction

Evolutionary theory based on natural selection has gained wide acceptance ever since Charles Darwin published his 'The Origin of Species' (1859). His theory is based on three postulates: (i) individuals differ in certain traits, (ii) these traits are inherited by the offspring, and (iii) individuals compete with each other (e.g., for territories, food resources, or mating partners). Consequently, individuals with advantageous traits are more likely to reproduce successfully and outcompete others; they have a higher Darwinian fitness. Fitness is a crucial concept in evolutionary biology and refers to the relative contribution of an individual to the gene pool of the next (or actually the second) generation. Thus, advantageous traits will increase in frequency from one generation to another. Likewise, disadvantageous traits are those that decrease the bearer's fitness, and will hence diminish. This process is called natural selection and results in organisms that become ever better adapted to their current environment, because well adapted organisms can allocate more resources to reproduction (Darwin, 1859).

But, what are these traits that influence an individual's fitness and that natural selection acts on? Potentially, it can act on any phenotype as long as the Darwinian postulates are satisfied: e.g., on a distinct kind of enzyme in the cell, a metabolic process or pathway, a morphological feature, or a specific behaviour. If a specific variant of a trait (or a new trait) is currently advantageous for the individual, it will spread in the population; it will evolve. How and why certain traits have evolved is thereby the question evolutionary biologists seek to answer.

In this thesis, I have concentrated on the evolution of behavioural traits and have investigated their role in increasing Darwinian fitness. My focus was on intraspecific interactions and communication. The first part examines how mate choice and the signalling of mate quality can influence an individuals' fitness. Mate choice is a major phenomenon of sexual reproduction that is absent in asexual organisms. Thus, if complex systems of finding and selecting the best mate have evolved, they must confer a fitness advantage. The second part deals with fitness consequences of cooperative behaviour and the connected communication of others' quality as cooperation partners. Cooperating with others means increasing their fitness at a cost for oneself. However, cooperative behaviour has evolved, especially in humans, and, thus, must as well confer an individual advantage. Both the evolution of sexual reproduction and the evolution of cooperation constitute major transitions in evolution (Maynard Smith & Szathmáry, 1995), and are therefore of great interest to evolutionary biologists.

Sexual reproduction

Sexual reproduction is abundant in animals and plants. Nonetheless, it is still difficult for evolutionary biologists to clearly answer the question: why do organisms reproduce sexually? Sexually reproducing organisms face the problem that only one of the sexes can bear offspring; the other sex is, evolutionarily speaking, a waste. In contrast, asexual organisms do not lose half of the population, because each individual can produce offspring. Hence, in a simplistic scenario, the asexual lineage will dominate the future population (Fig. I.1) (Maynard Smith, 1971a, 1978). Furthermore, if we assume an equal death rate for both variants, it is much more likely that the sexual as compared to the asexual variant will face extinction. This scenario lets us conclude that we should only find asexual organisms in the wild; they have a two-fold advantage over sexual organisms (Maynard Smith, 1978). Moreover, sexually reproducing organisms bear additional costs: costs of the search for mating partners (Vitousek, 2007), and costs of mating itself (e.g., harassment (Thornhill, 1980; Lee & Hays, 2004) or disease transmission (Thrall *et al.*, 2000)). Nevertheless, sexual reproduction is common and has been puzzling many a biologist.

It has been proposed that one advantage of sexual organisms is an increased ability to adapt to the environment due to a higher genetic recombination rate (Fisher, 1930; Muller, 1932). In any case, the advantage of sex has to compensate for its cost, and John Maynard Smith (1978) investigated the circumstances under which sexual lineages outcompete asexual ones mathematically. To achieve the desired outcome, the prevalence of sex, associations between environmental characteristics (e.g., temperature, day length, precipitation, presence of a particular predator) need to fluctuate extremely (see also Maynard Smith, 1971b). This means vast changes between successive generations: e.g., the correlation between ambient temperature and day length is positive in generation one, but negative in generation two. With respect to climate, this is clearly not what the majority of sexual organisms encounter.

Parasites, however, are a potential source of such changes (Hamilton, 1980; Hamilton & Zuk, 1982; Hamilton *et al.*, 1990). They are ubiquitous, impose costs by using host resources,

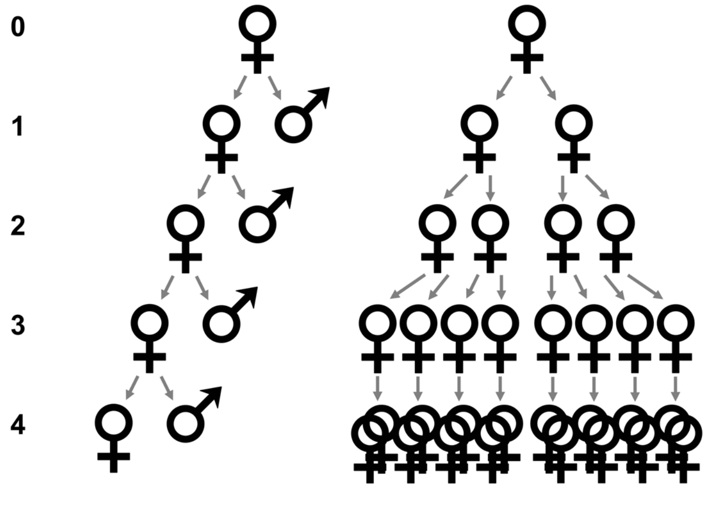

Fig. I.1. Graphical representation of the potential reproductive output of a sexual (left) and an asexual lineage (right). Starting with the parental generation, four subsequent generations are shown (indicated by the numbers on the left). Note that, for simplicity, an equal number of two offspring per generation is assumed for both lineages.

and usually have a shorter live span than their hosts, which makes them highly adaptable. To resist this threat, hosts need to adapt themselves and, therefore, need to rapidly change their genetic make-up (Levin, 1975; Bremermann, 1980; Hamilton, 1980; Bell, 1982; Tooby, 1982; Bell & Smith, 1987; Lively, 1987; Lively, 1996). Subsequently, the parasites adapt to their 'new' host which leads to an arms race between host and parasite. This phenomenon is commonly called the Red Queen Hypothesis, and was originally proposed by van Valen (1973). The name refers to the fictional character of the Red Queen in Lewis Carroll's 'Through the Looking-Glass' (1872), the sequel to his famous 'Alice's Adventures in Wonderland' (1865). Meeting the Queen, Alice has to run constantly to remain at the same spot as explained by the Queen: "[…] it takes all the running you can do, to keep in the same place." Likewise, hosts might have to constantly recombine their genes (e.g., immune genes of the major histocompatibility complex, see Milinski, 2006) just to keep up with the changes within their immediate environment, including parasites.

Sexual reproduction is characterised by meiotic cell division that halves the genetic information, and fertilisation that combines two halves to form a new organism. Consequently, to make it worth to discard half of the genes by cell division, genetic information gained via sexual reproduction needs to complement an individual's remaining set of genes (i.e., remaining in germ cells after meiosis). Therefore, the choosy sex has to search, evaluate and mate with an appropriate individual of the other sex. This process is referred to as mate choice.

But which is the choosy sex? In the simplest case of two sexes, one sex has been selected to produce small, vigorous gametes, whereas the other sex will produce large, nutrient rich gametes. The former are called sperm, and the respective sex is called male; the latter are called eggs, and their bearers are called females (Parker *et al.*, 1972). Due to their smaller gametes, males usually produce much more gametes and invest less energy in reproduction than females do; therefore, mostly males compete for females. Female gametes, in turn, end up as the restricted resource, and females can thus afford to be choosy. In extreme cases, however, where the parental care of males is extremely high and limited, males can become the choosy sex (Berglund *et al.*, 1989; Clutton-Brock & Vincent, 1991; Vincent *et al.*, 1992). Nonetheless, the choosy sex is always the one that is the limiting factor by investing, in total, more in the offspring.

Taken together, we expect (usually) females choosing their best match among males based on males signalling their quality. Consistent with this prediction, we find a multitude of male cues and signals on which females base their mating decision. These signals range from conspicuous visual features (such as antlers in deer (Malo *et al.*, 2005) or bright colouration in sticklebacks (Milinski & Bakker, 1990a)) to acoustic signals (bird songs (Searcy & Yasukawa, 1996), chirping in crickets (Gray, 1997)) to olfactory cues (sex pheromones in Lepidoptera (Costanzo & Monteiro, 2007)). If such cues or signals are costly (e.g., due to energetic costs for their production, or higher conspicuousness to predators), only males that can afford these costs are able to produce them (Zahavi, 1975, 1977; Iwasa & Pomiankowski, 1991). Thus, costly signals are honest signals from high-quality males. If a signal, however, could be produced without a significant investment of resources, low-quality males could try to increase their fitness by cheating and presenting this signal as well. Thereby, these males would attract and mate with more females than without cheating. Being inherently of low quality, such males would sire low-quality offspring. Consequently, females that respond exclusively to costly signals obtain high-quality mates, and, thus, produce high-quality offspring, which is highly viable and attractive for the other sex. Eventually, because per definition high-quality offspring is superior to low-quality offspring, the population will be dominated by both males featuring costly signals and females taking only costly signals into account. In general, the mechanism of favouring distinct features in mate choice and of thereby selecting for their development is called sexual selection (Darwin, 1871; Andersson, 1994).

The evolution of female choice based on exaggerated male traits (i.e., conspicuous signals) was first modelled as the runaway process (Fisher, 1930). According to this model, female preference for a certain male trait will increase the fitness of males bearing this trait. Hence, a male trait can become evolutionary favourable, simply because it increases offspring attractiveness. Furthermore, the preference and the trait will coevolve and increase ever more; they will runaway. This explanation fails, however, to incorporate a need for exchanging half of the genome for a high-quality replacement. Models comprising this role of mate (and genetic) quality are referred to as good gene models of sexual selection (Hamilton & Zuk, 1982; Grafen, 1990; Kirkpatrick & Ryan, 1991; Kokko, 2001; Kokko *et al.*, 2006).

A remarkable phenomenon in the context of signalling is that males of many species exhibit multiple signals to attract females (e.g. Zuk *et al.*, 1990a; 1990b; Moller & Pomiankowski, 1993; McLennan, 2003). According to the redundant signal hypothesis, additional cues enhance the assessment of a single quality (Zuk *et al.*, 1992; Moller & Pomiankowski, 1993; Iwasa & Pomiankowski, 1994; Johnstone, 1996). Receivers benefit by considering several traits to evaluate a mate's condition and quality more precisely. A second explanation is given by the multiple message hypothesis, according to which multiple signals serve as indicators of different qualities (Johnstone, 1995, 1996). A single cue might provide only partial information about the signaller's overall quality, and different aspects of this quality might use different signalling pathways. One signal might, for instance, transmit information about parasite resistance of an individual, whereas another signal might convey information about parental care quality. In this scenario, receivers would benefit by taking both cues into account. Another reason for multiple signalling might be the receiver's psychology (Guilford & Dawkins, 1991; Rowe, 1999). A signal is only useful if it is received and properly processed. This poses a selection pressure for the signaller to provide multiple cues, because multicomponent signals have a higher detectability, discriminability and memorability (Rowe, 1999).

To investigate sexual selection, female choice and the underlying signals and cues, the three-spined stickleback, *Gasterosteus aculeatus* L. (Fig. I.2), is an optimal model organism (Gibson, 2005). First, its genome is known since 2006 (Hubbard *et al.*, 2007) and freely accessible online (http://www.ensembl.org). Second, for stickleback populations in northern Germany, a large diversity of macroparasites can be found and has been described in detail (Zander *et al.*, 1999; Kalbe *et al.*, 2002). This is especially valuable for investigating the role of parasites in mate choice and its evolutionary consequences. But most importantly,

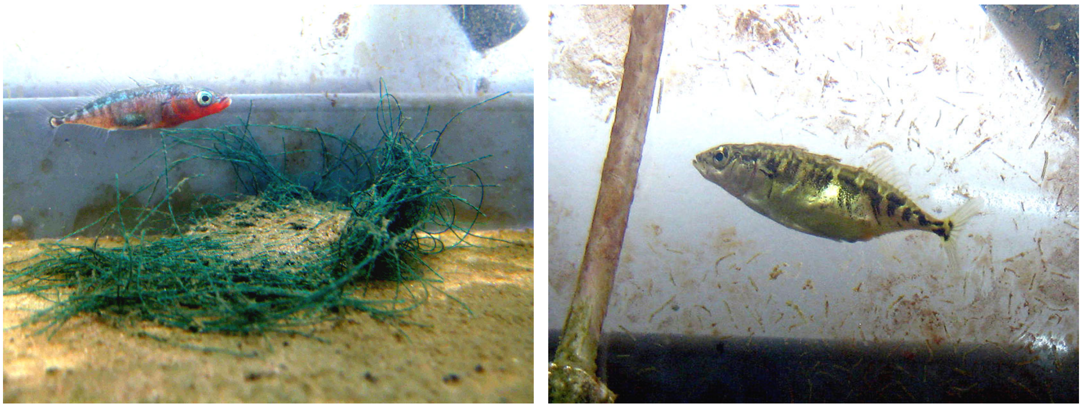

Fig. I.2. Left side: a male stickleback above his nest. Note the breeding colouration: a red throat and a blue iris. Right side: a female stickleback with an egg-laden belly. Photos by Ralf D. Sommerfeld.

sticklebacks exhibit many conspicuous signals, and their mating behaviour has been investigated intensely.

In our latitude, their breeding season starts in early spring (Wootton, 1976) when males develop an intense breeding colouration consisting of a red throat and blue irises (Fig. I.2). At this time, males enter shallow water and establish territories, where they build a nest out of algae and plant material (Fig. I.2). Forming a tiny cave, the building material is stuck together with glycoprotein glue secreted from the kidneys that is called spiggin (Jakobsson *et al.*, 1999; Jones *et al.*, 2001). As soon as a female has produced a mature egg clutch, it approaches the nest of a male, and a complex mating behaviour starts (Tinbergen, 1951; Wootton, 1976). The female presents its egg-laden belly to the male, which starts a distinct zigzag dance. After this courtship dance, which is often interrupted by nest behaviour (e.g., boring, fanning, glueing, and creeping-through), the male leads the female to the nest, and indicates the entrance by pointing at it with its snout. Once the female is inside, the male stimulates the female close to the base of the caudal fin by quivering. Having spawned, the female leaves the nest, and the male fertilises the eggs. Parental care is only provided from the male, which ensures oxygen supply by fanning and removes moulded eggs. The fry hatches after about a week.

This intricate reproductive behaviour is full of intersexual signalling, and the three-spined stickleback is thus perfectly suited for investigating the signalling of mate quality in the context of sexual selection.

Human Cooperation

As for sexual reproduction, I start with a simple framework to explain the noteworthiness of human cooperation. Imagine a small population of four individuals, all of them having the option to invest in a public good. The total investment will then be doubled and equally distributed among the group members, irrespective of their contribution. If each individual invests CHF 2, the total investment is CHF 8, doubled CHF 16 (Fig. I.3, left). In this situation, each individual gets CHF 4, which is equal to a net gain of CHF 2 each. If one individual, however, does not engage in the group action, and does not invest anything, the total investment is only CHF 6 (3x CHF 2), doubled CHF 12. As a consequence, the investors realise a net gain of CHF 1 each (CHF 12 divided by 4 is CHF 3, minus the investment of CHF 2), whereas the defector is better off with a net gain of CHF 3; he does not bear the costs for the original investment (Fig. I.3, right). The rational solution is not to invest at all, because, in summary, each invested CHF 1 yields only CHF 0.50 for its contributor (in economics, this value is commonly called the marginal per capita return, MPCR). Although the group has the highest payoff if everybody cooperates and invests in the public good, this framework results in a high incentive to withhold money from the public pool. Examples for public goods in human societies are free-to-air television and radio broadcasts, public health care, public roads, and pollution control.

From an evolutionary point of view, investment, costs, benefits, and, above all, final payoffs are interpreted as Darwinian fitness. Hence, if an individual strategy yields a higher payoff than others, this strategy is assumed to have a higher fitness, and, therefore, to spread in the population. As outlined before in the public goods scenario, a defector always has a higher payoff than a cooperator. Thus, the evolution and maintenance of cooperation seems to contradict Darwinian evolution. But why, then, is cooperative behaviour so common?

This question has been tackled by many scientists, including economists, sociologists, political scientists, anthropologists and evolutionary biologists. Their common tool is game theory: the study of strategic decisions of individuals trying to maximise their payoff given the strategies of all other individuals. Game theory was established by the seminal work of

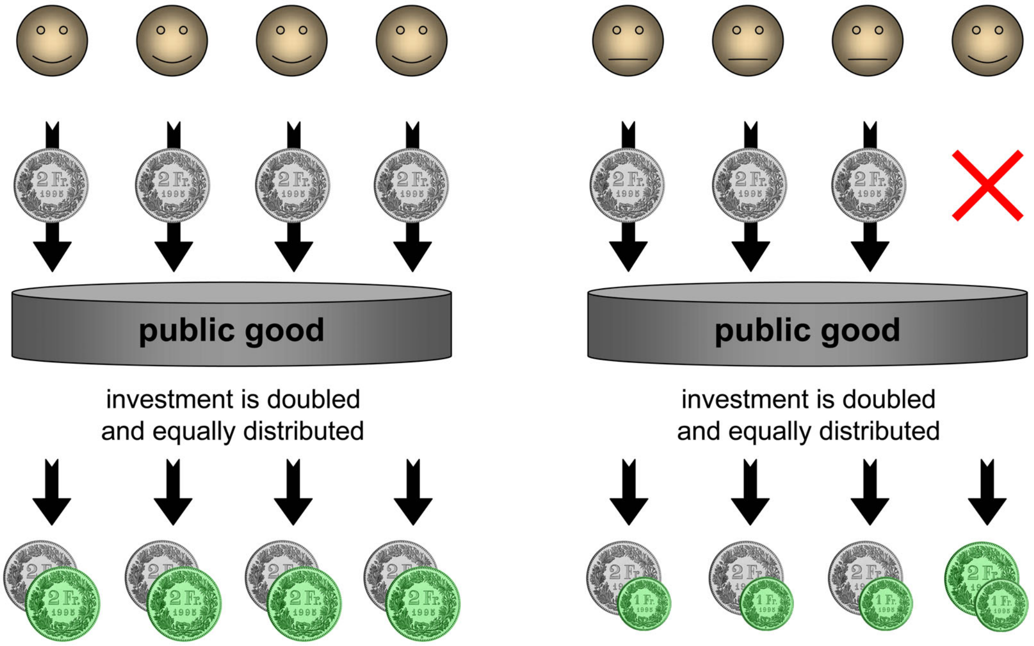

Fig. I.3. Illustration of a public goods game. Each individual can decide whether to invest in the public good or not. The total investment is doubled and equally distributed among all individuals, irrespective of their investment. The left side shows the result if all individuals invest CHF 2, the right side shows the outcome in a case where one individual does not invest into the public good. Green shaded coins indicate the net gain of each individual. In the right hand scenario, the defector (i.e., the one that invests nothing) has a higher net gain than the cooperators in his group.

von Neumann and Morgenstern (1944), and has later been adapted to evolutionary biology (Lewontin, 1961; Maynard Smith & Price, 1973; Maynard Smith, 1982; Nowak & Sigmund, 2004). A variety of games are used to investigate strategic behaviour. The social dilemma outlined in the first paragraph of this section resembles the 'tragedy of the commons' described by Hardin (1968), and has been used intensely under the name of public goods game (for a review see Ledyard, 1995). Further game theoretical frameworks are the prisoner's dilemma (Rapoport & Chammah, 1965; Axelrod & Hamilton, 1981), the chicken (or hawk-dove) game (Rapoport & Chammah, 1966; Maynard Smith & Price, 1973), and the ultimatum game (Thaler, 1988; Güth, 1995).

In the context of evolutionary biology and the evolution of cooperation, several mechanisms have been proposed to explain high levels of cooperation (see also Nowak, 2006): kin selection (Hamilton, 1964), reciprocal altruism (also known as direct reciprocity) (Trivers, 1971), group selection (Wilson, 1975), punishment (Yamagishi, 1986; Boyd & Richerson, 1992; Ostrom *et al.*, 1992; Fehr & Gächter, 2002; Gürerk *et al.*, 2006; but see Rockenbach & Milinski, 2006; Dreber *et al.*, 2008; Milinski & Rockenbach, 2008), and network selection (Nowak & May, 1992; Nowak *et al.*, 1994; Ohtsuki *et al.*, 2006). However, humans tend to help strangers that they will never meet again, they donate to charity organisations that are not part of their social network, and nobody punishes them if they do neither. A concept accounting for these universal processes in humans has been introduced by Alexander (1987): indirect reciprocity. In the standard game theoretical framework of indirect reciprocity, individuals are randomly paired and will never encounter each other in the future again. One individual, the donor, has to decide whether or not to help the other (the recipient) at a cost to itself. Mathematical modelling of this system has shown that the possibility to build a reputation can lead to the evolution of cooperation (Nowak & Sigmund, 1998). In their model, Nowak and Sigmund substituted reputation with an image score. The image score of an individual increases each time it helps (good reputation) and decreases each time it does not help (bad reputation). Extensive computer simulations have shown that a high level of cooperation is achieved and is stable if individuals adopt a discriminating strategy of helping only individuals with a high image score (i.e., cooperators). Later this finding has been corroborated with empirical studies documenting that people tend to direct their help towards those who helped others (Wedekind & Milinski, 2000; Seinen & Schram, 2006).

Other authors argued that the concept of standing (Sugden, 1986) is more realistic than image scoring (Leimar & Hammerstein, 2001; Panchanathan & Boyd, 2003). According to this concept, people start in good standing and only loose their good standing if they fail to cooperate with other people in good standing; they do not loose it if they refrain from helping individuals in bad standing. Thus, one has to know not only the standing of one's partner, but also of the partner's previous partners. This is a crucial difference from image scoring strategies where people always reduce their own image score if they do not help others irrespective of the partner's reputation or the partner's previous partners. Experimental tests have shown that people do not seem to use standing strategies in their decision making process (Milinski *et al.*, 2001). This might be due to the high memory demands of the standing strategy, and a limited working memory capacity (Milinski & Wedekind, 1998).

Eventually, all possible ways to assign a reputation to an individual based on his behaviour, his current reputation, and the recipient's reputation were theoretically examined (Ohtsuki & Iwasa, 2004). In the end, only eight strategies could maintain a high level of cooperation – the leading eight (Ohtsuki & Iwasa, 2004; Ohtsuki & Iwasa, 2006). The common characteristics of these conditional strategies are: (i) individuals with a good reputation cooperate with good individuals, and, thereby, keep their good reputation, (ii) defection against individuals with good reputation is seen as bad, (iii) individuals with good reputation refuse to cooperate with bad individuals and do not loose their good reputation, and (iv) bad individuals can restore good reputation by cooperating with good individuals.

Irrespective of theoretical findings, empirical studies show that reputation building has a remarkable influence on cooperative behaviour in experimental games (Wedekind & Milinski, 2000; Milinski *et al.*, 2002a; Seinen & Schram, 2006), and helps to increase cooperation levels in games of public goods (Milinski *et al.*, 2002b; Semmann *et al.*, 2004; Milinski *et al.*, 2006). But how do people get to know the reputation of others? For indirect reciprocity to work in natural situations, the spreading of and access to reputational information is a crucial prerequisite. An answer to this question might be found in gossip and gossiping, as argued by

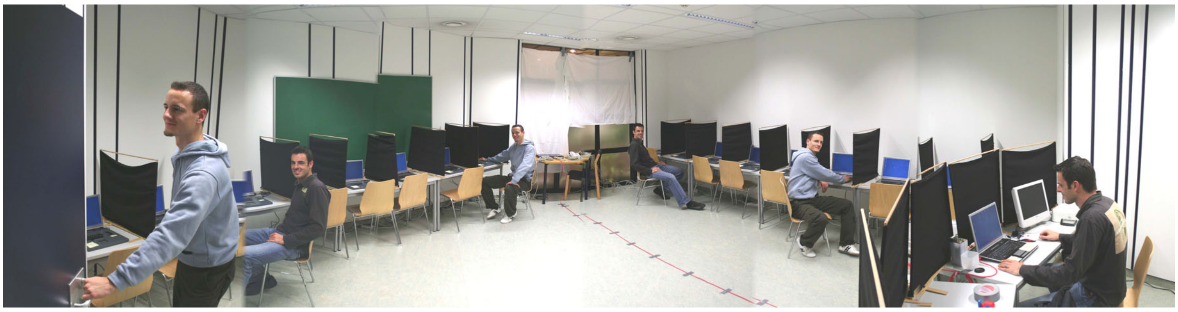

Fig. I.4. Setup for computer-based experiments with students (e.g., Vienna). Each student was seated in front of a laptop and between opaque partitions. A computer network enabled a server (on the right) to record every single decision from each laptop during the entire game. During experimental sessions, the experimenters sat also behind opaque partitions and could only watch a general game overview in order to help in case of computer problems. The photo was created by Dirk Semmann (on the right) and Ralf D. Sommerfeld (on the left).

many authors (Enquist & Leimar, 1993; Nowak & Sigmund, 1998; Mohtashemi & Mui, 2003; Panchanathan & Boyd, 2003; Nowak & Sigmund, 2005). Furthermore, there might be a strong connection between the large size of human social groups, high levels of cooperation, and the evolution of language (Dunbar, 1996; Nowak & Sigmund, 2005).

To investigate human cooperation experimentally, the use of computer-based games is a standard method and well established, especially in experimental economics (e.g., McCabe & Smith, 2000; Fehr & Gächter, 2002; McCabe *et al.*, 2003; Bolton *et al.*, 2005; Gürerk *et al.*, 2006; Croson, 2007). Participants (e.g., university students) usually play anonymously for real money and their reactions in defined game situations give thereby insight into human behaviour (see Fig. I.4).

Outline

In this thesis, I studied behavioural aspects in two major areas of evolutionary biology: mate choice (Chapters 1 and 2) and cooperation (Chapters 3 to 5). Each of the five chapters represents an independent experimental study that is structured in abstract, introduction, methods, results, discussion and references. In cases where the chapter has already been published, the section sequence of the original article has been maintained (Chapters 3 and 4). This outline gives an overview of the individual studies. All studies presented here are a result of collaboration with several colleagues. The individual contribution of each author is summarised in Table O.1.

Mate choice in the three-spined stickleback

Chapter 1: Seasonal Variation of Male Attractiveness in Sticklebacks

It has been shown that female three-spined sticklebacks base their mating decisions on major histocompatibility complex (MHC) genetics of potential partners. However, the corresponding olfactory signal does not elicit any female response if presented exclusively. In this study, male olfactory attractiveness to females was followed through an entire season (winter to summer, incl. nest maintenance, to the end of the reproductive phase of the male) by leading male tank water to a female and measuring its response. The experimental design allowed for measuring the female response independently of both female reproductive status and MHC signalling. The former was achieved by keeping females under such conditions that at each time point a sufficient amount of individuals was ready to be used for mate choice tests. To exclude any effect due to MHC signals, synthetic peptides resembling a males MHC signal were added to each test. Thus, a baseline MHC signal was always present, and any further change in male attractiveness found in the experiment was due to one or several additional olfactory cues. We found that male attractiveness peaks during nest maintenance in summer, and conclude that, in addition to the MHC signal, a further olfactory cue indicating male reproductive status is involved in female mate choice in the stickleback.

Table O.1. Contributions to individual chapters

	1	2	3	4	5
Idea & experimental design	MM, **RDS**	MM, MK, TBHR	FAR, MM, **RDS**	MM, **RDS**	MM, **RDS**
Programming	-	-	HJK	HJK	HJK
Research performance	MM, **RDS**, TB	ID, MK, MKW, **RDS**	MM, **RDS**	DS, MM, **RDS**	MM, **RDS**
Data analysis	**RDS**	CE	MM	**RDS**	**RDS**
Writing manuscript & supplemental material	**RDS**	CE, MK	FAR, MM	**RDS**	**RDS**

Abbreviations are given in alphabetical order. CE: Christophe Eizaguirre; DS: Dirk Semmann; FAR: Floyd A. Reed; HJK: Hans-Jürgen Krambeck; ID: Ilka Dankert; JM: Jochem Marotzke; MK: Martin Kalbe; MKW: Matthias K. Wegner; MM: Manfred Milinski; **RDS: Ralf D. Sommerfeld**; TB: Thomas Boehm; TBHR: Thorsten B. H. Reusch.

Chapter 2: Lifetime Reproductive Success and the MHC

According to Darwin's concept of natural selection and evolution, some individuals of a population have more and better adapted offspring than others, and their traits thus spread, resulting in evolution of the species. If mate choice has any evolutionary consequences, it should lead to inhomogeneous reproductive success with well adapted individuals having more offspring than others. In an enclosure experiment, the lifetime reproductive success of sticklebacks was measured under semi-natural conditions. Prior to release, the laboratory bred fish were infected with their natural spectrum of sympatric parasites. The results are consistent with previous studies, and document that an intermediate MHC variant number results in the highest lifetime reproductive success. MHC genes play a crucial role in immune defence, and it seems that individuals with an intermediate number of MHC variants are able to allocate more resources to reproduction.

Human cooperation

Chapter 3: Preventing Dangerous Climate Change: a Collective-Risk Social Dilemma

In this chapter, it was investigated whether the evolved behavioural repertoire which evidently leads to high levels of cooperation in human societies is also sufficient to face modern social dilemmas. The most challenging social dilemma is the prevention of dangerous climate change – a global dilemma. We characterised this dilemma as a collective-risk social dilemma, and designed a computer-based experiment to examine human behaviour in such a simulated scenario. Participants had to reach a target sum with their investments in a climate pool to prevent dangerous climate change and the connected severe financial loss. But, whatever they invested was lost from their individual account. Thus, they faced the dilemma of preventing loss due to dangerous climate change, and, at the same time, keeping the total investment minimal in order to realise a high personal payoff. We found that our participants managed to reach the target sum only if they faced a high risk of dangerous climate change and, thus, financial loss. Potential solutions for this social dilemma are discussed.

Chapter 4: Gossip as an Alternative for Direct Observation

Gossip has been proposed to be the means by which humans acquire and spread reputation-relevant, social information. Furthermore, it is believed that humans take such information into account to direct their help towards those that have helped others. In this way, indirect reciprocity can explain high levels of cooperation in human societies. The empirical study presented here investigates this function of gossip and focuses on the following questions: Do people describe the behaviour of others truthfully with comprehensible statements? Are such statements universal with respect to their valence? And do people hearing (or reading) these statements react accordingly? To answer these questions, we analysed how university students behaved in an experimental, computer-based game. In addition to the aforementioned questions, we investigated the manipulative potential of gossip, and the importance of information about the gossip's author. The results support the hypothesis that gossip meets the necessary prerequisites, but also document that gossip has a strong manipulative potential, even if hard facts are known.

Chapter 5: Multiple Gossip Statements, Reputation, and Trust

The last chapter extends the findings of the previous one. A similar experimental game was used to investigate the use of gossip in more detail. The design allowed for testing the effect of multiple gossip statements on the participants' response, as compared to single statements or direct observation. Do multiple gossip statements help to transfer the real behaviour of a person? In addition, to shed more light on the manipulative potential of gossip, we investigated the effect of single gossip statements of a valence opposing the valence of the majority of statements. Last, we measured the participants' trust in distinct scenarios to elucidate the connection between trust, reputation and reciprocity. In summary, our results indicate that an increased number of gossip statements helps to direct cooperation towards cooperators, and support the hypothesis that trust, reputation and reciprocity are tightly linked. Participants who gained a good reputation by helping others (i.e., reciprocating) were also perceived as more trustworthy.

Chapter 1

Seasonal Variation of Male Attractiveness in Sticklebacks

(Submitted for publication as: Sommerfeld RD, Boehm T and Milinski M. Desynchronising male and female reproductive seasonality: dynamics of male olfactory attractiveness in sticklebacks.)

Abstract

Olfactory cues play an important role in the process of mate choice in the three-spined stickleback. It has been shown that females take the MHC-genetic make-up of males into account for their choice; however, it seems unlikely that the highly diverse MHC can signal the reproductive condition of the male. We followed 17 individual males for up to 17 weeks through different seasons (winter to summer) and reproductive conditions (non-nesting, nesting, no longer nesting) and measured their olfactory attractiveness for females independent of the olfactory MHC signal. We kept females´ choosiness constant throughout the experiment by desynchronising their seasonality from the males'. Our results confirm that the MHC signal by itself is not sufficient to elicit any female response; it needs an additional olfactory cue. We show here that this additional cue renders males highly attractive during nest maintenance. This attractiveness drops significantly as soon as the nest is abandoned. We discuss possible candidates for this pheromone.

Introduction

Sexual selection, the preference for certain mating partners over others, is an important force shaping the outcome of evolution (Darwin, 1859, 1871; Kirkpatrick, 1982; Andersson, 1994). The behaviour that discriminates some mates from others due to their visual, acoustic, olfactory or any other perceptible features is a major mechanism of this process and is called direct mate choice (Wiley & Poston, 1996). Thus, certain cues need to be present for the choosing individual (1) to recognise conspecifics, (2) to recognise possible mates and finally (3) to discriminate between possible mates (Johansson & Jones, 2007). The discrimination can either be simultaneous (Milinski & Bakker, 1990a), or sequential (Milinski & Bakker, 1992), and should, according to good gene models (Hamilton & Zuk, 1982; Kokko *et al.*, 2002; Kokko *et al.*, 2006), be based on the quality of mates. This preference for higher-quality mates would result in more or higher-quality offspring and thus higher fitness for the choosing individual. Consequently, signals should evolve that reflect the quality of mates. To enhance the transmission of such information, multiple signals might have evolved to either transfer the same information repeatedly to increase the probability of reception (redundant signal hypothesis) (Moller & Pomiankowski, 1993; Johnstone, 1996), or to convey different aspects of the mate's condition or quality (multiple message hypothesis) (Johnstone, 1995, 1996).

While visual and acoustic signals have received intense attention (Andersson, 1994), research on chemical cues for the most part is comparably recent (Marchlewska-Koj *et al.*, 2001; Wyatt, 2003; El-Sayed, 2007; Johansson & Jones, 2007). However, there is increasing focus on chemical communication in fish during the last decade (McLennan & Ryan, 1997; Olsen *et al.*, 1998; Stacey & Sorensen, 2002; Stacey, 2003). Especially in the three-spined stickleback (Gasterosteus aculeatus L.), olfactory cues are important for species-specific (McLennan, 2003) and social recognition (Ward *et al.*, 2005; Ward *et al.*, 2007). Both visual and olfactory cues determine mate choice in the three-spined stickleback. For visual cues, it has been shown that female sticklebacks prefer more intensely red-coloured (Milinski & Bakker, 1990a; Bakker & Milinski, 1991; 1992; Bakker & Mundwiler, 1994; Kunzler & Bakker, 2001) as well as symmetrical (Mazzi *et al.*, 2003) males in choice tests. Fish in the wild seem also to take nest location and parasitisation level into account (Blais *et al.*, 2004).

In addition, there is now ample evidence that females also perceive chemical cues from males (Waas & Colgan, 1992) and take them into account for their mate choice decision (Reusch *et al.*, 2001; Aeschlimann *et al.*, 2003; McLennan, 2003; Häberli & Aeschlimann, 2004; Milinski *et al.*, 2005; Rafferty & Boughman, 2006). Experimental studies found that female sticklebacks are able to "smell" the males' number of MHC alleles and then prefer a mate that offers the optimal complement (Reusch *et al.*, 2001; Aeschlimann *et al.*, 2003; Wegner *et al.*, 2003a; Wegner *et al.*, 2003b). Furthermore, Milinski *et al.* (2005) were able to predictably modify MHC dependent female choice by adding a synthetic signal. Thus pheromones involved in this intersexual communication are most likely MHC peptide ligand molecules.

However, whereas the MHC signals a specific immune quality of the male as a basis for the discrimination between potential mates, we expect additional cues that convey information about the reproductive condition of the male and thus readiness to mate. This is further supported by the fact that MHC peptide ligands alone do not elicit a female response in mice (Leinders-Zufall *et al.*, 2004) and sticklebacks (Milinski *et al.*, unpublished data). Thus, there needs to be an additional olfactory cue to complete the signal for a potential mate being present.

In this study, we aim to investigate the seasonal aspect of olfactory signalling, i.e. "ready to mate" signals, in three-spined sticklebacks. We tested females provided with water from males held in different seasonal (from winter to summer) and reproductive (without a nest, maintaining a nest or having abandoned the nest) conditions. In this way we obtained a temporal resolution of the males' attractiveness, and thus the respective signal. To disentangle female preference from MHC-based signalling we added standardised MHC cues (MHC peptide ligands) to each male's water throughout the entire experimental period before each trial. Consequently the MHC-based signal is always present and any change in female reaction is independent of this cue. Furthermore, it is important to ensure that female preference is unaffected by the females' reproductive status. To achieve this major prerequisite we established several stocks of females held under winter conditions that could subsequently be taken through spring and summer conditions where they developed fully to reproductive females. This was done in a way that secured gravid and choosy females in summer condition throughout the entire period of the experiment (e.g. males in winter condition were tested with females in summer condition). Female choosiness was verified and standardised in a two-fold manner. First, we conducted choice tests with each female providing water from other, actually breeding males and neutral water. Only preceding preference tests of females that choose the male water in these choice tests were included in the analysis. Second, preference tests of females were only taken into account if the female spawned within 24h after this test.

If the MHC-independent male signal is costly to produce, we predict that is absent in winter, but not during summer conditions when males maintain their nests. Furthermore, we expect males that have abandoned their nests not to send the signal any longer. Accordingly, female preference for the respective male water should be low in winter, but high in summer conditions and again decrease for males that stopped any maintenance of their nests. Here we test for a costly male odour signal that complements the MHC signal and conveys information about the reproductive status. However, we may not detect this additional signal if it is produced in all seasons.

Materials and Methods

Animals

Fish were caught in December 2005 and January 2006 from the lake Großer Plöner See in northern Germany. After a few weeks in large tanks, they were placed individually in small tanks (16l). They were held in winter condition (day:night 8h:16h, water temperature 4°C) until they were transferred to spring conditions (12h:12h, 12°C) for ten days. Afterwards they were held in summer conditions (16h:8h, 18°C) for the rest of the experimental period. The experimental males were held separately from any female during the entire experiment.

Except from the winter and spring conditions, we distinguished four conditions in summer tanks (see also Appendix A): 'no nest', 'with nest', 'stimulated' and 'abandoned nest'. 'No nest' refers thereby to normal (light, temperature) summer conditions without any other stimuli. After a successful preference test (see below) under this condition, experimental males were provided with artificial nest material (i.e. sand and nylon threads). A few days later, males under this condition naturally developed red breeding colouration and built a nest. Having reached this condition, males were tested again ('with nest' condition). Following this condition and the respective preference tests, the experimental males were stimulated with a gravid female. To do so, a female in a small tank (1l) was placed in front of the male tank several times a week. Thus, the males entered the third summer condition referred to as 'stimulated'. Subsequently, having completed two or three preference tests under 'stimulated' condition, the stimulation treatment was stopped. Two to six weeks later, experimental males abandoned their nests and were tested a last time ('abandoned nest' condition). Abandonment was defined as stopping any maintenance of the nest by glueing, creeping-through or fanning

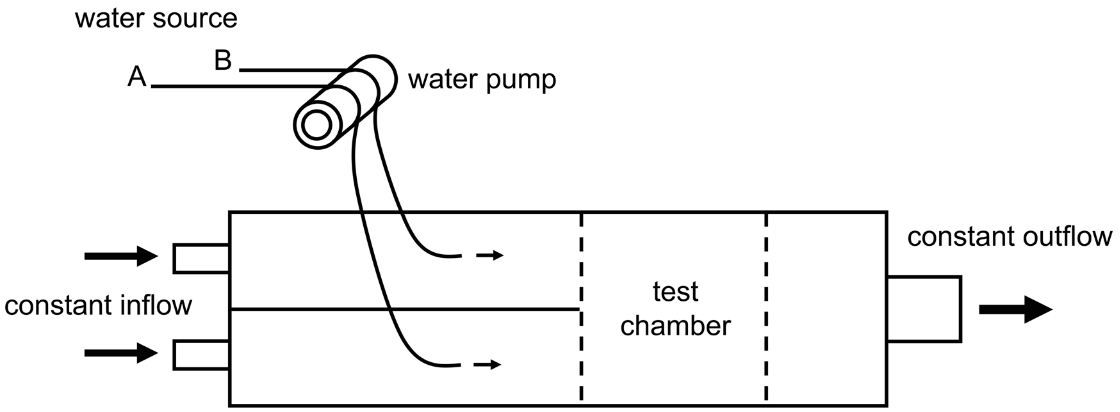

Fig. 1.1. Flow channel. This figure shows a sketch of the flow channel set-up. Within the channel a constant flow of neutral water was realised by a constant inflow and outflow. For experimental tests male water was added on both sides of the flow channel (water sources A and B) via hoses and a water pump. To verify female choosiness in the choice tests, male water was only presented on one side (e.g., water source A), whereas on the other side neutral water was provided (e.g., water source B). For both test situations females were placed in the test chamber. For further details of the procedures see text.

behaviour (Wootton, 1976). This condition was met when none of these behaviour patterns occurred during 10min observation periods on at least three consecutive days.

Females for experimental preference tests came from several stocks in winter conditions (16l individual tanks). These stocks were brought to summer condition as needed to secure a continuous availability of gravid females throughout the experiment. Like the males, females were held ten days under spring conditions before they entered summer conditions. From the moment the fish entered the experiment (after the period in large tanks under winter condition), they were fed twice a day with live food (chironomid larvae, tubifex, daphnids and artemia).

Sequential tests of a particular individual (male and female) were always separated by at least three days. Another three day break was realised after transfer to a new season (i.e. spring or summer).

Preference tests

The water used (1 litre) for a preference test was taken directly above a male’s nest (experimental males with nest) or from the middle of the water body (experimental males without nest). To this water a mixture of four MHC ligand peptides ('wild-type peptides' as described in Milinski *et al.*, 2005) were admixed to ensure the presence of the MHC signal in all seasons (see also Appendix A).

For an experimental trial a gravid female was caught with a glass pipe (e.g., Milinski & Bakker, 1992) and moved to a flow channel (Fig. 1.1 and Appendix A) (as described in Aeschlimann *et al.*, 2003). After an acclimatisation period (2-5min, i.e., 2 min after transfer we waited until the female crossed the middle of the tank) with neutral water, male water was continuously added to the flow channel. Female preference was measured as time the tip of her snout spent in the front half of the test chamber in the flow channel during two 5min experimental periods separated by a 2min break. A preference of the front half means that she tries to swim up to the male.

Each experimental male could be tested with several experimental females, whereas each experimental female was only used for one specific male.

Verifying female choosiness

After each experimental preference test, female choice tests were conducted to prove female choosiness. If we still detect choosiness in a sequential test, we can be sure that the female was choosy in the experimental test because choosiness is reduced in sequential tests (Milinski & Bakker, 1992). Choice tests took place between 1 to 3 hours after the preference test and were conducted in the same flow channel (Fig. 1.1). To test female choosiness male water without added peptides was tested against neutral water, whereby male water was taken from a brightly coloured non-experimental male that had glued its nest on the same day. A stock of such males was held under summer conditions (18h:6h, 18°C), provided with artificial nest material as well as stimulated with gravid females several times a week. Water from both sources (male and neutral) was added continuously to the current via two separated inflows (water sources A and B in Fig. 1.1). The experimenter was blind with respect to water source (a helper coded the bottles). To control for any side preference of the females from biasing the results inflow sides were exchanged from the first 5min experimental period to the second 5min period (again, these periods were interrupted by a 2min break with neutral water). Female choosiness was verified if the female spent more time in the front quarter close to male water inflow than in the quarter close to neutral water inflow. Respective experimental preference tests were omitted from the analysis if the choice test rendered a female non-choosy or if it did not spawn within 24 hours after the preference test.

Statistical analysis

Repeated tests with individual males in the same condition were averaged prior to analysis to provide one data point per condition per male. Choosiness of females (with respect to male condition) in the choice tests was compared to the expected time if no choice was assumed (no choice expectation: 150s out of 600s in the male quarter). Similarly, female preference in the experimental tests was compared with the no-preference expectation (300s out of 600s in the front half). For both analyses the one sample t-test in STATISTICA (version 6.1, StatSoft Inc., 2004) was used. Likewise, pairwise comparison of preference times across conditions by means of t-tests was also performed in STATISTICA. For the general ANOVA analysis of the choice tests R statistical package (version R 2.3.1) was used. It was ensured that the data meet all assumptions of the statistical tests used.

Results

In the choice situation tested females showed similar levels of preference for the male quarter of the flow channel (i.e. male water inflow side) throughout all conditions of the previously tested experimental male (Fig. 1.2a; ANOVA, $N = 115$, $F = 1.066$, $p = 0.30$). Thus, preference times obtained in the experimental test situations are not significantly influenced by any intrinsic differences in female choosiness across seasons and conditions. Notice that the distribution of mean preferences across conditions is slightly U-shaped (Fig. 1.2a). Therefore, the assumption that there is no difference is conservative with respect to the experimental results. Subsequently, we pooled the data to analyse the strength of the female choice in these tests. The mean time a female spent in the male quarter was 336s out of 600s (s.d. = 112.5s). Due to the experimental procedure of taking only choosy females into account, this is significantly different from the expected value for no-preference (i.e., 150s in the male quarter; one sample t-test, $N = 115$, $t = 17.716$, d.f. = 114, $p < 0.0001$).

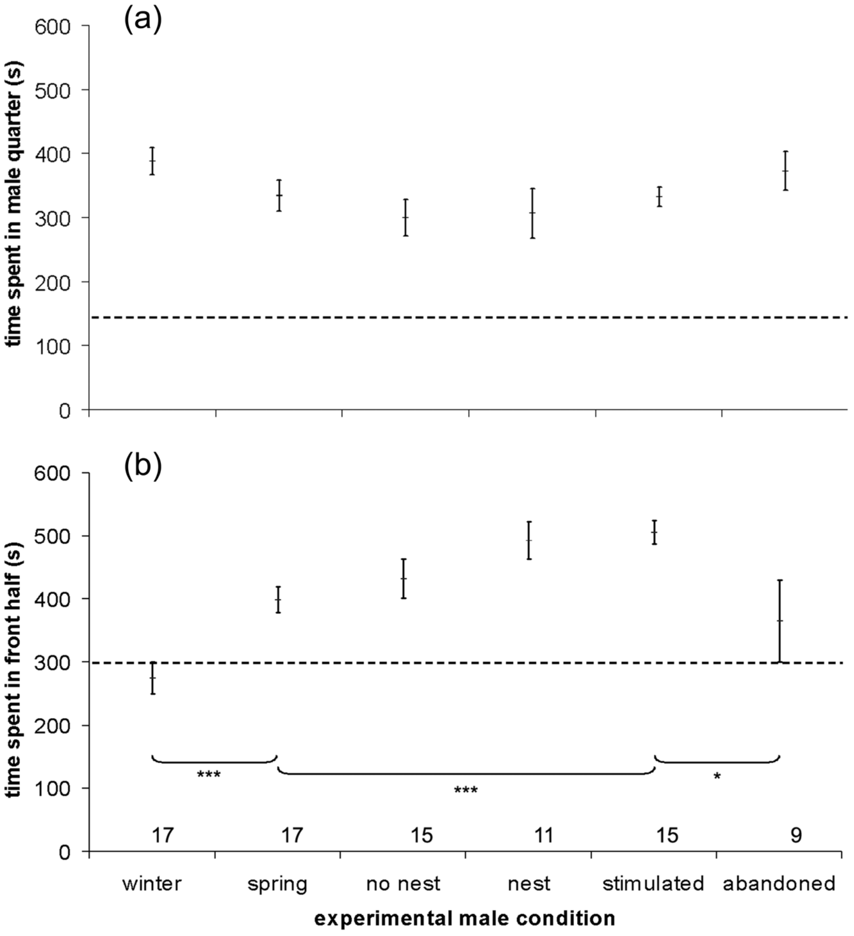

Fig. 1.2. Female choosiness and preference for experimental males. (a) This figure shows female choosiness as the time spent in the male quarter (mean +/- s.e.). In this choice situation water from a nesting male and neutral water was presented in the flow channel. Conditions indicated on the x-axis refer to the male condition of the respective experimental preference test the females were used for. For further details concerning male conditions see text. Note that 150s (dotted line), which is a quarter of the total time measured, mark expected values for random distribution, i.e., without any female choice. ANOVA, N = 115, F = 1.066, p = 0.30. (b) The time a female spent in the front half is given as seconds (mean +/- s.e.) according to the condition the test male was in. For further details concerning male conditions see text. Numbers above the x-axis indicate sample size, whereas the dotted line indicates expected time if females showed no preference (i.e., half of the total time). Significance levels of pairwise tests after Holm-Bonferroni correction: * $p < 0.05$, *** $p < 0.005$.

Preference tests: There was no significant female preference when experimental males were in winter condition compared to the expected value if there was no preference (Fig. 1.2b; mean = 275s, s.d. = 104.6, N = 17, t = -0.983, d.f. = 16, p = 0.34). However, a significant preference for male water was found in the following conditions (Fig. 1.2b): spring (mean = 399s, s.d. = 85.5, N = 17, t = 4.773, d.f. = 16, $p < 0.0005$), summer ‘no nest’ (mean = 432s, s.d. = 119.3, N = 15, t = 4.289, d.f. = 14, $p < 0.001$), summer ‘nest’ (mean = 493s, s.d. = 97.6, N = 11, t = 6.551, d.f. = 10, $p < 0.0001$) and summer ‘stimulated’ (mean = 505s, s.d. = 74.3, N = 15, t = 10.723, d.f. = 14, $p < 0.0001$). Female preference for males with abandoned nests differed not significantly from the no-preference expectation (mean = 365s, s.d. = 193.1, N = 9, t = 1.017, d.f. = 8, p = 0.34). After the experiment, three males started to rebuild their nest, two of which contributed to the ‘abandoned nests’ group. If we exclude those males from the analysis, female preference for males with abandoned nests is even lower (mean = 317s, s.d. = 193.1, N = 7, t = 0.233, d.f. = 6, p = 0.82). However, this preference is not significantly different from the female preference for those males that rebuilt their nest (mean = 535s, s.d. = 24.0, N = 2, t = 1.519, d.f. = 7, p = 0.17).

Subsequently, we compared female preference, and hence male attractiveness, pairwise with respect to experimental male condition. Given p-values were corrected for multiple testing using the Holm-Bonferroni method. From winter to spring male attractiveness increased significantly (paired t-test, N = 16, t = 5.304, p < 0.0005). Consecutively, attractiveness increased further until male reached a high reproductive status under the 'stimulated' condition (comparison spring vs. 'simulated'; N = 14, t = 4.514, p < 0.001). Thereafter, attractiveness decreased significantly at the moment the males abandoned their nests (N = 9, t = -2.417, p = 0.023).

Discussion

Intersexual communication is very elaborate in the three-spined stickleback. Males develop bright red breeding colouration as a visual cue which females evaluate for their mate choice decision (Milinski & Bakker, 1990a; 1992). This signal indicates health and parasite resistance and is therefore honest (Milinski & Bakker, 1990a; 1991). Furthermore, females choose their mate also according to olfactory stimuli carrying information about the MHC of the male (Reusch *et al.*, 2001; Aeschlimann *et al.*, 2003; Milinski *et al.*, 2005). However, in line with previous findings (Milinski *et al.*, unpublished data) this study shows that the MHC signal alone is not sufficient to elicit any significant preference in females. Water from males held under winter conditions did not elicit any female preference behaviour although it was enriched with MHC ligand peptide. This finding is further corroborated by a similarly low attractiveness of male water from individuals that had abandoned their nest.

Therefore, a second kind of olfactory cue is clearly active in the mating behaviour of three-spined sticklebacks and influences the female decision. Winter conditioned males do not seem to send any signal indicating "I am a mature male". However, from the moment the males enter spring condition, their attractiveness is high and there is clear female attraction. The same is true for early summer conditions under which males start to maintain a nest and begin to court females. Our results show that male attractiveness increases steadily with a peak during high reproductive status (Fig. 1.2b), i.e., maintaining a nest and engaging in mating behaviour triggered by repeated presentation of females (e.g., zigzag dance, glueing, fanning, creeping through). Moreover, our results show not only a strong seasonal dependence of this second signal, but also changes according to male breeding status. In late summer condition, when males abandon their nests, attractiveness decreases to a low level (comparable to winter condition). The signal seems to be switched off as soon as the males do not maintain a nest anymore and, therefore, are not able to care for eggs. Interestingly, three males rebuilt their nests after some time of abandonment and might then again switch on their signalling. The respective female preference for males that have an abandoned nest and rebuilt it afterwards (N = 2, mean = 535s, s.d. = 24.0) compared to the preference for males with abandoned nests that did not rebuild it within a week (N = 7, mean = 317s, s.d. = 193.1) supports this view, although the difference is not significant. Closer investigation of this aspect with higher sample size would be needed for clarification.

In this study, any influence of the intrinsic strength of preference by the female can be excluded. In a complex way of housing females, a permanent stock of gravid choosy females was maintained. In addition, all tests with potentially non-choosy females defined via choice tests were not taken into account for analysis. Furthermore, because all fish had been fed the same food throughout all seasons and conditions, the effect of dietary based cues as has been found in other studies (Olsen *et al.*, 2003; Ward *et al.*, 2004) can be excluded.

Our finding gives further insight in the multimodal communication between the sexes in the three-spined stickleback. However, one important question remains unanswered: what substance or mixture of substances does the MHC-independent male odour signal consist of? So far research on chemical communication in fish has mainly focused on pheromones released by females (Sorensen & Stacey, 1999; Stacey & Sorensen, 2002). Only a few studies provide insight in male-derived chemical communication in fish. Among the substances identified as pheromones sex steroids and their metabolites seem to be common as they are found in species as diverse as African catfish (Resink *et al.*, 1989; Vandenhurk & Resink, 1992), goldfish (Sorensen *et al.*, 2005) and gobies (Colombo *et al.*, 1980; Murphy *et al.*, 2001; Zielinski *et al.*, 2003; Corkum *et al.*, 2006). The latter have a similar mating behaviour to sticklebacks with respect to the males building nests and attracting the females to them. By contrast, arctic char males (*Salvelinus alpinus*) use a prostaglandin to attract females and elicit spawning behaviour (Sveinsson & Hara, 1995, 2000). Both arctic char and stickleback males become territorial and defend their selected sites against other males. Consequently, the females select their mates according to olfactory (and other) stimuli and then engage in their distinctive mating behaviour. Another similar mating behaviour is found in the unrelated sea lamprey (*Petromyzon marinus*) where males migrate into streams to find appropriate sites to build their nests. As in the other two species, the females are the choosy sex and select their mating partners. In this species it was found that a bile acid functions as a pheromone (Li *et al.*, 2002). As the authors speculate this might be due to high water solubility of these acids and the need for male lampreys to signal over large distances in running water to successfully attract females. The absence of a general pattern for substances involved in olfactory communication again suggests species-specific communication.

In the three-spined stickleback the missing cue might involve an androgen. Androgens have been investigated for more than a decade now in the stickleback (Borg & Mayer, 1995; 2002b; Pall *et al.*, 2002a; Mayer *et al.*, 2004). These studies indicate that 11-ketotestosterone plays an important role in this fish. It induces kidney hypertrophy (Borg *et al.*, 1993) and glue protein (spiggin) production (Jakobsson *et al.*, 1999), which are both connected to the distinct way males build their nests. Therefore, it is highly linked to the male nesting cycle (Mayer *et al.*, 1990; Pall *et al.*, 2002a) and might as well serve as a messenger for females. A recent study documented that male sticklebacks not only release 11-ketotestosterone into the surrounding water, but that its release is also linked to the reproductive cycle (Sebire *et al.*, 2007). Furthermore, Kurtz *et al.* (2007) showed that high levels of 11-ketotestosterone are costly. Thus all prerequisites for an honest signal are met. Its potential role in affecting mate choice has not been tested yet.

Acknowledgements

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Chapter 2

Lifetime Reproductive Success and the MHC

(Submitted for publication as: Kalbe M, Eizaguirre C, Dankert I, Reusch TBH, Sommerfeld RD, Wegner MK and Milinski M. Lifetime reproductive success is maximised with optimal MHC diversity.)

Abstract

Individual diversity at the Major Histocompatibility Complex (MHC) is predicted to be optimal at intermediate rather than maximal levels. The advantage of immunogenetic recognition of different parasite-derived antigens is traded off against disadvantages of an increased loss of T-cells from the repertoire through negative thymic selection. We showed previously that an intermediate MHC diversity is predominant in natural populations and provides maximal resistance in experimental, multiple parasite infections in the lab. However, what counts ultimately is lifetime reproductive success. Here we measured reproductive success of six laboratory-bred three-spined sticklebacks sib-groups – to minimize the influence of non-MHC genes – during their entire breeding period, each in a semi-natural enclosure in the lake of their parents, where they were exposed to the natural spectrum of parasites. We collected developing clutches at regular intervals and determined parenthood for a representative number of eggs (2279 in total) per clutch with 18 microsatellites. At the end of the reproductive season we could determine for each fish how many developing eggs it had fathered or mothered. Both males and females with an intermediate MHC class II*B* variant number had the highest lifetime reproductive success. The mechanistic link of MHC diversity and LRS differed between the sexes.

Introduction

Genes of the major histocompatibility complex (MHC) are the most polymorphic genes and play a fundamental role in the adaptive immunity of all jawed vertebrates. They encode cell-surface proteins, which present either self-peptides or peptides derived from phagocytosed pathogens to T lymphocytes, a prerequisite for production of pathogen-specific antibodies and the development of an immunological memory (Janeway *et al.*, 2005). The enormous allelic diversity found in natural populations is generally regarded as a consequence of parasite-mediated balancing selection (Clarke & Kirby, 1966; Takahata & Nei, 1990; Apanius *et al.*, 1997; Edwards & Hedrick, 1998; Jordan & Bruford, 1998; Penn & Potts, 1999; Penn *et al.*, 2002; Bernatchez & Landry, 2003; Mays & Hill, 2004; Milinski, 2006). Several reports have shown correlations between certain MHC genotypes and occurrence or severity of specific diseases and parasite infections (Briles *et al.*, 1983; Hill *et al.*, 1991; Godot *et al.*, 2000; Langefors *et al.*, 2001; Grimholt *et al.*, 2003; Bonneaud *et al.*, 2005; Harf & Sommer, 2005; Bonneaud *et al.*, 2006). This implies that individual MHC diversity should be maximised in order to achieve resistance against as many different pathogens as possible. However, although some studies show that MHC heterozygotes are more resistant than homozygotes (Doherty & Zinkernagel, 1975; McClelland *et al.*, 2003), the overall evidence remains ambiguous especially for species harbouring recently duplicated MHC loci (Penn *et al.*, 2002; Pitcher & Neff, 2006). A recent study showed that mice that were heterozygous at all MHC loci were even less resistant than mice that were homozygous at all loci when challenged with different strains of salmonella (Ilmonen *et al.*, 2007). Therefore, it seems to be disadvantageous to have too many different MHC alleles. Indeed, each time a distinct MHC molecule is added to the individual MHC repertoire, all T-cell clones that can recognise self-peptides bound to that molecule must be removed in order to maintain self-tolerance. This process of negative T-cell selection can prevent an efficient adaptive immune response if an individual has too many different MHC alleles (Lawlor *et al.*, 1990). Thus, theoretical models predict that maximal pathogen resistance is achieved by an intermediate, i.e. optimal, rather than a maximal number of different MHC variants (Woelfing *et al.*, submitted; Nowak *et al.*, 1992; De Boer & Perelson, 1993; Borghans *et al.*, 2003; Milinski, 2006). This prediction was recently confirmed by empirical studies, showing the lowest effect of parasite infections, a fitness trait, in fish (Wegner *et al.*, submitted; Wegner *et al.*, 2003a; Wegner *et al.*, 2003b), and reptiles (Madsen & Ujvari, 2006) with intermediate MHC diversity. Such a beneficial amount of individual MHC diversity may not only be maintained by parasite-mediated selection, but also amplified by MHC-based mate choice. For instance, female sticklebacks prefer males with a complementary number of MHC class II variants to their own set of variants, resulting on average in intermediate immunogenetic diversity in their offspring (Reusch *et al.*, 2001; Aeschlimann *et al.*, 2003; Milinski *et al.*, 2005). Recently, Forsberg *et al.* (2007) found evidence for a similar mating preference of female brown trout (*Salmo trutta*) for males with intermediate MHC dissimilarity. Thus fitness should ultimately, i.e., during an individual's lifetime, be maximised when MHC allele diversity is intermediate.

In this study, we tested the effects of individual MHC class II diversity on lifetime fitness by measuring the lifetime reproductive success of three-spined sticklebacks (*Gasterosteus aculeatus*) under natural conditions. Sticklebacks offer an exceptional system, because in populations of our geographical latitude they usually have only one reproductive period in their life (Wootton, 1976). Moreover, life history traits involved in reproduction have been studied extensively, such as breeding colouration that has been shown to be a good predictor of parasitation and body condition (Milinski & Bakker, 1990b; Frischknecht, 1993; Folstad *et al.*, 1994; Kraak *et al.*, 1999; Barber *et al.*, 2000). In a field enclosure system, we analysed mating combinations and individual reproductive output of laboratory-bred sticklebacks. Within each of six enclosures, fish (8 males and 8 females) were full siblings, which reduced variance in genetic background and fish differed almost only with respect to their MHC genotype. Experimental fish had been individually challenged twice with three common sympatric macroparasites from the lake of their parents to simulate a natural life history and to reach a status of immunological activation comparable to their free-living conspecifics. In the enclosures we collected all developing clutches of eggs until the end of the reproductive season and allocated the most likely parents to each clutch. Therefore, we could estimate the reproductive success of each individual fish. Immunogenetic optimality should ultimately contribute to lifetime reproductive success. Therefore, we expect that fish with an intermediate MHC class II*B* diversity have the highest reproductive success. This would explain why individuals with an intermediate MHC diversity predominate natural populations (Reusch *et al.* 2001).

Material and methods

Experimental fish

Three-spined sticklebacks caught from a natural population from the lake Großer Plöner See were used for breeding as described elsewhere (Kalbe & Kurtz, 2006). Several sibships per breeding pair were raised until the age of three months when offspring from the same pair were combined and transferred to 190L tanks in densities of 100 to 250 fish. Fourteen randomly chosen individuals and both parents of each sibship were analysed for their MHC class II*B* genotype (see below). Six sibships with segregating numbers of MHC class IIB alleles/variants were selected, as in Wegner *et al.* (2003a). In such families, with a similar genetic background, MHC genotypes with different numbers of sequence variants were present: 1) intermediate diversity (around 6 sequence variants), a sub- optimal number (< 5 sequence variants) and a supra-optimal number (> 7 sequence variants).

Experimental parasite infections and time schedule

From each sibship 30 randomly selected fish were each experimentally exposed twice to a combination of three of the most prevalent macroparasite species originating from their parents' habitat: the nematodes *Anguillicola crassus* and *Camallanus lacustris*, as well as a digenean trematode, the eye fluke *Diplostomum pseudospathaceum*. All parasites originated from the Großer Plöner See or contiguous neighbouring lakes and, therefore, are regarded as sympatric to the stickleback population examined here. Infection of fish was performed as described elsewhere (Kalbe & Kurtz, 2006; Krobbach *et al.*, 2007). Fish were exposed to the combination of all three parasites in December 2004, and again in May 2005. Between treatments, to mimic natural life history including parasite exposure, sticklebacks were stepwise brought to laboratory winter conditions (6°C, 10 h light per day) before re-experiencing summer conditions (18°C, 16 h light per day, see Fig. 2.1 for infection dosages and schedule).

Enclosures

The outdoor experiment was conducted in the lake Großer Plöner See, in northern Germany (54° 9'21.16"N, 10°25'50.14"E; see Appendix B) during the summer 2005. The enclosure system consisted of six stainless steel mesh cages (3 m x 3 m) installed on the lake ground in a row close to the shoreline, located in the natural breeding area, i.e., where the parents of the experimental fish had been in the previous year. The 5 mm meshes allowed only small particles and most invertebrates (food items and intermediate hosts of various parasite species) to pass through. A coarse meshed net protected the fish from bird predation. Prior to release into the enclosures, we weighed (+/-0.1mg), measured (+/- 1mm) the fish and counted the *Diplostomum* metacercariae in each eye lens under a dissection microscope.

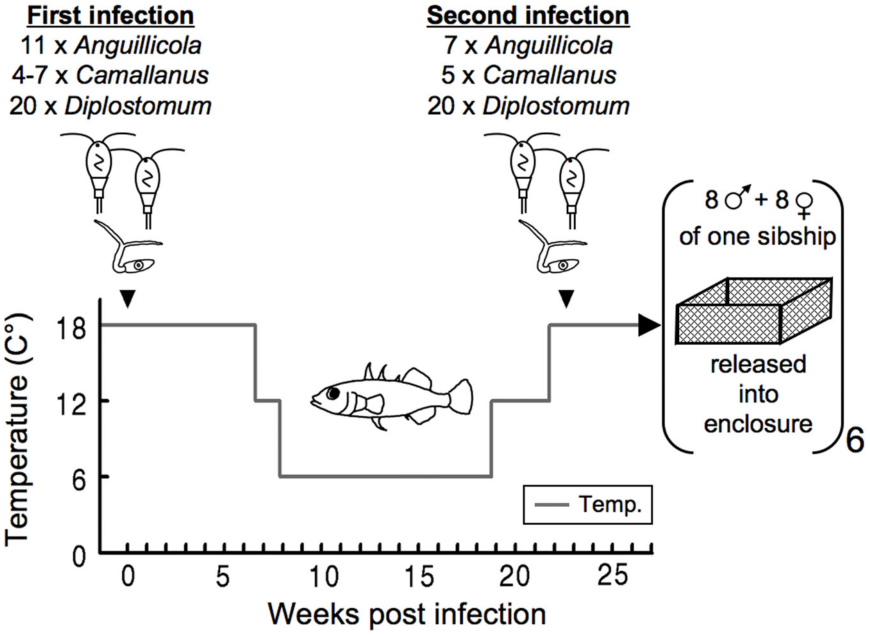

Fig 2.1. Schematic representation of experimental infection schedule and temperature regime in the laboratory, prior to release of the sticklebacks into the enclosure.

Finally, a 2-3 mm piece of the first dorsal spine was cut for later genotyping. Each of the six enclosures was stocked with eight males and eight females, one family per cage, on June 16, 2005.

Egg collection

Every week but one, because the weather did not allow it, all stickleback nests in each enclosure were detected by careful observation. All egg batches were removed and the nests carefully replaced in their original location. Egg batches were brought to the laboratory; clutches were separated on the basis of different developmental stages. If necessary, the individual egg clutches were incubated in aerated well water (with 0.04 ppm malachite green) at 18°C until dark eye spots and the neural tube developed, to ensure a sufficient amount of DNA for further analysis (see below).

Recapture and examination of sticklebacks

During the last egg collection on August 3, when nests no longer contained fresh clutches, all surviving fish were caught. Immediately following capture, a picture of each male's red throat was taken within a dark box using a digital camera (Olympus E20-p) with a 36 mm macro-lens. For the camera parameters and the handling of fish see Jäger *et al.* (2007). Intensity analysis of the red colouration was performed with IP Lab 3.6.2 for Mac OS 9.2.2 (Scanalytics, Inc.) delimitating a defined area of the red throat. Jäger *et al.* (2007) showed that method to be highly repeatable. Surviving fish were measured, weighed and dissected within three days after capture, including screening for macroparasites and weighting of organs (gonads, kidney, liver, spleen). General body condition of the fish was calculated according to Bolger & Connolly (1989).

All external and internal macroparasites and ciliates were determined to the lowest taxonomic level possible. In order to quantify the total parasite load of each fish, an individual parasite index was calculated (Kalbe *et al.*, 2002). This allowed for summarising different combinations of rare and frequently occurring parasites for each stickleback and comparing their total parasite burden quantitatively.

MHC and microsatellite typing

DNA extractions from dorsal spines were conducted using DNA Tissue kit (Invitek, Germany) following the manufacturer's protocol. All the fish were typed for 18 microsatellites (see Appendix B) combined in 5 different PCR protocols before release in the enclosures (Largiadèr *et al.*, 1999; Peichel *et al.*, 2001). This number of microsatellites was needed in order to guarantee a high parenthood resolution even within sibships. At the end of the experiment, survivors were re-typed for identification. The MHC class II*B* diversity was determined using capillary electrophoresis single-strand conformation polymorphism (CE-SSCP) as described in Binz *et al.*(Binz *et al.*, 2001).

Parenthood analysis and heterozygosity

From each egg clutch, 16 eggs were randomly picked for parentage analysis. Paternity assignments were performed with the software PAPA for every egg (Duchesne *et al.*, 2002). Accordingly, each egg was assigned to one of the following male categories: nest owner, sneaker and stolen. Males that fertilised the majority of the eggs in a nest were categorised as nest owners and these eggs were assumed to originate from females that have chosen this male. Eggs were assigned to be fertilised by a sneaker, if in one nest the same female had eggs fertilised by the nest owner and another male. Eggs were assigned to be stolen from other nests if the nest owner did not fertilise them and no further eggs of the same female were found in the nest. Moreover, we verified that the combination existed in other nests to exclude wrong affiliations from the software. We also calculated an heterozygosity index for each individual parent (Coulson *et al.*, 1998).

Data analysis

All statistical analyses were conducted in JMP 5.0.1 (SAS Institute). To start, a large multiple correlation was performed and occurring co-linearities were corrected by taking the residuals of the regressions. Stepwise model selections was performed based on the AIC criterion (Sakamoto *et al.*, 1986).

(i) Lifetime reproductive success: We aimed at estimating the lifetime reproductive success (LRS) of each fish. We performed an ANCOVA on the total number of eggs assigned to each parent, with enclosures, sex, parasite load, initial and final body condition (expressed as residuals of the regression with initial body condition) as dependent variables. Secondly, we correlated the residuals of the previous model for LRS with MHC class II*B* diversity with both linear and quadratic terms.

With our design we had to test the correlation between MHC genotypes and LRS within sibships. We used Wegner *et al.*'s method (2003a) extended from Aeschlimann *et al.* (2003) and Milinski (2003) to calculate reproductive success dependent on the number of individual MHC variants using each sibship as a statistical unit. Briefly, we averaged the number of eggs within each sibship over each MHC genotype and calculated all the possible slopes between these points. For a first purist test we used the average number of eggs and the average slope derived as described, and used this as one pair of data points from each sibship (see Results for detailed description of analysis). Further tests took individual fish and, thus, more information into account. Because we had clear predictions with intermediate genotypes to perform better, we used directed (not one tailed) statistical tests (Rice & Gaines, 1994). This analysis was performed with all introduced fish, as well as only with the survivors.

(ii) Parasite load, body condition, spleno-somatic index and redness: Surviving fish were tested for significant effects on parasite load with an ANCOVA incorporating body condition

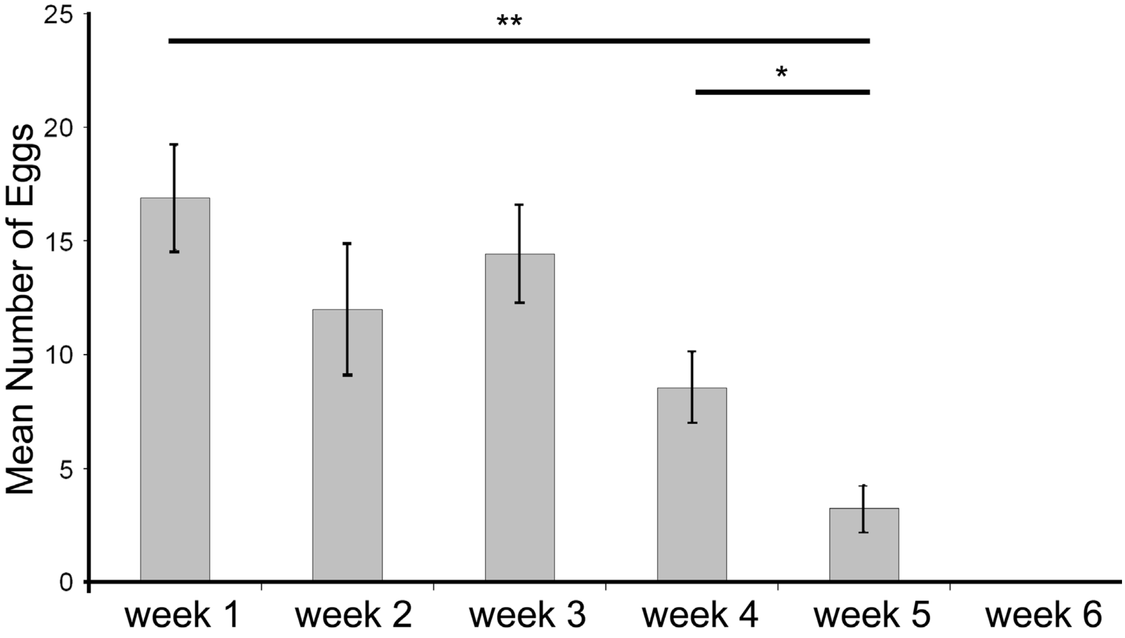

Fig. 2.2. Mean (+/- S.E.) number of eggs collected weekly during the experiment. The mean decreased significantly until the last collecting day, indicating that the reproductive period has finished until week 6. Significant differences between the first and last week and between the last two are depicted by solid horizontal lines.

at the beginning of the experiment, body condition at the end, sex and enclosure as predictors. We also included all two-way interactions in the model. Thereafter, we correlated the residuals with MHC individual diversity.

As an estimate of the sticklebacks' immunological activation, we calculated a splenosomatic index (SSI) as followed: SSI= (spleen weight/body weight)*100. We performed an ANOVA with SSI as dependent variable and enclosure, sex and their interaction as predictors. We then correlated the residuals with individual MHC diversity.

For the male breeding colouration, after an ANCOVA was performed to test for the effect of enclosures, body condition at the beginning and at the end of the experiment and of parasite load, we related the residuals of that model to individual MHC diversity.

Results

Lifetime reproductive success

Over the entire breeding we collected a total of 149 egg clutches until after 7 weeks the nests no longer contained fresh clutches (Fig. 2.2). Using 18 microsatellite loci, 2279 out of the total of 2384 (95.6%) offspring could be unambiguously allocated to a pair of parents. The remaining offspring were removed from subsequent analyses. Sneaking behaviour accounted for 12% of eggs, which is comparable to findings in natural populations (Rico *et al.*, 1992; Largiadèr *et al.*, 2001; Blais *et al.*, 2004), whereas 1% of eggs were evidently stolen from other nests. The total number of analysed offspring from surviving fish varied between 1 and 137 eggs. The lifetime reproductive success (LRS) of fish released in the enclosures was significantly correlated only to MHC diversity: fish with an intermediate number of MHC alleles had the highest LRS (Fig. 2.3a; N=96, t=-2.40, P=0.0185, Table 2.1.a and 2.1.a1). None of our other variables could predict LRS (Table 2.1.a). This result remained significant when restricted to surviving fish recaptured at the end of the experiment (N=53, t=-2.55,

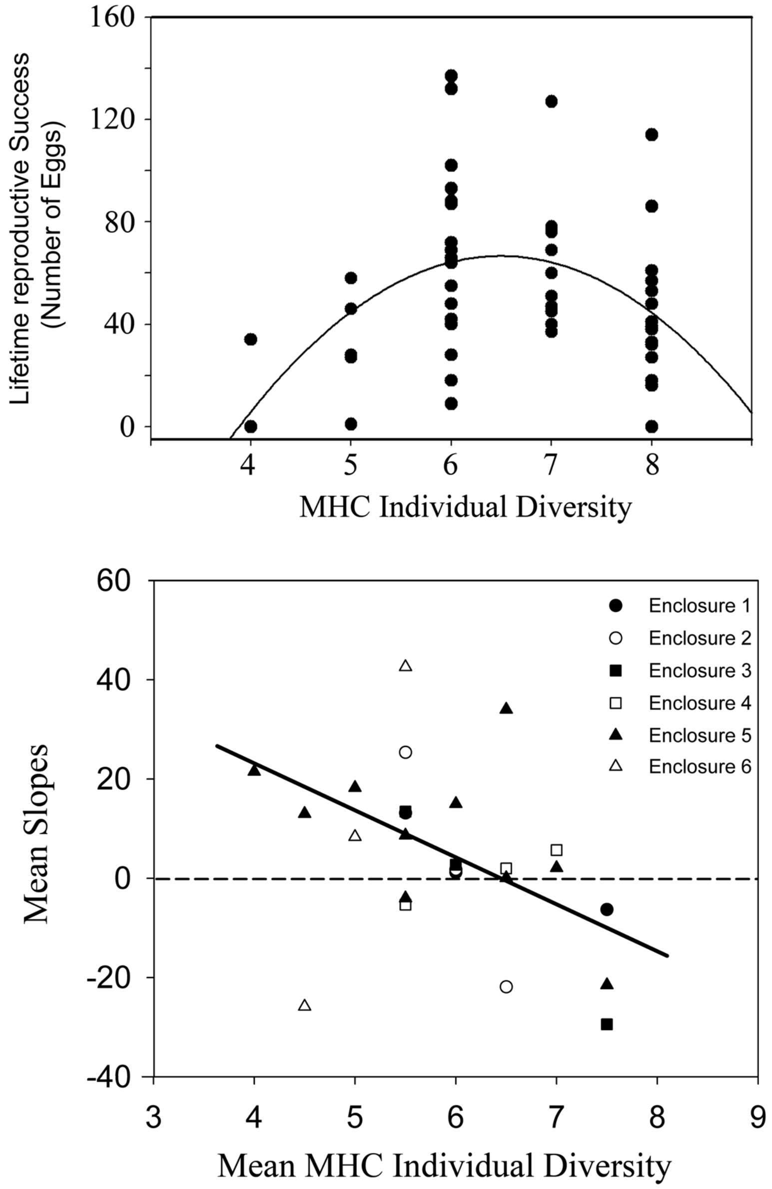

Fig. 2.3. a) Relationship between lifetime reproductive success (LRS) and MHC class II*B* diversity. Fish with an intermediate MHC II B diversity had the highest reproductive output ($N_{eggs}=-0.272+0.136N_{MHCIIB}-0.499(N_{MHCIIB}-6.679)^2$, $F_{2,52}=4.29$, P=0.019). For clarity, raw data are presented but tests were performed on residuals as stated in material and methods section.
b) Relationship between mean slopes of all potential pairs of surviving fish within an enclosure and their relative mean MHC diversity. All data points obtained from the same enclosure are depicted by the same symbol. The equation of the linear regression is f(x)=-27.94x+178.81, directed test $F(_{1,17})=33.71$, P=0.0001.

P=0.014, Table 2.1.a2) and when recaptured males and females were considered separately (female, N=28, t=-2.94, P=0.007; males, N=25, t=-2.46, P=0.022). Furthermore, LRS was not related to our individual heterozygosity index based on neutral markers (linear: $F_{1,53}=0.155$, P=0.695; quadratic: $F_{2,53}=0.207$, P=0.137).

In order to compare LRS among sibships, we assumed that a genotype with an optimal number of MHC alleles has the highest number of eggs, the slope between egg number of this genotype and of a genotype having less alleles should be positive, whereas it should be

Table 2.1. Variables correlated with (a) lifetime reproductive success, (b) parasite load, (c) spleno-somatic index, (d) redness. Models were chosen on the basis of AIC criteria.

Terms	D.F.	Sum of squares	F ratio	Prob>F	Terms	Estimates	Standard error	t ratio	Prob>t
(a) Lifetime reproductive success					**(a1) Lifetime reproductive success- *Polynomial regression- Optimum***				
- Enclosure	5	5156.117	0.992	0.434	- MHC class II *B*	0.055	2.907	0.02	0.985
- Sex	1	180.698	0.174	0.679	- MHC class II *B* (quadratic)	-4.378	1.826	-2.40	0.019*
- Parasite load (corrected for enclosure and sex)	1	1189.776	1.142	0.291	**(a2) Lifetime reproductive success surviving fish- *Polynomial regression- Optimum***				
- Initial body condition	1	1175.581	1.129	0.291	- MHC class II *B*	0.136	0.252	0.54	0.592
- Final body condition (corrected for parasite load and initial body condition)	1	0.006	0.00	0.998	- MHC class II *B* (quadratic)	-0.499	0.195	-2.55	0.014*
(b) Parasite load- *ANCOVA*					**(c) Spleno-Somatic Index - *Polynomial regression- Optimum***				
- Enclosure	5	2.212	4.145	0.0036**	- MHC class II *B*	0.02	0.0157	1.27	0.215
- Sex	1	1.401	13.123	0.0008***	- MHC class II *B* (quadratic)	0.0567	0.0169	3.36	0.0025**
- Body condition (corrected for sex)	1	0.086	0.8061	0.3742					
(d) Redness- *ANCOVA*									
- Parasite load (corrected body condition)	1	207.987	4.997	0.0364*					
- Body condition	1	194.716	4.6781	0.0422*					

*, p<0.05; **, p<0.001; ***, p<0.0001.

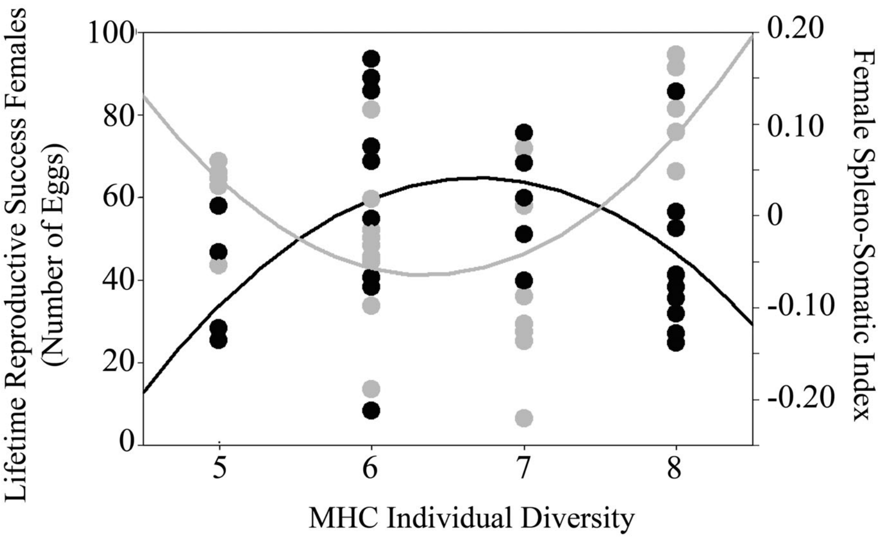

Fig. 2.4. Graph combining female lifetime reproductive success and spleno-somatic index (SSI) as function of MHC II B diversity. In black, females with an intermediate MHC II B diversity had the highest reproductive success (N_{eggs}=38.38+4.514 N_{MHCIIB}-11.98(N_{MHCIIB}-6.481)^2, $F_{2,26}$=4.63, P=0.02). In grey, females with an intermediate MHC II B diversity had the lowest SSI, representing a better immuno-competence status (SSI=-0.193+0.02 N_{MHCIIB}+0.057(N_{MHCIIB}-6.536)^2, $F_{2,26}$=6.698, P=0.004).

negative between the optimal genotype and a genotype with more alleles. Moreover, two genotypes equally distant from the optimum should have the same egg number and, thus, a slope of 0. Furthermore, the mean of the slopes should be positive when the mean of allele numbers is lower than the optimal number and vice versa. If there is an optimal MHC allele number per individual, all single sibship data points should fall on one straight line with the x-axis intercept at the hypothesised optimum (see Wegner *et al.*, 2003a for a similar analysis). Indeed, we could detect a significant negative linear relationship between the mean slopes of LRS and the mean number of MHC class II*B* sequence variants (all fish average per sibship, directed test F($_{1,5}$)=5.44, P=0.05; surviving fish, directed test F($_{1,5}$)=7.28, P=0.034; all fish, directed test F($_{1,23}$)=4.28, P=0.031; surviving fish, directed test F($_{1,16}$)=19.28, P=0.0001, see Fig. 2.3b). In the first case, the analysis resulted in an optimum at 6.55 MHC alleles while it resulted in an optimum of 6.40 when considering the surviving fish only. Males had a higher variance in their LRS than females (mean +/- SE, males: 55.4 +/-7.92 eggs; females: 53.11+/-4.57 eggs, Levene's test, $F_{1,52}$=5.495, P=0.023).

Spleen size

The spleno-somatic index (SSI), an indicator for immune activation, was different among enclosures ($F_{5,51}$=7.96, p<0.0001), and between the sexes with females showing higher values ($F_{1,51}$=6.87, P=0.012). Due to sex differences we split the data set and correlated SSI with individual MHC diversity for each sex separately. Male SSI did not show a significant relationship with MHC diversity (linear, $t_{1,25}$=-1.30, P=0.206; quadratic, $t_{1,25}$=-1.93, P=0.083). Females with an intermediate number of MHC variants had the lowest SSI (Fig. 2.4 and Table 2.1.c; quadratic, $t_{1,28}$=3.41, P=0.002; linear, $t_{1,28}$=1.28, P=0.212). Moreover, SSI correlated with the total egg number per individual for females (directed test, $t_{1,28}$=-1.84, P=0.049), but not for males (directed test, $t_{1,25}$=0.88, P=0.242).

Parasite load

We recorded 21 different parasites (for details see Appendix B) from 8 taxonomic groups: Protozoa (*Trichodina* sp., *Apiosoma* sp. and Ichthyophthirius multifiliis), Monogenea (*Gyrodactylus* sp.), Digenea (*Diplostomum* sp., *Apatemon cobitidis*, *Phyllodistomum folium*, *Cyathocotyle prussica*, *Echinochasmus* sp.), Cestoda (*Valipora campylancristrota*, *Proteocephalus filicollis*), Nematoda (*Anguillicola crassus*, *Camallanus lacustris*, *Contracaecum* sp., *Raphidascaris acus*), Acanthocephala (*Acanthocephalus lucii* and *A. clavula*), the crustaceans *Argulus foliaceus* and *Ergasilus* sp. and glochidia, the parasitic larval stages of freshwater mussels (Mollusca).

The total parasite load varied significantly among the enclosures (Table 2.1.b, $F_{5,53}$=4.145, P=0.004), and females were more infected than males (Table 2.1.b, $F_{1,53}$=13.123, P<0.001). Infection intensities by trophically transmitted parasites (all nematodes, cestodes and acanthocephalans found in this study) were higher in females than males ($t_{1,52}$=3.050, P=0.004), whereas there was no difference for directly and actively transmitted parasites (active, $t_{1,52}$=1.291, P=0.203; direct, Mann-Whitney test, Z=0.632, P=0.527, see Scharsack *et al.* (2007)).

Only for the eye fluke *Diplostomum* sp., but not for the two internal nematode parasites, we could determine the effect of the laboratory infection *in vivo* prior to release into cages. Here, parasite burden increased in the enclosure period significantly (paired t-test on log transformed data, $t_{1,52}$= 15.994, P<0.001) with fish that harboured the highest number of *Diplostomum* sp. at the beginning also showing the highest *Diplostomum* sp. intensity at the end (R^2=0.18, F=10.414, P=0.002).

Body condition and colouration

Body condition, a function of a species specific combination of body length and weight (Frischknecht, 1993), was estimated at the beginning and at the end of the experiment. The loss in body condition was only positively correlated to parasite burden ($F_{1,52}$=9.15, P=0.004) but not to MHC individual diversity (linear, $F_{1,52}$=0.001, P=0.979; quadratic, $F_{1,52}$=0.532, P=0.469).

Mature male sticklebacks develop distinctive red colouration of the throat, as a secondary sexual character. The intensity of breeding colouration was negatively correlated with parasite load (Table 2.1.d, $F_{1,25}$=4.997, P=0.036) but increased with a higher body condition (Table 2.1.d, $F_{1,25}$= 4.678, P=0.042, see figures in Appendix B). We did not find any differences among families ($F_{5,25}$=0.492, P=0.778), and the intensity of redness did not predict LRS ($F_{1,25}$=0.408, P=0.531). Finally, we found no correlation between breeding colouration and individual MHC diversity (linear, $F_{1,25}$=0.416, P=0.526; quadratic, $F_{2,25}$=1.00, P=0.384).

Discussion

Several studies have now identified natural or sexual selection for intermediate rather than maximal MHC diversity (Reusch *et al.*, 2001; Aeschlimann *et al.*, 2003; Wegner *et al.*, 2003a; Wegner *et al.*, 2003b; Bonneaud *et al.*, 2005; Milinski *et al.*, 2005; Madsen & Ujvari, 2006; Forsberg *et al.*, 2007). Here, we add a new important facet by showing that intermediate MHC diversity directly translates into Darwinian fitness, i.e. lifetime reproductive success (LRS). Our experimental design permitted the precise estimation of individual LRS under almost natural conditions, because most three-spined sticklebacks only reproduce during a single breeding season in their entire life (Wootton, 1976). We found that LRS was highest in individuals with an intermediate MHC diversity, which corresponds to an immunogenetic optimum (Wegner *et al.*, 2003a; Wegner *et al.*, 2003b; Kurtz *et al.*, 2004). While this result was significant for both males and females, the mechanistic link of MHC optimality to LRS might differ between the sexes. Our results indicate that body condition and parasite burden is probably directly linked to LRS probably only in females. Overall, females harboured more parasites than males, which does not necessarily indicate lower immunocompetence. The disparity arises mainly by differential infection intensities of trophically transmitted helminths and most likely reflects different feeding behaviours of females to cover their higher energy demand. The number of eggs a female stickleback can produce is dependent on its physiological capacity and nutritional status (Wootton, 1977; Kraak & Bakker, 1998). Hence, females need to consume more food, which also includes copepods and other potential intermediate hosts. Parasites with active transmission, like digenean trematodes, did not differ between the sexes in infection intensity.

In males, where the variance in LRS was higher than in females, the situation is more complex, because of different processes that define distinct optima. Firstly, an intermediate number of MHC variants is optimal in the sense of individual parasite resistance (Wegner *et al.*, 2003a; Wegner *et al.*, 2003b; Kurtz *et al.*, 2004). A second process that defines a males' optimum is MHC-based olfactory mate-choice; a male has to complement a female's MHC variants to achieve an intermediate MHC variant number in their offspring (Reusch *et al.*, 2001; Aeschlimann *et al.*, 2003; Milinski *et al.*, 2005; Milinski, 2006). Females, based on self-reference, prefer males where the combined MHC variant diversity (male plus female) is twice the optimum, as each parent provides only haploid gametes (Aeschlimann *et al.*, 2003; Milinski *et al.*, 2005; Milinski, 2006). In our design, males with an intermediate MHC variant number may have achieved the highest LRS because they appeared as better potential father, which was, however, not significantly reflected in any trait measured here at the end of the experiment.

Among condition dependent male traits in sticklebacks, the intensity of the red breeding colouration is one of the most conspicuous sexual traits that received a lot of attention (McLennan & McPhail, 1990; Milinski & Bakker, 1990a; Bakker & Milinski, 1991; Milinski & Bakker, 1992; Frischknecht, 1993; Bakker & Mundwiler, 1994; Candolin, 1999; Kraak *et al.*, 1999; Barber *et al.*, 2000). Parasite infections affect breeding colouration (Milinski & Bakker, 1990a; Folstad *et al.*, 1994) and body condition (Milinski & Bakker, 1990a; Tierney *et al.*, 1996; Blais *et al.*, 2004). Accordingly, as shown here, the redness of males recaptured from the enclosures correlated positively with body condition but negatively with parasite burden. However, in accordance with previous studies, the quality of sexual ornaments was not greater in males with optimal MHC diversity; but rather could reveal the possession of specific MHC alleles (Buchholz *et al.*, 2004; Jäger *et al.*, 2007). These respective alleles probably provide resistance against the currently predominating parasite species (Jäger *et al.*, 2007). Therefore, female mate choice is predicted to include two criteria: olfactory cues reveal a male's MHC variant diversity, whereas colour reveals the possession of currently protective alleles (Aeschlimann *et al.*, 2003; Milinski, 2006; Jäger *et al.*, 2007). Our present finding that optimal MHC variant diversity predicts LRS better than does breeding colouration suggests that females trade off olfactory, visual and other male signals in a way that favours males with intermediate MHC variant numbers. This trade-off needs to be studied experimentally, preferentially in non-related combinations, as female sticklebacks are known to prefer unrelated mating partners (Frommen & Bakker, 2006).

Also other traits correlating with individual MHC diversity in females was spleen size. Spleen size has been widely used in immuno-ecological studies as a measure of general activation of the immune system by multiple macroparasite infections, particularly in birds (John, 1995; Moller & Erritzoe, 1998; Morand & Poulin, 2000; Brown & Brown, 2002) and fish (Skarstein *et al.*, 2001; Kortet *et al.*, 2003; Lefebvre *et al.*, 2004; Ottova *et al.*, 2005). Females with an intermediate number of MHC class II*B* variants had the lowest relative spleen size (Fig. 4), which correlated (marginally significant) with the number of eggs assigned to the respective females. This link between reproduction, MHC genotype and spleen size is probably due to the activity of the immune system itself, rather than to the result of its efficiency, namely the individual parasite burden. This suggests a trade off between an individual's LRS and the costs of immunity. Sticklebacks with a more efficient adaptive (MHC-dependent) immune system, can afford to invest more into their offspring, whereas fish with less optimal MHC diversity need to allocate a higher proportion of their resources for defence mechanisms to maintain their parasite load at tolerable levels. Previous studies already showed that sticklebacks with an intermediate MHC diversity had the lowest oxidative burst activity, but were nevertheless more capable of limiting the growth of the tapeworm *Schistocephalus solidus* than fish with MHC variant number deviating from this optimum (Kurtz *et al.*, 2004). Fish with an optimal MHC diversity basis seem to perform a shift from this costly and self-damaging innate immune function towards a probably less costly, but efficient adaptive immune strategy, and use immunological mechanisms more concerted and economically. Costs of immunity are predominantly regarded as metabolic constraints (Lochmiller & Deerenberg, 2000). The results of this study indicate that immunological costs might directly affect LRS, but that their impact depends to a high degree on the individual MHC genotype. Therefore, these results further explain why sticklebacks with intermediate MHC diversity prevail in natural stickleback populations (Reusch *et al.*, 2001; Wegner *et al.*, 2003a).

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Chapter 3

Preventing Dangerous Climate Change: a Collective-Risk Social Dilemma

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Abstract

Will a group of people reach a collective target through individual contributions when everyone suffers individually if the target is missed? This "collective-risk social dilemma" exists in various social scenarios, the globally most challenging one being the prevention of dangerous climate change. Reaching the collective target requires individual sacrifice, with benefits to all but no guarantee that others will also contribute. It even seems tempting to contribute less and save money to induce others to contribute more, hence the dilemma and the risk of failure. Here, we introduce the collective-risk social dilemma and simulate it in a controlled experiment: Will a group of people reach a fixed target sum through successive monetary contributions, when they know they will lose all their remaining money with a certain probability if they fail to reach the target sum? We find that, under high risk of simulated dangerous climate change, half of the groups succeed in reaching the target sum, whereas the others only marginally fail. When the risk of loss is only as high as the necessary average investment or even lower, the groups generally fail to reach the target sum. We conclude that one possible strategy to relieve the collective-risk dilemma in high-risk situations is to convince people that failure to invest enough is very likely to cause grave financial loss to the individual. Our analysis describes the social window humankind has to prevent dangerous climate change.

Introduction

Whenever people have to maintain a public resource, such as avoiding overfishing the oceans or protecting the global climate, they find themselves in a social dilemma, which has been called “the tragedy of the commons” (Hardin, 1968). It is well known that over six billion “players” take part in a global climate tragedy of the commons, “a game that we cannot afford to lose” (Pfeiffer & Nowak, 2006). However, humankind faces a dramatic change of living conditions on Earth when the already-rising global temperature passes a certain threshold: Dangerous climate change will occur (Schneider, 2001; Alley *et al.*, 2003; Schellnhuber *et al.*, 2006; IPCC, 2007a). To reduce the risk of dangerous climate change, global greenhouse gas emissions should be reduced to ~50% of the present level by 2050 (IPCC, 2007b). A reduction of this magnitude is beyond the capability of any single country and requires international cooperation. Herein lies a dilemma: substantial emissions reductions are likely to have negative short-term economic effects, but failure to accomplish this reduction may well incur dangerous climate change later, resulting in substantial human, ecological, and economic losses (IPCC, 2007a). Thus, a special type of social dilemma has to be solved, which we call the collective-risk social dilemma. Will a group of people reach a collective target through individual contributions when everybody would suffer if the group fails to achieve the target?

The collective-risk social dilemma has characteristic features that, taken together, distinguish it from other social dilemmas: (i) people have to make decisions repeatedly before the outcome is evident, (ii) investments are lost (i.e., no refunds), (iii) the effective value of the public good (in this case, the prevention of dangerous climate change) is unknown, and (iv) the remaining private good is at stake with a certain probability if the target sum is not collected. Threshold public goods games have been studied intensely theoretically (Palfrey & Rosenthal, 1984; Bagnoli & Lipman, 1989) and experimentally (van de Kragt *et al.*, 1983; Dawes *et al.*, 1986; Erev & Rapoport, 1990; Bagnoli & McKee, 1991; Suleiman & Rapoport, 1992; Cadsby & Maynes, 1999; see Croson & Marks, 2000 for a review). Of the above-mentioned characteristics, several studies investigated the exclusion of refunding (see table 1 in Croson & Marks, 2000), and one study tested the effect of limited information about the value of the public good and its distribution (Marks & Croson, 1999). However, these economically focused studies are designed to simulate not a dilemma similar to the climate problem but rather the funding for bridges, public roads, railway lines (Suleiman & Rapoport, 1992), or a new coffee pot for a community office (Palfrey & Rosenthal, 1984). In contrast to these examples, the climate game involves investing in a public good, not to realize a gain but to avoid a loss. Thus, we expect the strategies adopted in the climate game to be risk-averse. Furthermore, many public goods games focus on a conflict between individual and group interests, but a major component of the climate problem is also a conflict between short- and long-term interests. Therefore, we propose the collective-risk social dilemma as a framework to investigate the inherent problems of avoiding dangerous climate change and other problems of this type.

The ability of people to assemble a target common good, such as food reserves, or to build up a collective defense system, i.e., a fence or a trench, might have been important at a time when humans lived in small communities that had to survive the winter or to defend their village. The building of an emergency sandbag levee by neighbors to protect their community from a flood has been important over the centuries. Half a fence or sand bag levee is hardly better than none. When there is no attack or high flood, the investment is lost. If the fence or sandbag levee is not complete and an attack or high flood occurs, all private goods are at stake. Many similar scenarios exist. Thus, there might exist a rich toolbox of social strategies of testing, signaling, or encouraging motivation to help collect a target common good in a collective-risk social dilemma. Nevertheless, the collective-risk social dilemma has not yet been analyzed by evolutionary theory. Our approach is experimental and might be an incentive for theoretical modeling.

Table 3.1. The expected account values at the end of the game under three pure strategies (all players share the same strategy for the entire game).

Loss probability, %	Free rider, €	Fair sharer, €	Altruist, €
90	4	20	0
50	20	20	0
10	36	20	0

Free riders contribute €0 each round, fair sharers €2, and altruists €4. At a 90% probability of account loss, the optimal strategy is to contribute € 2 each round to the collective. At a 10% probability of loss, the Free Rider strategy is rational, and at 50%, both of these strategies provide identical expected earnings.

In our simulation of the collective-risk social dilemma, every subject faces the same tradeoff: The more he or she invests in the collective good, the higher the probability that the group reaches the target sum, but the less money remains in his or her personal account, which he or she is guaranteed to receive in cash after the session if the target sum has been reached. In contrast, failure to reach the target sum implies a risk that the remaining money in the personal account will be lost. The social dilemma of this scenario adds another tradeoff: The more others invest, the less a subject needs to invest for the group still to reach its target sum. In this simulation, we interpret not reaching the target sum as failing to prevent dangerous climate change. Would others compensate, that is, pay more than their fair share, if someone invested nothing or less than his or her fair share per round? Subjects were anonymous in the experiment, but all subjects could see how much money other subjects contributed after each round. Decisions from the same person could be recognized as such: Altruists, fair sharers, and free riders would become recognizable during the experiment, as well as subjects that change their strategy. Clearly, our groups of six subjects cannot represent all players of the climate game who individually decide how to travel, use fossil fuel, etc. If we find that all groups of six subjects collect the target sum, we cannot conclude anything for the climate game. However, if some of our small experimental groups fail to collect the target, larger groups would certainly fail with higher probability, and other solutions of the climate problems would have to be found.

Thirty groups of six students each took part in a public goods game (Ledyard, 1995) modified to simulate the collective-risk social dilemma via an interactive computer program. We provided the students with an endowment of €40 each, and the students knew they would be asked in each of 10 rounds to invest anonymously €0, €2, or €4 in a “climate account.” They knew that, if the total contributions of the group reached or surpassed €120 at the end of the 10 rounds (equivalent to €2 per person per round on average), all group members would receive what they had not invested in climate change mitigation strategies in cash (for example, €20 if a person had invested €2 per round). If the group failed to reach this collective goal, the computer “threw dice,” so that with a probability of 90% all group members would lose all their savings. In two other treatments, also with 10 groups of six students each, this probability was 50% and 10%, respectively (see Methods). With these treatments, failure to reach the target sum is still interpreted as analogous to incurring dangerous climate change but with a much reduced risk of affecting individuals.

Independent of the treatment, groups who exactly reached the target sum collected, on average, €20 per player; the players then, on average, had invested their fair share. To maximize income, the best possible strategy would thus be to collect the target sum when failure would result in complete loss of money with a probability of 90%: If no one invests anything, any subject would receive his or her saved €40 only in one of 10 cases, that is, €4 on average (Table 3.1). This is much less than if the fair personal share is invested and the average €20 would be gained after the session. The groups taking part in the 50% treatment, on average, would gain €20 per person, either by investing the fair share and safely collecting

€20 each or by investing nothing and on average gaining €20, that is, €40 in half of the cases. Groups in the 10% treatment on average gained most from investing nothing: If no one invested anything, any subject would receive €36 on average, because he or she would lose the saved €40 only in one of 10 cases (Table 3.1).

In the 90% treatment, each course of the game that leads to exactly reaching the target sum of €120, irrespective of who contributes how much as long as each player invests less than €36, is a Nash equilibrium: No single player can gain by deviating from his or her strategy (Colman, 1998; Camerer, 2003; Holt & Roth, 2004). Once a single subject irrationally switches either to a strategy that jeopardizes reaching the target sum or that may exceed the target sum (both of which lowers his or her expected earnings), the remaining subjects' best strategies also involve a switch (Table 3.1; a description of equilibrium points and rational decisions is available in Appendix C). Depending on the current public sum and stage in the game, this switch might be either to "cut their losses" and also become free riders or to "maintain their investment" and increase the level of altruism. The latter is expected when one knows that the target might be missed because of some free riders; one invests more to secure some money. This represents a "snow drift game" scenario (Doebeli & Hauert, 2005), where the best strategy is to cooperate when you know your partner will defect. Irrational responses such as the first switch stated above (that is, those that lower personal expectations) have been reported in several other game designs (e.g., Thaler, 1988). These responses appear to be related to a sense of fairness, that is, situations that are perceived as unfair often result in players making less than optimal choices. In addition to purely self-interested people, there appears to be a fraction of people who are also motivated by these fairness considerations (Fehr & Schmidt, 1999). One explanation for this behavior is that humans are better adapted to repeated game situations where fairness can become adaptive (e.g., Nowak *et al.*, 2000). A lot of opportunity exists in this climate protection game for unfair choices to be made, that is, free rider strategies can be adopted requiring other subjects to choose altruist strategies for the group still to reach the target sum (see Appendix C), which, because of human behavior, jeopardizes the goal of preventing dangerous climate change.

Results and Discussion

Despite the difficulties outlined above, we found that 5 of the 10 groups in the 90% treatment successfully collected the target sum. This is significantly different ($n = 10$, $P < 0.0001$, binomial test) from the rational outcome of all groups reaching the target. Only one group in the 50% treatment and, as expected, none of the groups in the 10% treatment achieved the collective goal of preventing simulated dangerous climate change (Fig. 3.1). Surprisingly, almost all groups provided €2 per person in the first round, an all fair-sharer situation. However, in subsequent rounds, some subjects supplied nothing, which others clearly noticed, as stated in a questionnaire after the game; probably as a consequence, the motivation to contribute declined steadily. This was particularly noticeable for the 50% and 10% treatments, where many subjects reduced investments after round six. Providing €118.2 ± 1.9 (mean ± SE), the groups in the 90% treatment just failed on average to reach the target sum of €120 (Fig. 3.2). The five groups that did not reach the target sum collected on average (€112.8 ± 1.2). Just failing to reach the target represents the worst possible outcome: low individual savings and no collective benefit. The groups involved in the 50% and 10% treatments missed the target sum by far with €92.2 ± 9.0 and 73.0 ± 4.4, respectively (difference among the three treatments: $P = 0.0001$, $n = 30$, $df = 2.29$, $F = 13.784$). However, even the groups in the 10% treatment did not try to gain most on average by investing nothing (Fig. 3.2); against the rational strategy, they collected >50% of the target sum. This irrational behavior may indicate a high potential motivation also to protect the real climate and suggests future experiments where responses to other motivation factors could be studied. Perhaps this surprising behavior also stems from strong risk aversion, which has been shown to result in departures from standard Nash-equilibrium predictions (e.g., Goeree *et al.*, 2003). Some free riders did invest nothing and in 8 of 10 groups won their big savings. Group members invested differently in the climate account. Of the six members of each group, there were 3.3 ± 1.3, 2.1 ± 0.6, and only 1.1 ± 0.3 subjects in the 90%, 50%, and 10% treatments, respectively ($P = 0.003$, $n = 30$, $df = 2.29$, $F = 7.137$), that provided at least their fair share of €2 per round. The rest were free riders; the extreme free rider per group provided only €1.4 ± 0.1, 0.9 ± 0.2, and 0.5 ± 0.2 per round in the 90%, 50%, and 10% treatments, respectively ($P = 0.0003$, $n = 30$, $df = 2,29$, $F = 11.137$).

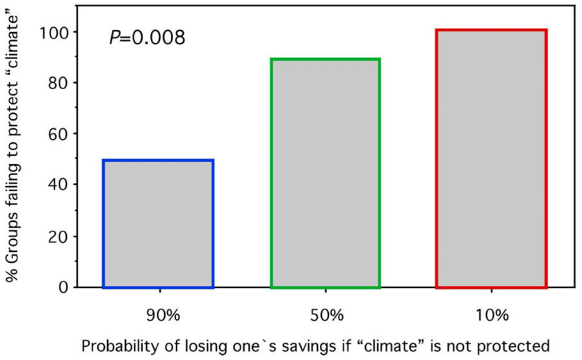

Fig. 3.1. Groups that either reach the target or fail. Displayed is the percentage of groups of six subjects each that fail to invest the target sum of at least €120 during 10 climate rounds, when they have a probability of 90%, 50%, or 10% of losing all their savings if the target sum is not reached. There are differences in not reaching the target among treatments ($P = 0.008$, $n = 30$, $df = 2,29$, $\chi^2 = 9.66$). The percentage of groups not reaching the target is significantly different from all groups reaching the target in each treatment (in each case: $n = 10$, $P = 0.0001$, binomial test).

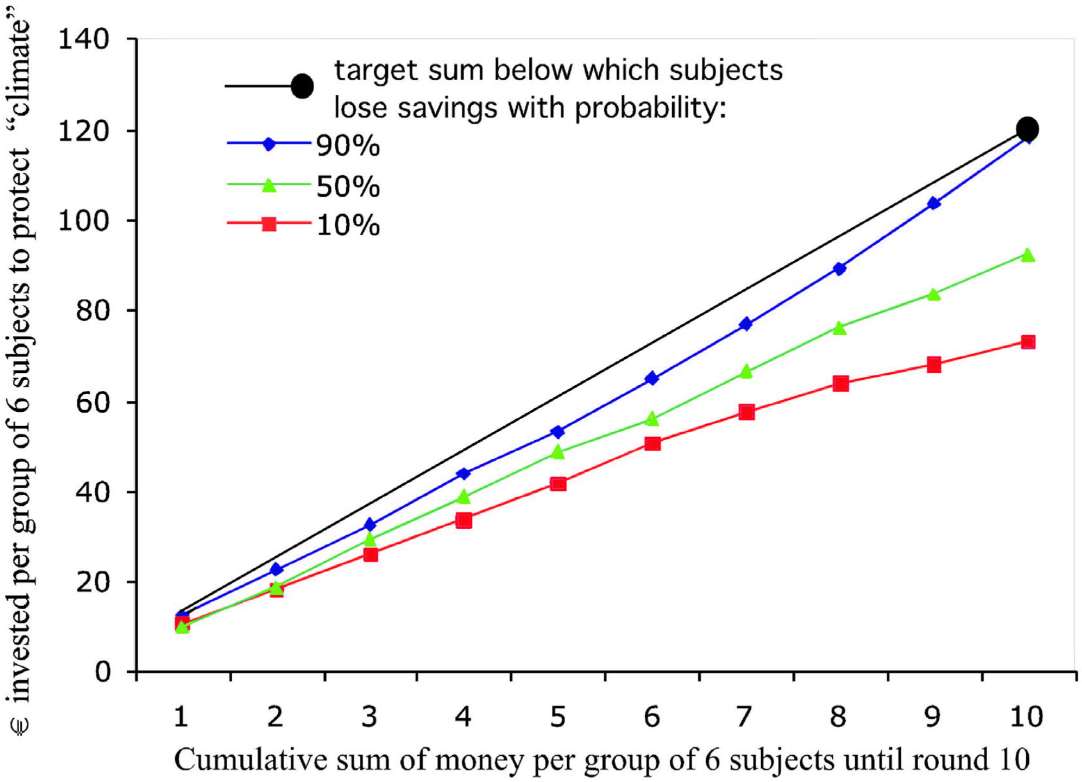

Fig. 3.2. Cumulative sum of money per group and round provided for the climate account. The target sum to be achieved after 10 rounds was €120; the treatments differed in the probability, i.e., 90%, 50%, and 10%, with which all subjects in a group lost their individual savings when the group did not supply the target sum for the climate account.

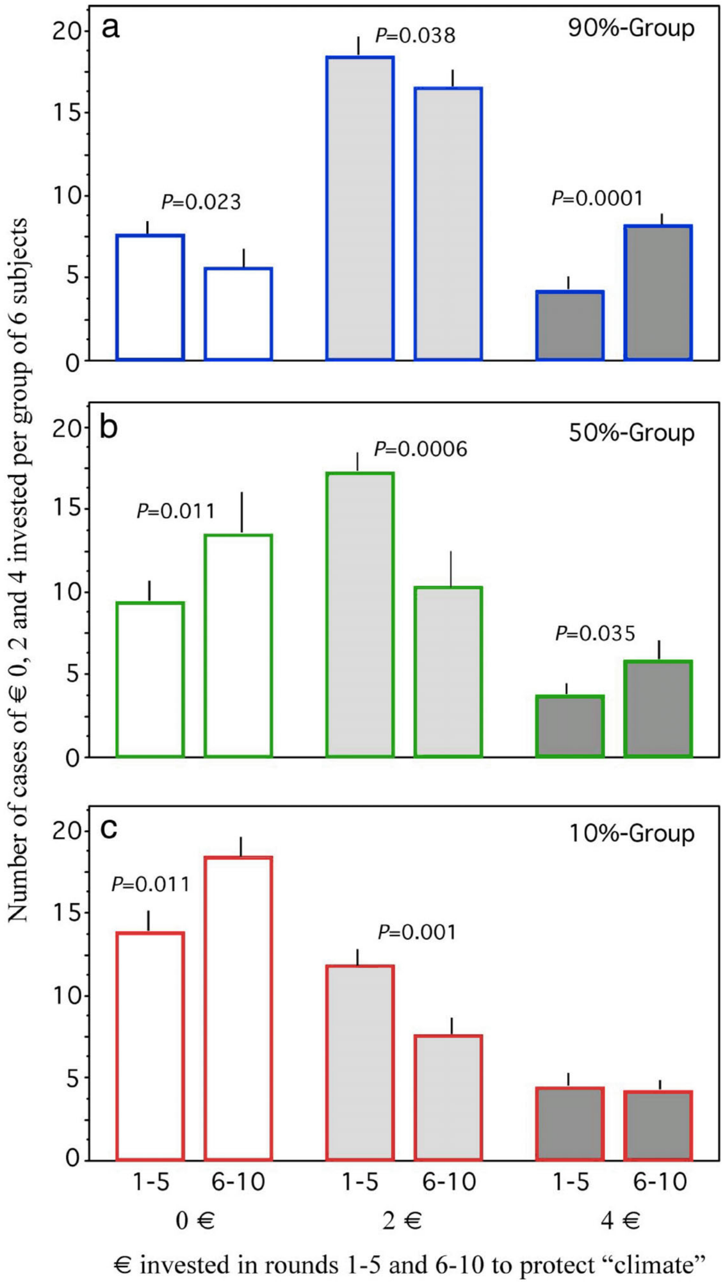

Fig. 3.3. Strategic behavior of subjects depending on the risk of losing all savings. Number of selfish acts, i.e., providing €0 (unfilled columns); fair-share acts, i.e., providing €2 (light-gray shading); and altruistic acts, i.e., providing €4 (dark-gray shading), per group of six subjects in the first (rounds 1–5, left in column pair) and second halves (rounds 6–10, right in column pair). The probability of losing all savings if the target sum is not reached was 90%, 50%, or 10%, for *a*, *b*, and *c*, respectively. See text for statistics.

Interestingly, the dynamics of selfish acts (providing €0), fair-share acts (providing €2), and altruistic acts (providing €4) differed among and within treatments (Fig. 3.3). In the 90% treatment, selfish acts decreased from the first to the second half of the session (P = 0.023, z = 2.739, paired t test, two-tailed), as did fair-share acts (P = 0.038, z = 2.433), but altruistic acts strongly increased during the session (P = 0.0001, z = -6.325). This is mirrored by the slightly U-shaped curve describing the cumulative approach of the target sum: It is almost reached after round 10 on average (Fig. 3.2). This shift of strategies during the 90% treatment also illustrates the importance of short-term, in contrast to long-term, interests in individual strategy decisions during game play. Conversely, in the 50% treatment, selfish acts increased (P = 0.011, z = -3.188), but fair-share acts strongly decreased (P = 0.0006, z = 5.161), and altruistic acts slightly increased (P = 0.035, z = -2.473) (Fig. 3.3). In the 50% treatment, altruists obviously tried to compensate free riding of others, but usually in vain. In the 10% treatment, selfish acts increased from the first to the second half of the session; from an already high level (*P* = 0.011, *z* = -3.196), fair-share acts decreased (*P* = 0.001, *z* = 4.776), and altruistic acts were maintained at a low level (*P* = 0.8, *z* = 0.259).

In the 90% treatment, failure to achieve the target sum sometimes occurred in an extremely irrational way. Occasionally in the last round, it became clear that all of the contributions to the cumulative sum would have been in vain unless a large proportion of the players made a maximal contribution. Nevertheless, an insufficient number of players made this contribution, and the group just failed to reach the target sum (see also Appendix C). Not contributing more at the end of the game, despite the risk of personal loss, may stem from a reluctance to reward behavior that is perceived as unfair.

When the risk of loss was no higher than the necessary average investment, our experimental groups generally failed to reach the target sum, which represented a threshold for preventing dangerous climate change. In contrast, groups with a high probability (90%) of losing their savings either succeeded in preventing simulated dangerous climate change or, half the time, came close to preventing it. Groups of six subjects may not represent the real climate game; our findings probably underrate the problems of the global challenge, because achieving cooperation is more difficult for larger than for smaller groups (Boyd & Richerson, 1988). Nevertheless, a proportion of the target could be achieved even in larger groups.

However, the number of countries with political representatives at climate summits or G8 summits is small compared with all individual players in the game. Perhaps our experimental setup may best be interpreted as representing such summits, with their smaller group size. Furthermore, in contrast to our experiments, climate or G8 summits are not anonymous, and it has been shown that anonymity is a strong impediment to preserving a common good (Milinski *et al.*, 2006). Despite its conceptual simplicity, our climate game thus holds promise for representing the social dilemma inherent in preventing dangerous climate change.

The strict cut-off of €120 for any common benefit to be realized may not be realistic for some hazards of climate change. However, many elements of climate change have "threshold" properties, consistent with our game design; adaptation to these abrupt changes is expected to be particularly difficult (Alley *et al.*, 2003). Unlike in our game, real climate change, which is already underway, will not affect everyone equally; some countries and regions might even profit from it (IPCC, 2007a). However, this is different when dangerous climate change occurs, which is expected to cause such disruption that in a globalized world, no one would remain unaffected by it (Schneider, 2001; Schellnhuber *et al.*, 2006; IPCC, 2007a).

The collective-risk social dilemma seems to be a frequent phenomenon of human social life. Preventing dangerous climate change is but one example, albeit important, of this type of social dilemma. We therefore tried to simulate the inherent problems of preventing dangerous climate change in the present experiment. There are three conclusions from our experiment: (i) To achieve an effective level of voluntary individual cooperation, people have to be convinced of the very high probability that individuals will be affected by dangerous climate change, should the set target for the reduction of global greenhouse gas emissions not be met by the set date (here, 50% of the present level by 2050) (Schneider, 2001; IPCC, 2007b). If they believe in a lower probability, climate protection may fail, as it did in our 50% and 10% treatments. The high motivation to invest in the collective good that we found even in the 10% treatment suggests that informing people is worth the effort. (ii) We cannot rely on people to always behave rationally (Thaler, 1988) (see also Appendix C). Climate protection programs that appeal to a human sense of fairness (Fehr & Schmidt, 1999), that is, all players contribute a "fair share" to the collective goal, are more likely to avoid irrational self-detrimental behavior. (iii) Because even our small experimental groups had difficulty preventing simulated dangerous climate change, the many players in the global game will certainly have more problems and may fail to prevent dangerous climate change. Climate or

G8 summits may well have increased probability of success because of their smaller group sizes. Also, incentives for investing in climate protection, other than the fear of suffering from dangerous climate change in the future, need to be offered, such as improved social reputation with its inherent benefits (Milinski *et al.*, 2006) or a combination of reputation and sanction institutions (Rockenbach & Milinski, 2006). Otherwise, the short-term advantages of free riding may fulfill Hardin's (1968) prediction that "freedom in the commons brings ruin to all."

Methods

We tested 180 undergraduates who participated in 30 groups of six subjects each in a computerized experiment (e.g., Milinski *et al.*, 2006; Rockenbach & Milinski, 2006) at the University of Cologne and the University of Bonn. Our goal was to see whether they would contribute their own money, which they had received as the initial endowment, to prevent simulated dangerous climate change in a collective-risk social dilemma. The subjects knew they would obtain their money after the game in a way that did not disclose their identity. They were separated by opaque partitions and each had a laptop computer, on which they received the instructions for the experiment (see Appendix C for original introduction pages) and with which they communicated their decisions to invest €0, €2, or €4 in the "climate account" to the main computer. After each of 10 rounds, the decisions of the six subjects were displayed on all computers simultaneously without any clue to a subject's identity. However, each subject's decision was listed in the same position after each round to allow individual strategies to be observed; thus, individual players were not anonymous within the game. Yet, they could not build a reputation from which to profit in another situation (e.g., Milinski *et al.*, 2006). Note that the cumulative sum of contributions was not displayed on the computer screen. Instead, the students were given pen and paper, and they were encouraged to take notes during the game.

The students knew that the total sum of money in the climate account, accumulated from all groups, would be used to publish a press advertisement on climate protection in a daily German newspaper simultaneously with the publication of the present study. However, they received the "little information" version from Milinski *et al.* (2006) to explain the climate account, so that we could expect very weak motivation to invest in publishing the advertisement *per se*.

Acknowledgements

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Chapter 4

Gossip as an Alternative for Direct Observation

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Abstract

Communication about social topics is abundant in human societies, and many functions have been attributed to such gossiping. One of these proposed functions is the management of reputations. Reputation by itself has been shown to have a strong influence on cooperation dynamics in games of indirect reciprocity, and this helps to explain the observed high level of cooperation in humans. Here, we designed a game to test a widespread assumption that gossip functions as a vector for the transmission of social information. This empirical study (with 14 groups of 9 students each) focuses on the composition of gossip, information transfer via gossip, and the behavior based on gossip information. We show that gossip has a strong influence on the resulting behavior even when participants have access to the original information (i.e., direct observation) as well as gossip about the same information. Thus, it is evident that gossip has a strong manipulative potential. Furthermore, gossip about cooperative individuals is more positive than gossip about uncooperative individuals, gossip comments transmit social information successfully, and cooperation levels are higher when people encounter positive compared with negative gossip.

Introduction

The use of language in human societies has been widely investigated, and several studies have shown that most conversations are about social information (Haviland, 1977; Emler, 1992; 1994; Dunbar *et al.*, 1997). Commonly, such communication about social topics, especially of third parties, is called gossip (Eder & Enke, 1991; Foster, 2004; Mesoudi *et al.*, 2006). Thus, gossip is regarded as an important phenomenon (Gluckman, 1963; Paine, 1967; Haviland, 1977; Levin & Arluke, 1987; Noon & Delbridge, 1993; Goodman & Ben-Ze'ev, 1994). In recent years, it has received increasing attention (Foster, 2004) from disciplines such as economics, sociolinguistics, psychology, anthropology and evolutionary biology.

The functions attributed to gossip are as diverse as the disciplines engaging in its study. Gluckman (1963) proposed gossip as a tool for social control to hold the community together by preserving its morals and values and controlling competing cliques and aspiring individuals. A study on Californian ranchers, for instance, supported this view (Ellickson, 1991). Through a series of interviews, Ellickson showed that, in this small-scale society, group norms were enforced by gossip. Later findings corroborated this hypothesis further by showing that self-serving, compared to group-serving, gossip is highly disapproved of (Wilson *et al.*, 2000), as well as by documenting the use of gossip to reward group beneficial behavior and deride violations of group norms (Kniffin & Wilson, 2005).

Baumeister *et al.* (2004) used questionnaires to show that gossip is a means of cultural learning. About two thirds of the participants stated that they learned something from gossip that was useful for their own lives. This finding suggests that gossip is a way of communicating rules and other formal information (Noon & Delbridge, 1993). Among the best-known views about gossip is Dunbar’s (1993; 1996; 2004) social grooming hypothesis, according to which language has evolved to cope with the increasing size of social groups resulting in an increasing number of social connections. Therein, language (and thus gossip) functions as a mechanism for social bonding by increasing the potential number of interaction partners. The effect of strengthening social bonds also was discussed by Noon and Delbridge (1993) in the context of business organization. They state that gossip can aid the coordination of organizations by maintaining social networks within that organization through periods when this coordination is not required for the operation of the company.

Other authors have stressed the use of gossip to promote self-interest and individual benefits (Paine, 1967; Emler, 1994; McAndrew & Milenkovic, 2002). It was found that participants were mainly interested in information about people of the same age and gender (McAndrew & Milenkovic, 2002). In addition, negative information about high-status people (e.g. professors) and positive information about friends were especially valuable and likely to be passed on to others. These findings support an evolutionary perspective about gossip, according to which people, among other things, try to enhance their own status by damaging the reputation and status of higher ranked members of the social group. Therein, gossip serves as an important means to gather reputation-relevant information about others (Emler, 1990; 2001) and, furthermore, to manage one’s own reputation by spreading positive gossip about oneself.

Reputation, however, has been shown to have an important effect on cooperation dynamics in human societies. Recently, it was found that reputation can solve the ”tragedy of the commons.” This social dilemma, described by Hardin (1968), refers to the fact that a public resource will be overused if everybody is free to do so. Milinski, Semmann and Krambeck (2002b) showed in an experiment with students that the opportunity to build up a reputation prevented a public good from being overused. This finding was applied to the global climate problem, where students could invest into climate protection anonymously in one treatment and while being observed in another (Milinski *et al.*, 2006). When the investment in a pool for climate protection had reputational consequences (by being observed by others), donations were substantially higher than in anonymous rounds.

These studies support the view that the presence of reputations has a strong effect on the maintenance of high-level cooperation. Reputation can be acquired through indirect reciprocity (Alexander, 1987). Accordingly, people who help others gain reputation and will thus be helped, whereas those who refuse to help will lose reputation. This dynamic leads to the evolution of cooperation if partners' reputations are known. Nowak and Sigmund (1998) showed by computer simulations of evolution that discriminating cooperators (i.e., individuals who base their decision of whether to help on the partner's reputation) eventually dominate the population. Since then, many authors have been investigating indirect reciprocity theoretically with computer generated agents competing for prevalence (Leimar & Hammerstein, 2001; Mohtashemi & Mui, 2003; Panchanathan & Boyd, 2003; Brandt & Sigmund, 2004; Ohtsuki & Iwasa, 2004; Brandt & Sigmund, 2005; Nowak & Sigmund, 2005; 2006), and it is accepted as a major mechanism leading to cooperation (Nowak, 2006).

Experimental studies confirmed that humans cooperate through indirect reciprocity (Wedekind & Milinski, 2000; Milinski *et al.*, 2001; Milinski *et al.*, 2002a; 2002b; Semmann *et al.*, 2005; Seinen & Schram, 2006). However, these dynamics rely on complete information. Computer agents base their decisions on scores reflecting past behavior of their artificial partners, and participants of experimental studies were presented with similar scores or directly with past decisions of their partners. Clearly, the acquisition of knowledge about others' reputation is important. Nowak and Sigmund (1998) suggested that only a fraction of the population may have the opportunity to directly observe an interaction of two specific individuals. Incorporating respective parameters, the outcome of their computer simulations depended on the probability with which a given individual witnessed another's decision, as well as on group size. The larger the group (and, therefore, the less likely interactions were to be observed), the lower the level of cooperation.

Although human societies tend to be large groups, they show a remarkably high level of cooperation. We assume that there is abundant information transfer to compensate for low levels of direct observation. And there is widespread belief among anthropologists and evolutionary biologists that gossip can serve this function (Enquist & Leimar, 1993; Dunbar *et al.*, 1997; Nowak & Sigmund, 1998; Panchanathan & Boyd, 2003; Nowak & Sigmund, 2005).

Here, we combine cooperation games based on reputation with the possibility to gossip about other group members. We examine whether gossip transfers information successfully in such a context and whether it can maintain cooperation by indirect reciprocity. In this study, gossip refers to short comments of participants about other players in the experimental setup. This gossip is based on direct observation, and we expect them to be positive when a cooperative player is observed and negative when an uncooperative player is observed. Furthermore, to be a functional vector of social information, gossip should not only reflect the quality of observed behavior (i.e., cooperation vs. defection), but also needs to be comprehensible. A given gossip intended by the author to be a positive statement also should be perceived as such by other members of the group. Therefore, we expect high correlation between one's own and other's ratings (positive or negative) of gossip comments. Furthermore, we test whether gossip has an effect in a situation where the respective group member also is directly observed. Especially, we focus on conflicting information between gossip and direct observations. In these situations, participants see, for instance, cooperative decisions of another player, but also can read a negative gossip about that person. Our prediction is that, in such cases, gossip is ignored.

Results

Students played a computer game in groups of nine (see Materials and Methods for details). They started with six 'observer' (i.e., with access to past decisions of the potential recipient) indirect reciprocity rounds (block A) to create a history of their cooperation behavior (Fig. 4.1). These were followed with gossip rounds in which participants wrote a short gossip about other players' decision behavior. These gossips were then the only information about the potential recipient in further indirect reciprocity rounds. Afterwards, the students again played six observer indirect reciprocity rounds (block B) and two gossip rounds as before. However, the following indirect reciprocity rounds showed a mixture of information (gossip and past decisions, or gossip and a comment about the author) (Fig. 4.2) to the active player. Finally, the participants played another three observer indirect reciprocity rounds (block C). At the end, each participant had to rate each gossip he or she encountered during the game on a scale from 1 (negative) to 7 (positive).

In all three blocks of observer indirect reciprocity rounds (A, B and C), the cooperation was on a high level (means in percent/SD, A: 66/12.6, B: 65/15.8, C: 68/17.9) and did not rise or fall significantly (paired *t* test, A and B: $n = 14$, $t = 0.1496$, $P = 0.882$; B and C: $n = 14$, $t = -0.354$, $P = 0.726$).

To analyze general giving behavior based on direct observation, decisions of those rounds in which individuals were provided with six former decisions of another player were taken into account (special rounds I). We grouped each individual player according to the number of YES decisions she saw in this round (i.e., 0,1,2,… or 6), and calculated a cooperation level for each group (i.e., the number of players who decided YES in this round divided by the total number of players in the group). The resulting data show a significant correlation between number of YESs observed and the resulting cooperation level as percentage ($y = 8.6x + 27.4$, $r^2 = 0.86$, $F(1,5) = 30.78$, $P < 0.005$) (Fig. 4.3). This result is to be expected in an indirect reciprocity game and shows that the design of the game allows for

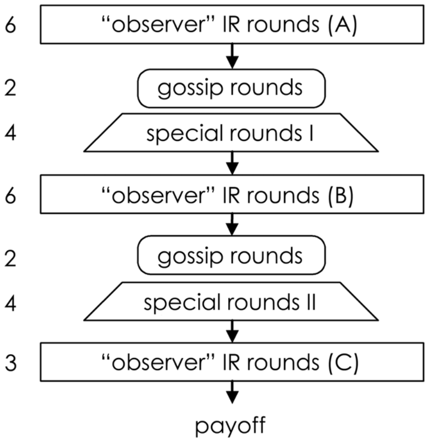

Fig. 4.1. Flow diagram of the game. The exact design of single rounds is described in the text. IR refers to indirect reciprocity. The special rounds I block consists of rounds in which participants had access to either six former decisions, two former decisions, or **gossip** information (based on either all six or two former decisions), respectively. Round types of the special rounds II block are explained in Fig. 4.2. Numbers on the side indicate number of rounds of a particular kind played.

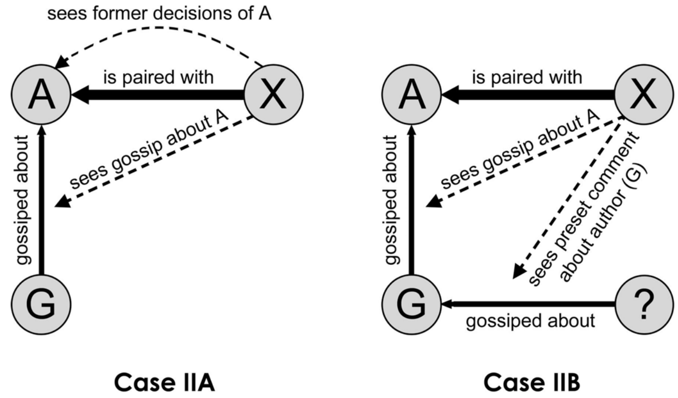

Fig. 4.2. Schematic overview of the two round types in the block special rounds II, cases IIA and IIB. The X represents the focus players, A is the potential recipient, and G is another player who gossiped about A earlier in the game (thin arrows). Thick arrows indicate pairing of players (X and A). Dotted arrows indicate the information X had access to before making his decision. Question mark represents another player who had gossiped about G. However, in these special rounds, the respective gossip was replaced with preset comments.

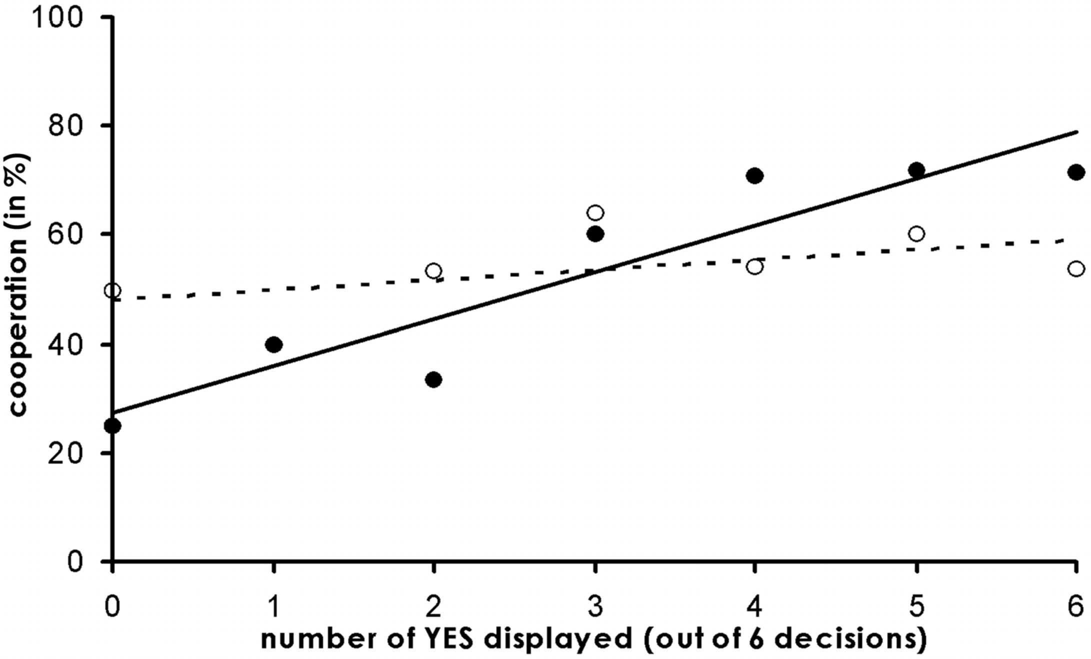

Fig. 4.3. Elicited cooperation dependent on observed cooperation. Filled circles and line show the percentage of players cooperating and regression line ($y = 8.6x + 27.4$, $r^2 = 0.86$, $F\ (1,5) = 30.78$, $P < 0.005$) dependent on how many YES decisions they saw out of six decisions of their partner. Open circles and dotted line ($y = 0.02x + 0.48$, $r^2 = 0.29$, $F\ (1,5) = 2.028$, $P = 0.21$) represent the resulting cooperation after the original information (*x* axis) was transmitted by gossip.

normal indirect reciprocity dynamics to work (Wedekind & Milinski, 2000).

The same analysis was done for rounds in which the players only had access to one third (i.e., two former decisions) of the same information. Would a third of all former decisions reliably mirror the actual decisions? The actual number of YES decisions (of six) was correlated with the number of YES decisions displayed (of two). There was a highly significant correlation ($y = 0.33x + 0.07$, $r^2 = 0.54$, $F\ (1,124) = 145$, $P \ll 0.0001$), which means the random selection of two decisions mirrored effectively the original behavior of the player. Consequently, as before, the players were again grouped dependent on the number of YES decisions provided, resulting in three groups (0, 1 or 2 times YES displayed). A correlation with the respective cooperation level, however, failed to be significant ($y = 9.7x + 54.3$, $r^2 = 0.95$, $F\ (1,1) = 18.56$, $P = 0.15$).

To analyze the use of gossip, we pooled the rounds in which players had access to six former decisions of another player and then had to write a gossip about that player. The pooled data showed that the more YES decisions were observed, the better the rating of the resulting gossip by its author ($y = 0.57x + 2.57$, $r^2 = 0.96$, $F\ (1,5) = 108.4$, $P < 0.0005$). This analysis, which was done on individual-level, was justified by the fact that individuals knew the ratings cannot be used in the game and the explicit statement that the ratings should not be given strategically. The same was found for those cases where gossip was only based on two former decisions ($y = 0.75x + 3.55$, $r^2 = 0.9975$, $F\ (1,1) = 394.1$, $P = 0.032$).

Furthermore, the author's rating of a gossip was significantly correlated with the subsequent rating of the same gossip by a player encountering it later in the game. This finding was true when gossip was based on 100% information (i.e., six former decisions) ($y = 0.27x + 2.98$, $r^2 = 0.10$, $F\ (1,124) = 13.15$, $P < 0.0005$), as well as when it was only based on

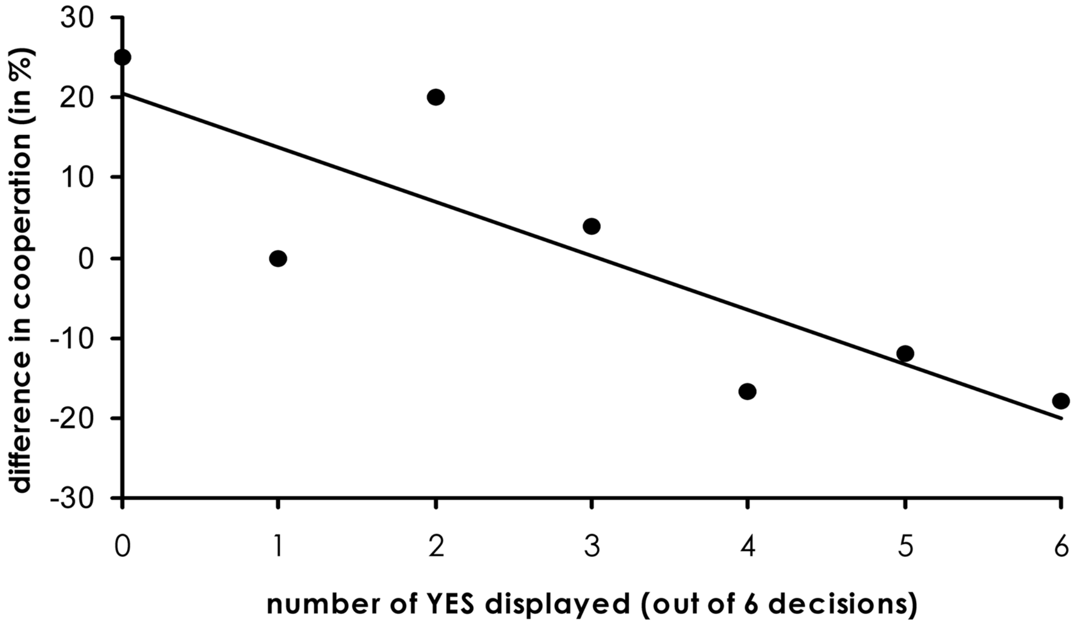

Fig. 4.4. Difference between cooperation based on direct observation and cooperation based on gossip. This graph shows the difference between the elicited cooperation level by gossip minus the cooperation level based on direct observation (i.e., expected cooperation). The *x* axis represents the actual number of YES decisions (of six) from the potential recipient. Positive values indicate that players cooperated more with gossip information than expected, and negative values document a lower cooperation level than expected ($y = -6.8x + 20.6$, $r^2 = 0.72$, F (1,5) = 12.74, $P = 0.016$).

33% information (i.e., two former decisions) ($y = 0.27x + 2.95$, $r^2 = 0.05$, F (1,124) = 7.162, $P < 0.01$).

While investigating participants' reactions to gossip, we grouped players according to their ratings of an encountered gossip. Thus, seven groups (gossip ratings from 1-7) were obtained; we calculated the cooperation level as before (number of players deciding YES divided by total number of players in the respective group). We found a significant correlation for both cases: gossip based on 100% information ($y = 5.7x + 33.2$, $r^2 = 0.61$, F (1,5) = 7.69, $P = 0.039$) and gossip based on 33% information ($y = 9.2x + 18.7$, $r^2 = 0.88$, F (1,5)= 35.86, $P < 0.005$).

To directly analyze the effect of gossip, we compared cooperation levels in rounds where the decision is based on direct observation with cooperation levels in rounds where the decision is only based on gossip (about the same information). Therefore, we used the same grouping of individuals as before (i.e., according to the number of YES decisions displayed) and correlated the resulting amount of cooperation with the resulting cooperation these groups received in rounds where the decision is based only on gossip. The resulting regression is not significant ($y = 0.02x + 0.48$, $r^2 = 0.29$, F (1,5) = 2.028, $P = 0.21$) (Fig. 4.3). Fig. 4.3 shows a larger difference between the two regression lines in the extremes than in an intermediate cooperation level. This finding suggests that the transfer by gossip processes the original information in a way that positive and negative gossip are qualified as less extreme. To investigate this effect, the resulting cooperation (after information transfer by gossip) is compared with the expected cooperation (taken from decisions of the same players based on direct observation). The analysis documents a significant correlation ($y = -6.8x + 20.6$, $r^2 = 0.72$, F (1,5) = 12.74, $P = 0.016$) (Fig. 4.4). If the observed cooperation is very low (0 on the *x*

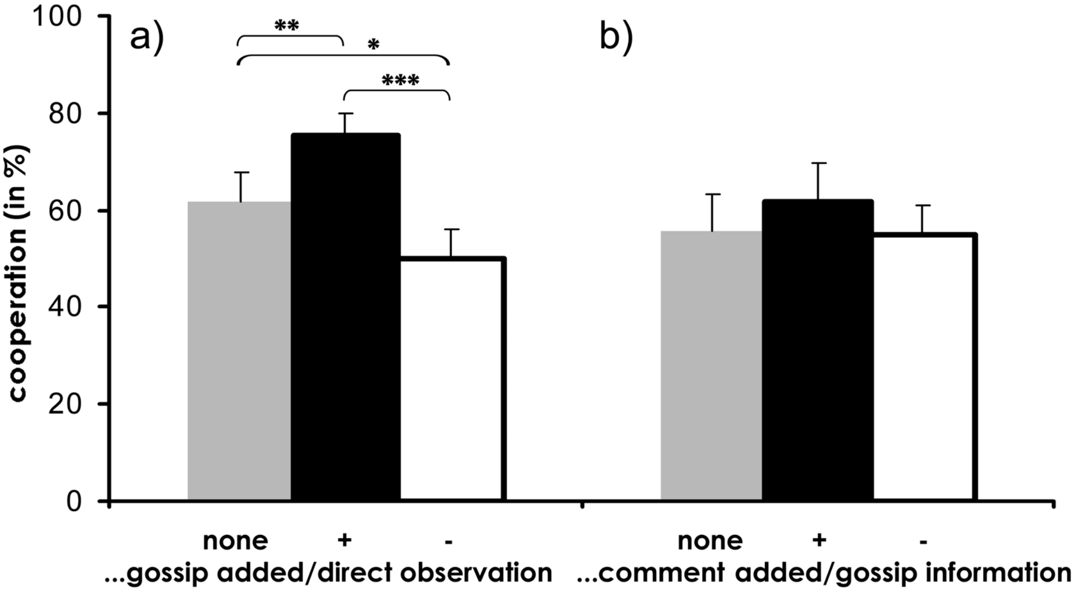

Fig. 4.5. Cooperation levels of rounds with added preset gossip/comments. (a) Bars represent mean cooperation levels (+ SE) of rounds in which players were provided with six former decisions (direct observation) of another player without (none, grey bar) or with preset positive (+, dark bar) or negative (-, light bar) gossip pretendedly being about the same decisions (case IIA in Fig. 4.1). (b) Mean cooperation levels (+ SE) of rounds in which players were provided with gossip about their potential recipient and without (none, grey bar) or with a preset positive (+, dark bar) or negative (-, light bar) comment pretendedly being about the author of the gossip (case IIB in Fig. 4.1). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

axis in Fig. 4.4), the elicited cooperation after information transfer by gossip is higher than expected and vice versa for high observed cooperation levels (e.g., 6 on the *x* axis in Fig. 4.4).

Last, we analyzed preset gossip and its effect in rounds where participants had access to direct information and preset gossip about their partner (case IIA in Fig. 4.2). The preset gossip intended to be positive was rated significantly higher (mean 6.0 +/- SE 0.12) than preset gossip intended to be negative (mean 2.6 +/- SE 0.17; paired *t* test, t (13) = 12.58, $P \ll 0.0001$). Group-level analysis of the cooperation behavior in these two rounds (direct observation with positive gossip/direct observation with negative gossip) showed a strong effect of the added gossip statement despite access to direct information. Comparing the cooperation in the round with positive added gossip (mean 75%) with the cooperation in the case where negative gossip was added (mean 50%) yielded a significant difference (paired *t* test, t (13) = 4.85, $P < 0.0005$) (Fig. 4.5a). Furthermore, with reference to the cooperation level of the respective round without any added gossip information (mean 62%) there was a significant increase in cooperation in the positive gossip round (paired *t* test, t (13) = 3.64, $P < 0.005$) and a decrease in the negative gossip round (paired *t* test, t (13) = 2.27, $P = 0.04$) (Fig. 4.5a).

The situation presents itself differently, however, if we look at rounds in which students were provided with a gossip statement about a potential recipient and with a preset comment about the author of this gossip statement (case IIB in Fig. 4.2). Although our preset comments were again significantly different from each other (mean rating of positive comment, 6.0 +/- SE. 0.18; mean rating of negative comment, 2.4 +/- SE 0.16; paired *t* test, t (13) = 12.53, $P \ll 0.0001$), there was no significant effect on the cooperation level in these two rounds (paired *t* test, t (13) = 1.02, $P = 0.33$) (Fig. 4.5b). Consequently, no difference in cooperation levels was found in comparison to the respective round without any added comment (mean

Table 4.1. Usage, perception, and influence of gossip in the game.

Effects	Based on … past decisions six	two
Direct		
Resulting cooperation ~ observed cooperation* (pos. corr.)	**$P < 0.005$**	$P = 0.15$
Gossip rating/quality[†] ~ observed cooperation (pos. corr.)	**$P < 0.0005$**	**$P = 0.032$**
Subsequent gossip rating ~ original rating (pos. corr.)	**$P < 0.0005$**	**$P < 0.01$**
Resulting cooperation ~ rating of observed gossip[‡] (pos. corr.)	**$P = 0.039$**	**$P < 0.005$**
Indirect		
Resulting cooperation after information transmission by gossip ~ resulting cooperation based on direct information (pos. corr.)	$P = 0.21$	
Difference between cooperation based on direct information and based on gossip: dampening effect through gossip (neg. corr.)	**$P = 0.016$**	
Gossip as supplement to direct information[§] (*t* test)	**$P < 0.0005$**	
Information about the gossip author[¶] (*t* test)	$P = 0.33$	

Significant results are in bold. pos. corr., positive correlation; neg. corr., negative correlation.
*Information the player had access to when making his decision (i.e., the number of YES decisions displayed).
[†] High quality meaning a high rating (on a scale from 1-7).
‡This rating is equivalent to the subsequent gossip rating.
[§] See case IIA in *Materials and Methods* and Fig. 4.2.

cooperation in no preset comment, 56%; positive preset comment vs. no added comment, *t* (13) = 1.33, *P* = 0.21; negative preset comment vs. no added comment, *t* (13) = 0.23, *P* = 0.82) (Fig. 4.5b). To further test the absence of an effect, we conducted a power analysis for these rounds assuming the same effect size as found in the rounds combining preset comment and direct observation. The calculated power for a sample size of 14 and an effect size of 25.40% (+/- SD 19.70%) of a paired *t* test is 0.9935. This indicates that our sample size was large enough to detect a similarly strong effect.

In summary, third-party observers of social interactions gave truthful gossip about the potential donor of such an interaction. This written information was perceived by others as intended and, thus, transmitted the original information successfully. Furthermore, people acted according to the quality of a given gossip statement. However, when directly compared, the expected and observed cooperation after information transfer by gossip differed. Further analysis documented a dampening effect of this transmission in a sense that originally negative behavior is not acted on as negatively and vice versa for positive behavior. In addition, we showed that gossip strongly influenced a player's behavior even if she had access to real information about her game partner by direct observation. This was not the case, however, when the gossip statement was a second-order comment (i.e., a comment about the gossip author).

Discussion

In our experiment we followed the sequence of gossip composition, gossip transfer, and resulting behavior (these direct effects are summarized in Table 4.1). For gossip to function, people first need to trustfully describe other people's behavior. These statements should be unambiguous and generally comprehensible. People encountering these comments should assign them the quality (positive or negative) intended by the author. Last, hearing (or, as in our experiment, reading) such gossip, people should act accordingly, which means that they would need to cooperate with people about whom they heard positive gossip and defect otherwise. The participants of our study acted as expected. The higher the cooperation of a player they had observed, the more positive was the gossip they wrote. This finding indicates that gossip is used by a third-party observer to truthfully transmit information to a potential recipient. Apparently, the author had the intention to spread this information in the population despite not having any immediate (or monetary) benefit from it. Obviously, this outcome would be expected if the gossiper would risk his reputation by gossiping dishonestly. Concerning transmission of gossip information, we found that positive comments (as rated by the authors) were rated higher by other players than negative comments. Thus, people believe in gossip, and gossip, in turn, is an efficient vector for information transfer. Last, people reading positive gossip about their partner were more likely to cooperate than those reading negative gossip. Accordingly, language provides individuals with access to information about others without the need for direct observation. As speculated by many proponents of indirect reciprocity theory (Nowak & Sigmund, 1998; Mohtashemi & Mui, 2003; Panchanathan & Boyd, 2003), we found that gossip is a possible means of information transmission among individuals.

A further test to see whether gossip serves as a means of transmission of social information about other group members is the comparison of behavior based on direct observation, with the respective behavior based on gossip information (Table 4.1). Here we found that transmission by gossip had a dampening effect on the cooperation levels compared with acting on direct observation. The more extreme a gossip was, the less impact it had on the reader (Table 4.1). This finding was apparent despite successful intermediate steps, as explained earlier, which could be due to the fact that people tend to question extreme gossip statements more than less extreme ones. Therefore, we would expect the documented strong effect (changes of 18-25% in the extremes) (Fig. 4.4) of decreased cooperation based on gossip, compared with direct observation of a cooperative individual, and, respectively, an increase of cooperation by gossip in the group observing very uncooperative individuals.

In the present study, individuals had access to only one gossip statement about another person. People may sometimes have access to gossip about the same person from different sources. Such access to multiple sources could reduce the dampening effect. If individuals hear several gossip comments about another person, the mean quality of these gossips (very bad, bad, neutral, good, very good etc.) might reflect the original behavior much more precisely than a single comment. In line with this assumption is a recent finding of Hess and Hagen (2006), who studied the psychology of gossip. In their study, participants had to scale the believability of given gossip in a (written) scenario about their working environment. According to the experimental condition, the participants read the same information from up to four sources. Hess and Hagen found an increase in believability with an increasing number of sources.

Surprisingly, the hypothesis that gossip has no effect if an individual has access to direct information (i.e., observation) clearly has to be rejected (Table 4.1); 44% of all participants changed their decision in the respective rounds (case IIA in Fig. 4.2). Of these players, 79% said YES in the round with added positive gossip and NO in the round with negative gossip, although they were informed that the gossip was precisely about the direct information they saw. Thus, gossip has a strong manipulative potential that could be used by cheaters to change the reputation of others or even change their own. This finding suggests that humans are used to base their decisions on gossip, rumors, or other spoken information. Such a strategy could be successful in an environment where ample gossip/information focusing on friends or other people known to the individual is available and where direct observation is potentially less common than indirect information about others. In such a world, individuals gather a lot of information indirectly by gossip from different sources. The resulting picture of any person with whom the individual is in social contact would be much more refined than the picture based on the small amount of direct observation of these people.

In accordance with a previous series of experiments (Milinski *et al.*, 2001), second-order information (here further information about the source of information) had no significant impact on an individual's behavior. More precisely, it did not matter whether there was additional information about the author of given gossip available (case IIB in Fig. 4.2 and Table 4.1). A power analysis showed that our sample size was large enough to potentially detect a similarly strong effect as found in rounds with first-order direct and gossip information. Thus, there is strong evidence that people do not take into account whether the source of information is a cooperative player. First, this could be due to the fact that second-order information might be too demanding for the working memory anyway (Milinski & Wedekind, 1998). Second, people do not think that cooperative players are more honest in the role of gossipers. This notion supports the view that a person's acts are taken into account irrespective of whether the person is in good or bad standing (Milinski *et al.*, 2001).

A limitation of this study is the fact that participants could not interact further with gossip authors. In natural situations, the possibility to ask for more details about the gossip target might result in a more detailed picture of that individual than a single statement could ever give. However, Eder and Enke (1991) found that evaluative statements are rarely challenged. Thus, we would not expect a change in the essence of this information (i.e., from negative to positive). If an individual hears something bad about another person, talking about the gossip with the gossipmonger would not change the content into something good about the other person. However, it might adjust the degree from very negative to slightly negative.

Our results suggest that it may be worthwhile to study the manipulative potential of gossip in more detail in the future. Controlling free riders is a major problem in theories explaining the evolution of human cooperation, and Enquist and Leimar (1993) found that gossip counteracts free riding in their mathematical model. However, if cheaters are successful in altering their reputation in the population by gossiping, this result might be difficult to achieve. The question remains how individuals detect liars.

Materials and Methods

This experiment was conducted at the Universities of Kiel and Münster, Germany, as well as Vienna, Austria, where 126 first-semester biology students played a computer-based game in 14 groups of nine subjects each. The sessions took place from November 2006 to January 2007. Each participant was seated in front of an individual laptop between opaque partitions. All nine experimental computers were connected to a server. Each computer, including the server, ran the experimental program under Windows XP and recorded each decision of the respective player. The server recorded the entire game (i.e., all decisions of all players and the contents of each individual screen). Before the start of the game a short oral introduction guaranteed the following points: Participants knew how to operate the computer and knew about their total anonymity during and after the game (in particular, they will be provided with their earnings in a way that would not reveal their identity).

At the beginning of the game, introduction pages explained the rules of the game (see Appendix E for original pages). These pages were not turned before each participant clicked on an OK button. The following information was given to the students. They were endowed with starting money of 10 Euro each. Participants were anonymous and provided with a pseudonym that was only used for the payoff at the end of the game. To ensure anonymity, they were not allowed to talk to each other or draw attention towards themselves. For each round, they were assigned a partner by the computer.

The game consisted of 27 rounds (see Fig. 4.1). In the first six rounds, they had to decide whether to give (click YES) or not to give (click NO) a preset amount of their money (donor, -1.25 Euro; recipient, +2.00 Euro) to their game partner. To facilitate the decision, they were provided with all former decisions of the potential receiver. During these first rounds, each participant was paired with two other players and interacted with each 3 times alternately (without explicitly knowing).

After the first introduction and the first six indirect reciprocity rounds, the students played two gossip rounds with the same partner (rounds 7 and 8). In such rounds, they saw all six or one third (i.e., two in a random sequence) of the former decisions of another anonymous participant and had to give any comment they wanted (within a 50-character limit). They were informed that this comment could be the only information a player might have in the following rounds of the game on which to base his YES/NO decision. The sequence of these two different kinds of gossip rounds was alternated across players to control for any sequence effects.

After these gossip rounds, a first block of four connected rounds was played (rounds 9 to 12; special rounds I in Fig. 4.1). In these four rounds, players saw either all six or one third (i.e., two in a random sequence) of the former decisions of another player or they saw gossip about this player (based on either all six or two former rounds).

This block was followed by six more observer indirect reciprocity rounds (rounds 13-18). Here the participants could observe all past YES/NO decisions of their potential recipient, except the decisions from the first six rounds at the beginning of the game. Thus, they have information about their game partners from just after the gossip rounds (starting with round 9).

As before, these observer indirect reciprocity rounds were followed by another two gossip rounds with the same partner (one with access to six past decisions and the other with access to two past decisions). The decisions shown to the participants were drawn from rounds 13 to 18 (i.e., the second block of six observer indirect reciprocity rounds).

In the rounds 21 to 24, a second block of four connected rounds followed. In these special rounds II (see Fig. 4.1 and 4.2), preset statements were used as supplement information. These statements were taken from preliminary sessions and were as follows: “ein richtig toller typ” (“a really cool guy”; positive), “übler geizkragen” (“nasty miser”; negative), “spendabler spieler!” (“generous player!”; positive) and “ein sehr unkooperativer spieler” („a very uncooperative player“; negative). (Note that the missing capitalization in the original German statements was done purposively to mimic comments typed by students during the game.)

In case IIA, such preset gossips were paired with six former real decisions of another player (Fig. 4.2) to investigate whether people would still pay attention to gossip information despite having access to the original and real information. Each student played one round with a positive preset gossip and another round with negative preset gossip, in addition to identical direct information. It was explicitly stated that the gossip was about the information they saw.

In case IIB, preset statements functioned as a comment about the author of gossip concerning the actual game partner. The focus player was paired with a player A and saw gossip about that player A. In addition, the focus player was shown one of the preset comments, and it was explained that this is a comment about the author of the gossip about A (Fig. 4.2). This round served to investigate whether participants paid attention to whether the gossip they read (i.e., gossip about A) was written by a “nice” (positive preset comment) or “bad” (negative preset comment) player.

In both blocks (special rounds I and II), the different types of round were ordered randomly for each player to control for any sequence effect. Moreover, to exclude upstream reciprocity (Nowak & Sigmund, 2005), that is, any effect based on whether participants earned money in previous rounds, the payoff from special rounds I and II was shown only after the entire blocks. Participants were informed about all of these round types (gossip rounds, special rounds I, special rounds II) before the respective rounds by further introduction pages.

The monetary part of the game was ended with three observer indirect reciprocity rounds. Here participants had access to past decisions starting with round 21 to ensure the previous decisions (rounds 21-24) still had reputational consequences. After that the game was over, but participants were asked to rate every comment they had given themselves, as well as those they had encountered. Each student had to assign a number between 1 (very negative) and 7 (very positive) to 10 different comments. An introduction page defining the scale was shown beforehand. Thus, each of the four preset gossip statements was rated by every student, and two comments of each player were rated twice: by the author as well as by another player.

Finally, all students were paid off with their exact earnings in Euro after the game (mean payoff was 21.05 Euro). To ascertain anonymity, envelopes with the players' pseudonyms were used as described in Semmann *et al.* (2005).

To exclude direct reciprocity during the entire game, pairings were designed in a way that no potential donor of A was a former potential recipient of A. In addition, players who already played indirect reciprocity rounds with each other (in the role of donor or recipient) never gossiped about the other; thus, the gossiper was always a third-party observer. Furthermore, our design did not permit any standing strategy in the game (Sugden, 1986; Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001). There was no information provided to decide whether a single decision was justified or unjustified.

All data were analyzed using an *R* statistical package (version 2.3.1) for Windows XP. If not stated otherwise, data were tested for normality using a Shapiro-Wilk test to justify *t* tests, which were then conducted two-sidedly. Furthermore, the analyses were done on group level, except for those cases where individual-level analyses are explicitly justified in the text.

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Chapter 5

Multiple Gossip Statements, Reputation, and Trust

(Submitted for publication as: Sommerfeld RD, Krambeck H-J and Milinski M. Multiple Gossip Statements and Their Effect on Reputation and Trustworthiness.)

Abstract

Empirical and theoretical evidence from various disciplines indicate that reputation, reputation building, and trust are important for human cooperation, social behaviour and economic progress. Recently it has been shown that reputation gained in games of indirect reciprocity can be transmitted by gossip. But it has also been shown that gossiping has a strong manipulative potential. We propose that this manipulative potential is alleviated by the abundance of gossip. Multiple gossip statements give a better picture of the actual behaviour of a person and, thus, inaccurate or fake gossip has little power as long as it is in the minority. In addition, we investigate the supposedly strong connection between reciprocity, reputation and trust. The results of this experimental study (with eleven groups of twelve students each) document that gossip quantity helps to direct cooperation towards cooperators. Moreover, reciprocity, trust, and reputations transferred via gossip are positively correlated. This interrelation might have helped to reach the high levels of cooperation that can be observed in humans.

Introduction

Reputation and reputation building is important for the evolution of human cooperative behaviour. It seems to explain high levels of cooperation between anonymous partners in one-shot interactions in a global market (e.g., modern e-commerce systems such as eBay and Amazon, see Resnick *et al.*, 2000), and cooperation between non-relatives in general (Nowak & Sigmund, 2005). Function and effect of reputation building have been studied by several researchers from various disciplines (Alexander, 1987; Emler, 1990; Kreps, 1990; Pollock & Dugatkin, 1992; Nowak & Sigmund, 1998; Ostrom, 1998; Wedekind & Milinski, 2000; Leimar & Hammerstein, 2001; Milinski *et al.*, 2002b; Fehr & Fischbacher, 2003; Semmann *et al.*, 2004; Bolton *et al.*, 2005; Seinen & Schram, 2006; Röhl *et al.*, 2007). The development of a reputation is important for the process of indirect reciprocity (Alexander, 1987; Nowak & Sigmund, 2005; Brandt *et al.*, 2007). In principle, indirect reciprocity occurs when people have the possibility to decide whether to help others, and thereby base their decision on (social) information about these people, i.e. their reputation. Here, it is important to distinguish indirect reciprocity from direct reciprocity (Trivers, 1971), where the helped individual could directly reciprocate and subsequently help the helper; this situation is excluded in the indirect reciprocity framework (but see Roberts, 2008). Indirect reciprocity can therefore be summarised by the phrase “I help you and somebody else helps me” (Nowak & Sigmund, 2005) if people know my reputation.

In line with theory (Nowak & Sigmund, 1998), such an opportunity to build up reputation has been shown to increase cooperative behaviour in experimental games (Wedekind & Milinski, 2000; Milinski *et al.*, 2002b; Semmann *et al.*, 2004; Milinski *et al.*, 2006; Seinen & Schram, 2006). However, in these experimental studies, people were always directly informed about other people’s behaviour, which resembles a situation in which people would first directly observe others and then decide whether to help or not. Furthermore, people had access to complete information about their partners – they saw all previous decisions of their partners about helping others or not. Thus, previous studies included direct observation and complete information. Yet, the natural situation is different: We cannot observe everybody all the time, especially not those people we possibly meet and interact with in the future.

To overcome this lack of information, especially in large groups, it has been argued that language and gossip might have evolved as a substitute for direct observation (Enquist & Leimar, 1993; Dunbar, 1996; Nowak & Sigmund, 1998; Mohtashemi & Mui, 2003; Panchanathan & Boyd, 2003; Nowak & Sigmund, 2005). As gossip and gossiping is regarded as one of the most important social and cultural phenomena (Gluckman, 1963; Paine, 1967; Fine & Rosnow, 1978; Noon & Delbridge, 1993; Emler, 2001), it has been investigated for decades (e.g., Cox, 1970; Haviland, 1977; Suls, 1977; Levin & Arluke, 1987; Eder & Enke, 1991; Ellickson, 1991; Goodman & Ben-Ze'ev, 1994; Wilson *et al.*, 2000; McAndrew & Milenkovic, 2002; Baumeister *et al.*, 2004; Foster, 2004; Bosson *et al.*, 2006), but only recently it has been shown that gossip can serve as a substitute for direct observation in the context of indirect reciprocity (Sommerfeld *et al.*, 2007).

In an experimental game in which students could write a short comment – i.e., gossip – about other people’s behaviour, Sommerfeld *et al.* (2007) showed that gossip reflected the people’s cooperative behaviour and transferred this information to other members of the group who, in turn, relied on this information, although only marginally when gossip described extremes. However, in a situation where everybody would totally rely on single gossip statements it would be evolutionary favourable to cheat and lie about one’s own behaviour or the behaviour of close relatives and, thus, manipulate reputations. Lying defectors would not bear the costs of cooperation, but gain the benefit from those that would otherwise help only cooperators; they would spread in the population and cooperation could not be maintained (Nakamaru & Kawata, 2004). Consequently, for the evolution of cooperation by indirect reciprocity it is important that a partners' reputation is reliably known (Nowak & Sigmund, 1998; Roberts, 2008), and that cheaters can be effectively detected (Nakamaru & Kawata, 2004; see also Hess & Hagen, 2006).

We suggest that gossip can help to meet these prerequisites by its quantity. A single gossip statement may only be a poor indicator of a person's reputation. However, in our daily life we rarely know just one gossip statement about another person. We know plenty of gossip, and it has already been shown that repetition of specific gossip increases its believability (Hess & Hagen, 2006). Yet, such a repetition would only give a more reliable picture of a single situation, but not a complete picture of the person concerned. Thus, we propose that multiple gossip statements approximate the complete picture much better than single observations or comments do. In order to investigate this experimentally, we designed a computer-based game in which participants encounter one or several gossip statements about other people's cooperative behaviour and have then to decide whether to cooperate or not. It has already been shown that a single gossip statement does not lead to the same behaviour as direct observation does (Sommerfeld *et al.*, 2007). Our expectation is that the participants' response upon reading several statements is closer to the response they show with complete information (i.e., after direct observation) than the response upon reading a single statement. Furthermore, the game includes predefined situations concerning gossip quantity and valence in order to measure the effect of single statements of opposing valence. Thereby, we intend to simulate situations in which, for instance, a person tells nice stories about a close friend, but in which others report the friend's real behaviour and gossip negatively about him. We also include the contrary situation of little negative and plenty of positive gossip.

At last, we extend our experimental design to incorporate another, highly connected social phenomenon: trust – a concept that seems to contribute substantially to the success of human societies and their economic progress (Knack & Keefer, 1997; Zak & Knack, 2001). According to a model proposed by Ostrom (1998), trust, reciprocity and reputation are linked by a positive feedback mechanism, and Dasgupta (1999) points out that 'trust is based on reputation, and reputation is acquired on the basis of observed behaviour over time'. Trust has been a topic in economic research for some time (Gambetta, 1988; Berg *et al.*, 1995; Güth *et al.*, 1997; McCabe & Smith, 2000; McCabe *et al.*, 2003; Krueger *et al.*, 2007; Rigdon *et al.*, 2007), as well as the connection between trust and reputation (Lahno, 1995; Diekmann & Przepiorka, 2005; King-Casas *et al.*, 2005), but only recently the connection between trust, reputation and reciprocity has been investigated (Bravo & Tamburino, 2008). Using evolutionary modelling, Bravo and Tamburino have shown that trust and reciprocity – and therefore cooperation – are indeed dependent on reputation building and the spread of information about others' reputation in the population.

In order to investigate this connection experimentally, we combine an indirect reciprocity game with the well established trust game designed by Berg *et al.* (1995). Thereby, we aim to investigate the effect of reputation transferred via gossip in the trust game, as well as the connection between cooperative behaviour, trustworthiness and trustfulness.

Materials and Methods

We conducted this experiment in November and December 2007 at the Universities of Kiel, Germany, and Vienna, Austria, where we recruited 132 first semester Biology students. The volunteering students were randomly divided in 11 groups of 12 people each. Each participant of a group played the experimental game on an individual computer that was connected to a server. Opaque partitions prevented participants to watch one another. Before each experimental session, the participants were orally informed about how to operate the computers, about their total anonymity concerning their decisions within the game and the payment of their earnings at the end, and that they play with real money (Euro) in the game (see also Sommerfeld *et al.*, 2007).

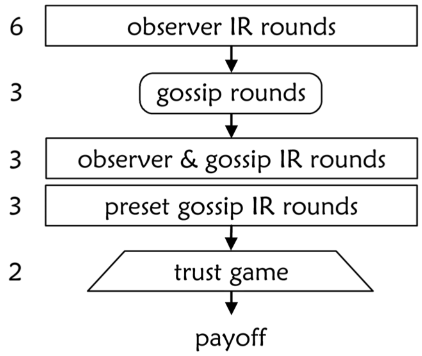

Fig. 5.1. Flow diagram of the game. 'IR' refers to indirect reciprocity. Numbers on the left side indicate number of rounds of each particular type played. Ratings of gossip valence took place between the trust game and the payoff. A detailed description of single rounds is found in the text.

The experimental game consisted of 17 rounds in which participants encountered different game situations. Each new game situation was introduced by a series of text pages explaining details and rules. In addition, the first introduction pages informed the participants about the following details: (i) each participant was endowed with starting money of 10 Euro each, (ii) each participant was provided with a pseudonym in order to preserve their anonymity during the final payment of their earnings, and (iii) they must neither talk during the game nor draw attention towards them in any way.

Three major game situations were encountered during the game: indirect reciprocity rounds, gossip rounds and a single trust game at the end. In indirect reciprocity rounds, participants acted as potential donors and were asked whether they wanted to give 1.25 Euro to another player, their receiver. Upon clicking YES, the donor paid 1.25 Euro from his account and the other player received 2.00 Euro (the additional 0.75 Euro were paid by the experimenters). If the answer was NO, no money was exchanged. During the game, indirect reciprocity rounds varied in the information provided about the potential receiver. In the first round, potential donors had no additional information about their potential receiver; in rounds 2 to 6, the donors were informed about all previous decisions of their receivers. This type of rounds is called observer indirect reciprocity rounds (Fig. 5.1). Further types of indirect reciprocity rounds were encountered later in the game and are explained below.

The second major game situation was encountered in rounds 7 to 9: gossip rounds (Fig. 5.1). Here, each participant was provided with all previous decisions of another participant and was asked to write a short (50 characters) comment about that person.

After these three gossip rounds, participants played again indirect reciprocity rounds (rounds 10 to 12; Fig. 5.1) with the following information about their potential receiver: either (i) all previous YES/NO decisions of this player from rounds 1 to 6, (ii) a single gossip statement about this player written by another participant, or (iii) a set of three gossip statements about this player written by three different participants. To control for sequence effects, each participant played these three different situations in rounds 10 to 12 in random sequence. Furthermore, without them knowing, participants were paired with the same receiver throughout these three rounds.

Rounds 13 to 15 consisted again of indirect reciprocity rounds providing preset gossip information about the potential receiver (Fig. 5.1). In these rounds, each participant encountered three of five possible combinations of preset gossip statements: (i) three negative and one positive statement (hereafter referred to as nnnp), (ii) two negative and one positive statement (nnp), (iii) one negative and one positive statement (np), (iv) one negative and two positive statements (npp), or (v) one negative and three positive statements (nppp). The sequence of the three combinations encountered by a single participant was randomised, as was the sequence of the individual gossip statements displayed in each round. The preset gossip statements were based on original student gossip from a previous study (Sommerfeld *et al.*, 2007) and randomly selected by the computer programme (see Appendix E for further details).

In the last two rounds (round 16 and 17; Fig. 5.1), participants played a trust game (Berg *et al.*, 1995). In our version of this game, a sender is endowed with 6.00 Euro and is asked how much (if any) he wants to give to a recipient. The money sent in this way is tripled before it reaches the recipient. Subsequently, the recipient is asked how much (if any) he wants to return to the sender; the rest he keeps for himself. The returned amount of money reaches the sender unchanged. Because the recipient can only lose money by returning something to the sender, he is rationally expected to return nothing. Consequently, by anticipating this choice, a rational sender is expected to send nothing to the recipient (Berg *et al.*, 1995).

In our experimental game, participants played the trust game first in the role of a recipient (round 16). Here, they were asked to answer the question of how much they would return for each possible sender decision (i.e., if the sender gives 0, 1, 2, 3, 4, 5, or 6 Euro and the recipient would receive 0, 3, 6, 9, 12, 15, or 18 Euro, respectively). In the following round (round 17), each participant was endowed with 6.00 Euro and acted as sender; she was asked how much of the 6.00 Euro she wanted to give to her recipient. To facilitate this decision, each sender was provided with gossip information about their recipient. Of the five aforementioned possible combinations of positive and negative preset statements, one combination was displayed per sender. Prior to the trust game, participants were informed that their decisions as both sender and recipient will not be disclosed to anyone later in the game. After the sender decisions, participants were paired and the computer calculated and displayed the payoff for each participant individually.

At the end of the game, participants were asked to rate the valence of each gossip statement they encountered or wrote during the game on a scale from 1 (very negative) to 7 (very positive) with 4 representing neutral valence. Each experimental session ended with the anonymous payment of the individual earnings to the participants (mean payoff = 26.22 Euro) as described in Semmann *et al.* (2005).

The design of the entire game did neither allow for any direct reciprocity (Trivers, 1971), nor permit any standing strategy (Sugden, 1986). Furthermore, participants composed gossip only about players they encountered neither in indirect reciprocity nor in trust game rounds; they were always third-party observers.

All data were analysed using the R statistical package (version 2.6.2) for Windows XP. To verify normality of residuals, we used the Shapiro-Wilk test procedure. If not stated otherwise, data were analysed on group-level. Furthermore, all r^2 values refer to adjusted r^2 and p values are corrected for multiple testing if applicable.

Results

In the observer indirect reciprocity rounds at the beginning of the experiment (rounds 1 to 6; Fig. 5.1), participants reached a mean cooperation level of 59% (s.d. 12.2%). Thereby, individual behaviour varied from 0% to 100% cooperation with only 10 participants (7.6%) that cooperated never or just once, and 39 participants (29.5%) that cooperated five or six times (out of six).

To analyse the gossip rounds (Fig. 5.1), we used gossip ratings provided by each participant as a measure of the individual gossip's valence. Furthermore, we grouped the participants according to the number of YES decisions they saw on their individual screen when asked to write a gossip about their game partner. This yielded a total of 7 groups (0, 1, 2,…, or 6 out of 6 YES decisions displayed) of which we calculated the cooperation level as the number of YES responses divided of total number of people in the respective group. As in a previous study (Sommerfeld *et al.*, 2007), the more YES decisions participants saw, the more positive the gossip they wrote ($y = 0.69x + 2.01$, $r^2 = 0.92$, $F(1,5) = 55.35$, $P < 0.001$). Furthermore, subsequent ratings of gossip were positively correlated with the original rating of the same gossip by its author ($y = 0.45x + 2.11$, $r^2 = 0.20$, $F(1,394) = 102.3$, $P < 0.001$). The same was found for gossip triplets where we compared the average original ratings by the gossip authors with the average rating of these statements by the participant encountering them ($y = 0.66x + 1.16$, $r^2 = 0.39$, $F(1,130) = 81.74$, $P < 0.001$). This analysis was performed on individual-level, justified by the explicit statement not to give ratings strategically because they will not be used later in the game.

Two different situations encountered in the game allowed for analysing the response on gossip written by participants. First, participants encountered only a single gossip statement as basis for their YES/NO decision. For this situation, we grouped participants according to their subjective rating of the provided gossip (i.e., the subsequent rating as compared to the author's rating) and calculated the cooperation level in percent for each of these seven groups (i.e., gossip rating is 1, 2, 3, 4, 5, 6, or 7). We found that the participants' cooperation is the higher, the more positive they rated the provided gossip ($y = 9.54x + 8.23$, $r^2 = 0.68$, $F(1,5) = 10.66$, $P = 0.022$). In a second situation, participants encountered three different gossip statements. In order to calculate a cooperation level from binary YES/NO decisions, we grouped participants according to their average rating of the three statements in the following groups: average rating is (i) lower than 2, (ii) between 2 and 3, (iii) between 3 and 4, (iv) between 4 and 5, (v) between 5 and 6, or (vi) higher than 6. Note that integer numbers belong to the higher interval (e.g., an average rating of 3 would fall in interval iii). As before, a higher average gossip rating led to increased cooperation ($y = 12.54x – 7.79$, $r^2 = 0.95$, $F(1,4) = 71.03$, $P = 0.001$). For both situations (single gossip and three gossip statements), we used the R function 'anova()' to estimate the best model, and for reasons of parsimony kept the simplest, i.e. in both cases a linear model.

To measure the effect of gossip compared to direct observation, we grouped participants again according to the number of YES decisions (0, 1, 2,…, 6 out of 6 decisions) they were provided with in our control observer indirect reciprocity round (round 10, 11, or 12, depending on the individual random sequence; see Materials and Methods), and calculated the cooperation levels for these 7 groups according to the information regime (i.e., direct observation, single gossip statement, or multiple gossip statements; Fig. 5.2). To keep our results conservative, we decided to exclude the group of participants that encountered zero YES decisions from the following analysis; the low sample size in this group ($N = 2$; see Fig. 5.2) would result in a weak representation of the population mean and potentially lead to unjustified conclusions. We then performed a MANOVA with the actual cooperation of a participant's partner as independent variable and with the cooperation levels according to information regime as three dependent variables. The reaction of participants according to the actual cooperation of their partners differed significantly between information regimes (MANOVA, Wilk's lambda < 0.0005, $F(3,2) = 2047.8$, $P < 0.001$). The individual linear responses within each information regime are as follows (see Fig. 5.2): (i) direct observation: $y = 8.58x + 28.78$, $r^2 = 0.46$, $F(1,4) = 5.33$, $P = 0.082$; (ii) single gossip statement: $y = 9.80x + 16.09$, $r^2 = 0.61$, $F(1,4) = 8.85$, $P = 0.041$; multiple gossip statements: $y = 13.53x + 2.69$, $r^2 = 0.98$, $F(1,4) = 207.6$, $P < 0.001$.

Preset gossip rounds (cf. Fig. 5.1) were analysed by grouping participants according to the number and valence (positive, p, or negative, n) of gossip statements they encountered: nnnp, nnp, np, npp, nppp (see Materials and Methods). Analysis of how preset gossip was rated by the participants (using the average rating for several statements of the same valence) documents a significant difference between designed positive and designed negative statements for each of the five groups (paired t test, $t(10) > 9.6$, $P < 0.001$ for each group). Due to violation of parametrical test assumptions, non-parametrical tests were used for

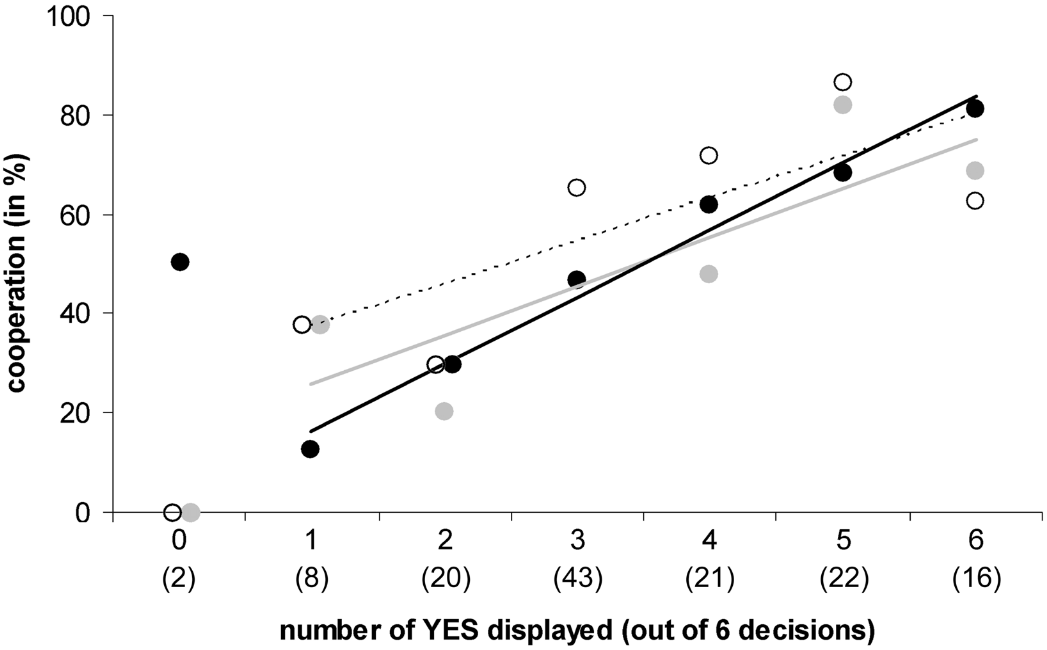

Fig. 5.2. Elicited cooperation based on observed cooperation or gossip information. Open circles show the percentage of participants cooperating dependent on the observed cooperation (as number of YES decisions out of 6 decisions) of their game partner. Regression line (dotted line): $y = 8.58x + 28.78$, $r^2 = 0.46$, F(1,4) = 5.33, $P = 0.082$. Grey circles represent the resulting cooperation after the original information (x-axis) was transmitted via a single gossip statement (grey line: $y = 9.80x + 16.09$, $r^2 = 0.61$, F(1,4) = 8.85, $P = 0.041$). Black circles represent the resulting cooperation after transmission via three gossip statements (black line: $y = 13.53x + 2.69$, $r^2 = 0.98$, F(1,4) = 207.6, $P < 0.001$). Numbers in brackets indicate sample size for each group. Note that data points were displayed side by side for clarity if they superimposed exactly.

between-group analysis of mean gossip ratings. A general test showed significant differences (Kruskal-Wallis chi-squared = 41.77, df = 4, $P < 0.001$) which were further examined using a multiple comparison test (R function ‘kruskalmc()’). Following pairs of groups showed significant differences (N = 22 for each comparison): nnnp-nppp ($P < 0.001$), nnnp-npp ($P < 0.001$), nnp-nppp ($P < 0.001$), nnp-npp ($P = 0.002$). For the analysis of the corresponding cooperation levels a parametrical test was applied and showed a similar picture (overall: F(4,50) = 10.890, $P < 0.001$; significant pairs with each N = 22: nnnp-nppp, $P = 0.002$; nnnp-npp, $P < 0.001$; nnp-nppp, $P = 0.009$; nnp-npp, $P < 0.001$); pairs that showed significant differences in mean gossip ratings also showed significant differences in cooperation level, and vice versa.

In order to analyse the effect of a change of a single gossip statement’s valence, we examined rounds in which triplets of gossip statements were encountered. We compared the following situations: nnn, nnp, npp, and ppp. For the extremes (nnn and ppp), we included those participants that rated all three gossips encountered in a gossip indirect reciprocity round (round 10, 11, or 12; see Materials and Methods) as either negative (i.e., each rating < 4 for the nnn group) or positive (i.e., each rating > 4 for the ppp group). Between these groups mean gossip ratings were significantly different (Fig. 5.3; Kruskal-Wallis chi-squared = 35.99, df = 3, $P < 0.001$; with the following significant group differences: nnn-npp, N = 20, $P < 0.001$; nnp-ppp, N = 20, $P < 0.001$; nnn-ppp, N = 18, $P < 0.001$). However, although the overall analysis of the corresponding cooperation levels was significant (Fig. 5.3; Kruskal-Wallis chi-squared = 13.19, df = 3, $P = 0.004$), a more detailed analysis did not reveal the

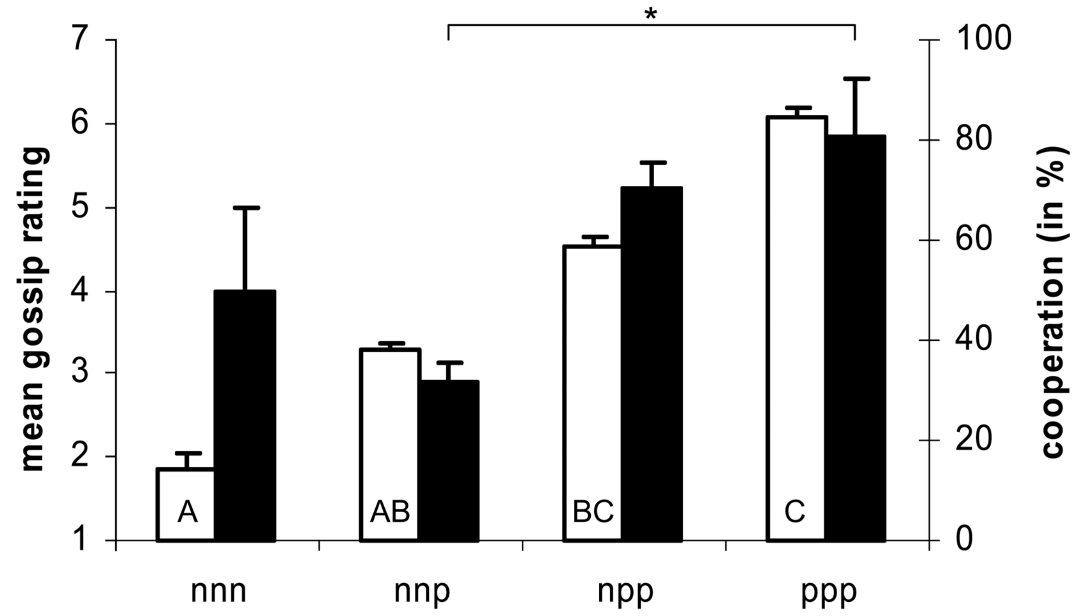

Fig. 5.3. Mean gossip rating and resulting cooperation in rounds in which three gossip statements were encountered. This graph shows the mean (+ s.e.) gossip rating (white bars, left y-axis) and the cooperation level (black bars, right y-axis) according to the number and valence (positive, p, and negative, n) of gossip statements encountered. Note that the extreme groups (nnn and ppp) refer to gossip written by participants, whereas intermediate groups (nnp and npp) refer to preset gossip. Different letters show significant differences (each P < 0.001) for gossip ratings (white bars), whereas the asterisk marks the significant difference for cooperation levels (black bars, asterisk indicates P = 0.005).

same effects (significant group differences: nnp-ppp, N = 20, P = 0.005). This was due to unexpectedly high cooperation in the group in which participants encountered three negative statements (nnn: 50 ± s.e. 16.7% cooperation). Furthermore, we found a much higher variance in the extreme groups (mean/variance; nnn: 44/25%, nnp: 32/1%, npp: 71/3%, ppp: 81/12%; Levene's test, F(3,36) = 6.70, P = 0.001).

All analyses of the trust game are based on individual-level, justified by the explicit statement that the participants' decisions as sender and as recipient will not be used or disclosed in any way later in the game. Overall, the average sender decision was 2.60 Euro (s.e. 0.17 Euro), which is about 44% of the 6.00 Euro senders were endowed with. Note that this result is not biased by the gossip they encountered, because the different gossip conditions (nnnp, nnp, np, npp, nppp) are balanced among all participants. Furthermore, the mean gossip rating across all conditions was close to neutral (3.9 ± s.e. 0.1).

A detailed analysis showed that participants' sender decision was positively correlated with mean gossip ratings of the encountered gossip statements (Fig. 5.4; $y = 0.47x + 0.81$, $r^2 = 0.06$, F(1,130) = 9.926, P = 0.002). Using the grouping according to gossip condition as mentioned above showed an overall effect (Kruskal-Wallis chi-squared = 21.12, df = 4, P < 0.001) and the following significant multiple comparison results: nnnp-npp, N = 55, P < 0.001; nnnp-nppp, N = 44, P = 0.003. The amount of money sent by a participant in the sender role was positively correlated with the initial cooperation of the participant at the beginning of the game (t = 3.08, df = 130, P = 0.003). The more cooperative a participant is in indirect reciprocity rounds, the more money she sent in the trust game. Note that the correlation between mean gossip ratings and sender decision remains significant after

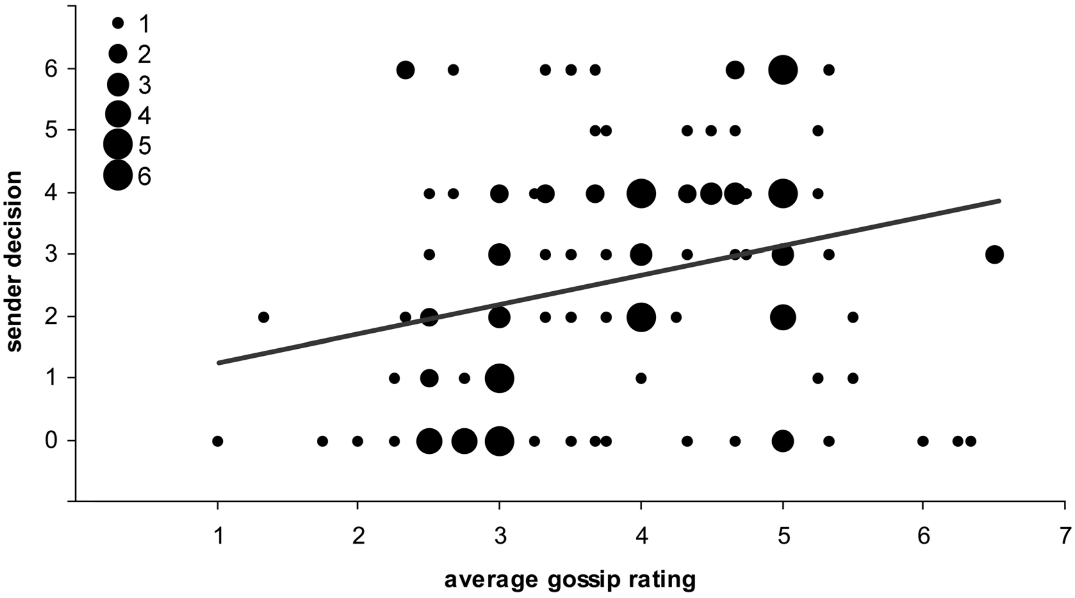

Fig. 5.4. Sender decision according to average rating of encountered gossip. Circle area represents number of participants that decided accordingly (see legend in the top left of the graph). Regression line: $y = 0.47x + 0.81$, $r^2 = 0.06$, F(1,130) = 9.926, P = 0.002.

correcting for the senders' cooperation in indirect reciprocity rounds ($y = 0.46x - 1.80$, $r^2 = 0.07$, F(1,120) = 10.42, P = 0.002).

For the analysis of recipients' decisions, note that the recipients' decisions were not influenced by any gossip. First, we focused on the general return behaviour of the recipients. As a measure for the general return behaviour, we calculated the average return for each possible sender decision as a percentage of the respective sender decision. In this way, a recipient who returns 0, 1, 2, 3, 4, 5, and 6 Euro of the possible 0, 3, 6, 9, 12, 15, or 18 Euro has a general return behaviour of 33%. A recipient who returns always the total amount received from the sender has a general return behaviour of 100%. The mean general return behaviour of the participants in our study was 29% (s.e. 1.3 %). Analysing the recipients' return behaviour according to the amount of money the recipients potentially will receive from the sender, but independent of actual sender decisions, we found a significant effect (Friedman chi-squared = 126.23, df = 5, P < 0.001). The more money they potentially receive, the higher the fraction they would sent back to the sender. Note that the situation where the sender sends 0.00 Euro is omitted from the analysis, because recipients had no choice in this situation. A post-hoc multiple comparison revealed the following significant differences according to the potential amount sent by the sender (using the R function 'friedmanmc()'; for each difference N = 44, 55, or 66, and P < 0.002): 1-3, 1-4, 1-5, 1-6, 2-4, 2-5, 2-6, and 3-6. Furthermore, we found general return behaviour to be positively correlated with initial cooperation (t = 3.33, df = 130, P = 0.001) as was the sender decision (see above). Looking at the actual money exchange in the game, the average relative return was 28% (s.e. 1.8%) with 31% of the participants returning more money than the sender originally sent.

Discussion

The results of this experimental study support earlier findings about people's behaviour in games of indirect reciprocity and the use of gossip therein: people cooperate more often with cooperators than with defectors (Wedekind & Milinski, 2000), people write more positive gossip about cooperators than about defectors (Sommerfeld *et al.*, 2007), and people cooperate more with people about whom they read positive gossip than with people about whom they read negative gossip (Sommerfeld *et al.*, 2007). This corroborates the hypothesis that gossip is a vector for socially relevant information further (Nowak & Sigmund, 1998; Mohtashemi & Mui, 2003; Panchanathan & Boyd, 2003; Nowak & Sigmund, 2005).

Against this background, the present study investigates the effect of multiple gossip statements and the reaction of people encountering them. Our results document that the original cooperation was a significantly better predictor of participants' responses when they had access to multiple gossip statements, as compared to single statements or direct observation. Whereas in the direct observation regime the original cooperation of the partner accounts for 46% of the variation in participants' responses, the percentage increases in the single gossip statement regime (61%), and reaches the highest value in the multiple gossip statements regime, where it accounts for 98% of the variation. Thus, the more gossip was provided, the better it represented the behaviour of the person concerned. Furthermore, gossip even represented this behaviour better than direct observation did. This finding might be connected to an earlier finding that people are influenced by gossip even if they knew hard facts about the other person (Sommerfeld *et al.*, 2007). In both cases, a distinct behaviour has already been judged by other people. Humans might adjust their own behaviour in order not to depart from the public opinion of their local group; they do not want to stand out. Following other people's judgement is potentially easier than making one's own, and might be rooted in a fundamental need to belong (Baumeister & Leary, 1995).

In the preset gossip scenarios of this study, where people could base their decision on several preset judgements, we could investigate the effect of a single contrasting gossip statement. In the balanced situation (one positive and one negative statement, i.e. the np group), participants acted neutrally (average gossip rating of both statements 4.0/s.e. 0.2; mean cooperation 47%/s.e. 8.4%). In unbalanced situations, people reacted in accordance with the majority of statements: they were more likely to cooperate if the majority of statements were positive, and they were more likely to defect if the majority of statements were negative. This indicates that a single gossip statement does not have a strong impact on the donor's decision. Thus, if the valence of most of the gathered gossip is in line with a person's real behaviour, the power of single inaccurate statements is very limited. In this way, cooperators seem to be able to detect defectors reliably by the use of gossip.

However, the present results also indicate that people have more difficulties reacting on an actually clear-cut situation: the variance of responses was higher in situations where participants had to react on three similar either positive or negative statements than in situations where they encountered a mixture of positive and negative gossip. The highest variance of responses was observed in the all-negative group; it was more than twice as high as in the all-positive group. Somehow, people seem to be reluctant to believe in absolute cooperation or defection. Especially, people facing purely negative gossip showed an unexpectedly high cooperation. They might have told themselves "he/she can't be that bad". This finding is in line with a previous finding by Hess and Hagen (2006) who found that people preferred benign alternatives to negative gossip. Furthermore, it is consistent with a previously found dampening effect of gossip (Sommerfeld *et al.*, 2007). This dampening effect refers to a discrepancy between the response upon gossip about a person and the response upon directly observing the same person. Reading gossip, students cooperated less often with cooperators, and more often with defectors than compared with the situation involving direct observation (Sommerfeld *et al.*, 2007). Although the present study does not document a dampening effect in a situation similar to the one of the previous study (cf. Fig. 5.2 and Fig. 4.3), the higher variation in extreme situations (Fig. 5.3) and the highly cooperative response towards all-NO participants (Fig. 5.2) still indicate its presence.

The absence of a dampening effect in the data of Fig. 5.2 is potentially due to a difference in design. In our previous study, participants encountered situations in which they had to write gossip based on only a fraction (i.e., two out of six) of all previous decisions of their partners (in addition to the complete information situation, i.e. facing six out of six decisions). Thus, participants could not be sure that the gossip they encountered was based on complete information. To adjust for this shortcoming, they might have dampened their response. In contrast, in the present study the students played only gossip rounds where they knew all of the previous six decisions; they always had complete information and knew that all gossip was based on such. In summary, the following results are known: single gossip statements based on complete information lead to no dampening effect (this study); multiple gossip statements based on complete information lead to no dampening effect (this study); and single gossip statements based on potentially incomplete information lead to a dampening effect (Sommerfeld *et al.*, 2007). The missing piece is a situation in which multiple gossip statements are based on potentially incomplete information. This last condition might also approximate the natural situation best. In our everyday life, we are aware that gossip is not fully reliable, because of our limited possibility for observation. Here, a dampened response does make sense, and obtaining a more precise picture of another person by gathering plenty of gossip might alleviate this dampening effect. Thereby, in situations with only little information, the dampening might be a mechanism to avoid high cooperation with defectors that seem to be nice, and, at the same time, to avoid risking the own good reputation by defecting against potentially nice people that seem to be bad.

In the trust game of the present study, participants behaved in general similarly as in previous studies implementing the trust game and rewarded trust (Berg *et al.*, 1995; Cox, 2004; Sutter & Kocher, 2007). In addition, our results document that reputation gained via reciprocating also helps in the trust game; sender decisions were strongly influenced by gossip that was based on reciprocating behaviour (Fig. 5.4). This shows the strong relationship between reciprocity, trust, and reputation as described by Ostrom (1998). People that reciprocate often gain a high reputation, which results in high perceived trustworthiness, which is, in turn, more likely to be honoured by these people. These positively reinforcing interrelations may have fostered the evolution of cooperation (Bravo & Tamburino, 2008).

Surprisingly, the sender decision was positively correlated with the basic cooperative behaviour of individuals; cooperative participants sent more money to their recipients and were, thus, more trustful. This finding might be connected to a general attitude towards investing/handling money, affecting both indirect reciprocity and trust game situations. In addition, it might be connected to an inner assumption about the recipient's behaviour (Dawes *et al.*, 1977). As Orbell and Dawes (1991) pointed out, cooperators generally expect higher cooperation in their environment (in this case the recipient) than defectors do (see also Croson, 2007).

In conclusion, our results document that multiple gossip statements optimise human responses in a way that cooperation can be more accurately directed towards cooperators. Furthermore, we showed that single inaccurate statements have only limited power to influence people's responses. Given this and the fact that people react on other's reputation transferred via gossip, important prerequisites to allow for high levels of cooperation are met (Bravo & Tamburino, 2008). Furthermore, as proposed by Ostrom (1998), reputation seems to be universal, at least in our experimental settings, and tightly connects trust and reciprocity. This connection might have led to an upward spiral increasing cooperative behaviour to the level we experience it today, in modern societies.

Nonetheless, our design represents a benign world without any incentive for gossip authors to cheat. Apparently, the real world is different, and future research needs to investigate the power of gossip in situations where cheaters might profit from lying.

Acknowledgements

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Conclusion

In the main introduction, I pointed out that the evolution of both sex and cooperation is of major concern to evolutionary biologists. Many researchers have tried to find an answer to the question of why we observe these evolutionary paradoxical phenomena in nature, and this thesis adds on to their work.

My colleagues and I have shown that female sticklebacks incorporate multiple cues and signals about male quality in order to choose their mate (Chapter 1). By doing so, females try to achieve an intermediate number of major histocompatibility complex (MHC) variants in their offspring. Having such an intermediate variant number leads to high immunocompetence and maximal reproductive output (Chapter 2); it thus directly translates into high Darwinian fitness. In the light of Darwin's theory of evolution – according to which higher fitness results in spreading of the trait –, this finding indicates that the need for fast host adaptation in an environment of fast-adapting parasites might have been a pivotal factor for the success of sexual reproduction, and, hence, the evolution of sex.

These results show an intriguingly clear-cut picture. Nature, however, is highly complex, and experimental studies try to condense this complexity to a manageable level in order to find unambiguous results. Clearly, this is a needed and fundamental approach, but it leaves open an important question: how is the situation in nature really?

Even though previous laboratory studies have shown that female sticklebacks strongly react on the MHC signal (Milinski *et al.*, 2005, and references therein), I demonstrated that they also react on a MHC-independent cue/signal (Chapter 1). How many more signals are taken into account by females under natural conditions? Do females also react on these specific signals when they have access to potential mates not only during a limited time defined by the experimenter? Experimental studies under semi-natural conditions shed some light on these aspects (Chapter 2). Nonetheless, evolutionary biologists ultimately want to explain the evolution of sexual reproduction in an extensive manner – not just in the three-spined sticklebacks of northern Germany. In other organisms, different factors might be crucial. A female's perception machinery, for instance, might limit the detection and the evolution of signals and cues (Guilford & Dawkins, 1991; 1993; Boughman, 2001). The transmission of signals, in turn, is influenced by environmental factors: bright breeding colouration is useless in highly turbid water where a visual signal would not travel far enough to reach potential mates (Boughman, 2002). All these factors have to be taken into account if we try to comprehensively solve the puzzle of the evolution of sex.

A similar picture can be drawn in the case of human cooperation. Several mechanisms have been proposed to be conducive to cooperative behaviour, one of them being indirect reciprocity and the use of reputation (see Introduction). Our results support the hypothesis that the required spread of information about other people's reputation is achieved by gossiping (Chapter 4). On the one hand, this indicates that the uniquely high levels of cooperation found in humans are connected to another unique ability of humans: the use of language. On the other hand, gossiping seems to be a powerful tool to reduce the risk of cooperating with a defector (Chapter 5), and, thus, potentially even against cheating and cheaters – a major problem in the context of human cooperation, whether of the first order, or of the second or a higher order (e.g., the problem of cooperators that free-ride on the punishment of others and do not engage in costly punishment themselves).

In the cooperation experiments presented here, we have shown that people observe other people's behaviour, interpret it, and then judge the actors based on this interpretation – even if they do not know all circumstances that caused the actors' behaviour. Apparently, humans judge people not only on the basis of their own interpretation, but also on the basis of the interpretation of others' interpretations (i.e., gossip). In our studies, students paid attention to gossip in an experimental setup where gossip authors were third-party, and, therefore, neutral agents (Chapters 4 and 5). But how do people react in real world settings where social relationships are present? What role play emotions (e.g., Leuba & Lucas, 1945), and what selective pressures led to their evolution? The complex judgment of others can lead to misinterpretation and misunderstanding, which might eventually result in interpersonal conflict (Wall & Callister, 1995) – possibly a consequence that also affects people's behaviour. Students have further been reported to invest irrational high amounts of money in various situations, even if their reputation is not at stake – including our collective-risk scenario (Chapter 3). So, other factors need to be considered that evoke these decisions. How strong, for instance, is the influence of learned rules and norms, and how did they evolve? Knowing such details could help us design strategies to solve modern social dilemmas and avert major future disasters (e.g., Chapter 3).

Taking all studies presented in this thesis together, I conclude the following. In order to achieve the optimal outcome of an inter-individual interaction (e.g., mating and cooperation) and to protect themselves against cheaters, all organisms face the same problem: they need to trade off the gathering of information about their interaction partners against the associated costs of doing so (e.g., time expenditure). Yet, single signals or cues are only incomplete information, in both sticklebacks (e.g., breeding colouration, MHC signal) and humans (e.g., single gossip statements). Thus, individuals try to obtain several signals or take multiple cues into account to approximate the real quality of a mate, or the real behaviour and character of a person. Thereby, they have to balance individual against group interests, and short-term against long-term benefits to optimise the amount of information they need.

It is the aim of scientists to answer the aforementioned and many more questions by investigating from the small (controlled laboratory studies), to the intermediate (semi-natural field experiments), to the large (descriptive real world surveys). Each of these levels is important to understand the complete picture – or rather, approximate the complete picture. But, I think it also is important to be aware of each level's limits. One should always keep in mind that a laboratory study can never give proof about the importance of its results under natural conditions, as a descriptive survey can never connect cause and effect.

Science is like our sticklebacks or students; it trades off the gathering of knowledge against the associated costs of doing so (e.g., funding, time expenditure, work load, opportunities) to reach its ultimate goal: a complete picture of nature.

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Appendix A

This part contains supplementary information for Chapter 1, Seasonal Variation of Male Attractiveness in Sticklebacks. Figure A.1 provides detailed information about the time points of male water extraction with respect to the test males and condition. Figure A.2 shows a photo of the flow channel. The following paragraph describes the peptides used for simulating the MHC-signal and was kindly provided by T. Boehm.

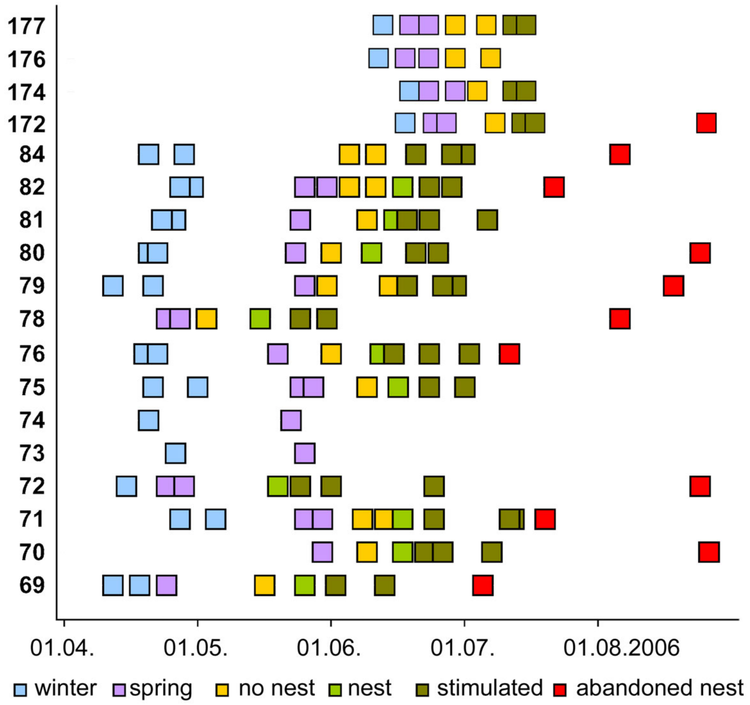


Fig. A.1. Timetable for male water extraction. Numbers represent individual males. Squares indicate days on which water was taken from a male tank, and colours indicate the housing condition or reproductive status of each male at that time. Note that the interval between two consecutive extractions was at least three days.

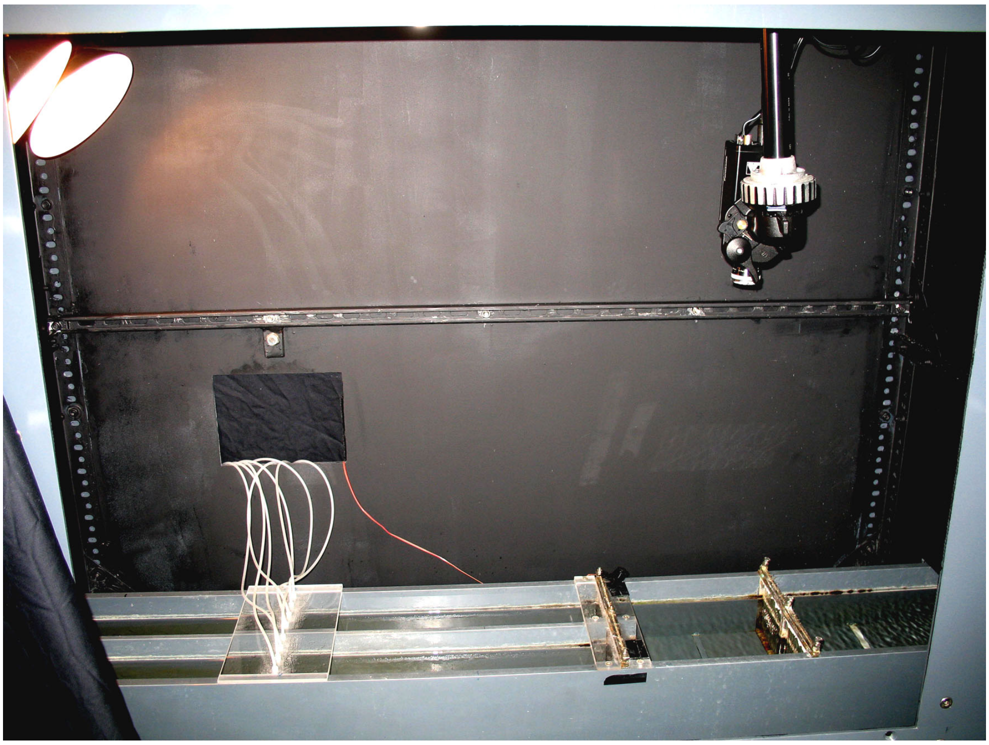


Fig. A.2. Flow channel for olfactory mate choice tests. A camera (right top) was mounted above the test chamber for the female (right bottom). The test water was added through the white hoses (left) to the constant inflow of water (from the left). Two light bulbs (left top) provided light as for each trial black curtains were closed to reduce disturbance for the females.

Derivation of Stickleback Peptides

Peptide ligands of stickleback MHC molecules have not yet been described; furhermore, their binding properties have not been defined. However, the analysis of ligand motifs of mammals and birds has indicated a substantial degree of evolutionary conservation (summarised in Rammensee *et al.*, 1997). To derive putative MHC ligands from conceptual translations of stickleback cDNA sequences, a cDNA library from mRNA isolated from adult stickleback head kidney in the pCMVSport6 vector (Invitrogen) was constructed (Haas-Assenbaum & Boehm, unpublished work). Individual cDNA clones were sequenced, and the derived protein sequences were compared with database entries by using the BLAST suite of search algorithms at the National Center for Biotechnology Information (NCBI) server (www.ncbi.nlm.nih.gov). Given the evolutionary conservation of motifs in MHC class I peptides, the derived protein sequences were subjected to motif predictions using algorithms implemented in the SYFPEITHI database suite of programs (www.uni-tuebingen.de_uni_kxi) (Rammensee *et al.*, 1999). In this manner, the following peptides were selected (sequences given in single-letter code): VDPDNFKLL was derived from *Gasterosteus aculeatus* β-globin; amino acids 99–107, GenBank accession no. AY184355; NYGVTKTDI was derived from *Gasterosteus aculeatus* neuronal protein 22, amino acids 47–56, GenBank accession no. AY184357; SYKEKNIFL was derived from *Gasterosteus aculeatus* signal peptidase complex 25-kDa subunit (Spc25), amino acids 93–101, GenBank accession no. AY184358; and KLYEQGSNK was derived from *Gasterosteus aculeatus* proteasome subunit α-3, amino acids 57–65, GenBank accession no. AY184356. Peptides were chemically synthesized, purified, verified by MALDI-TOF-MS, and dissolved in PBS.

Appendix B

This part contains supplementary information for Chapter 2, Lifetime Reproductive Success and the MHC. During the study the males in enclosure five were colour tagged and regularly observed. The tagging and the results are provided in this appendix. The remaining information found in this appendix is submitted alongside with the manuscript for publication as supplementary online information.

Colour tagging and behavioural observations

To obtain data on male nesting behaviour, we tagged all male fish of one enclosure with coloured pieces of plastic tubes (Silicone analytical hose, 0.5x0.7 mm, Reichelt Chemietechnik Heidelberg). Each male received two 2mm long pieces on each of two back spines. With three colours (black, green and blank) and two colours per fish, we achieved individual-specific tagging for all 8 males. Tagging was conducted just after weighing and measuring of the fish. Otherwise, the tagged fish were handled exactly the same way as the other fish of the study (see Chapter 2, Fig. 2.1). After release, they were observed on a daily basis as the weather permitted. On each observation day, I observed the males for one hour and documented their nesting sites. After 15 days of which 11 days could be used for observation, I had to stop the observation due to loss of or unrecognisable colour tags. Furthermore, we could only get data for 7 of the 8 males due to the death of one individual within 2 days after the start of the experiment.

Out of the 11 observation days, each male maintained a nest on 8 to 10 days (mean = 9.7) and had an average of 2.4 nests (SD = 1.0). Only one male had just one nest during the entire period. Even after egg sampling events, they mainly maintained their nests (in 64% of all cases). Usually, the male strategy attributed to each male contributing to a given egg clutch is defined by the proportion of eggs fertilised by this male. Accordingly, the male contributing the highest amount of fertilised eggs to one clutch is defined as the nest owner. Eggs that were neither sired nor mothered by any of the parents encountered in a distinct clutch were assumed to be stolen from other nests by the nest owner. To confirm the respective assignment of parents to such eggs, it was checked whether this parental combination was also found in other nests in the same period. Last, a sneaker strategy was attributed to those males (except the nest owner) that fertilised eggs of females that also mothered other eggs in a clutch. Comparing these data with the behavioural data on nest ownership revealed that 94% of all attributed male strategies with respect to individual eggs are correct for the investigated enclosure. Only in two of the 28 egg clutches in this enclosure the standard procedure yielded wrong results, which might be due to the fact that in these cases the owner did not fertilise a single egg. Note that stolen eggs could not be identified by behavioural observation. This single case in the observed enclosure was excluded from the comparison. Furthermore, each male but one suffered at least two sneaker events during the 15 days observation period.

Fig. B.1. The enclosure system viewed from above. The six stainless steel mesh cages can be seen as squares on the left. Behavioural observations took place in the second enclosure from the bottom. This picture was obtained from Google Earth (version 4.2).

Supplementary tables and figures

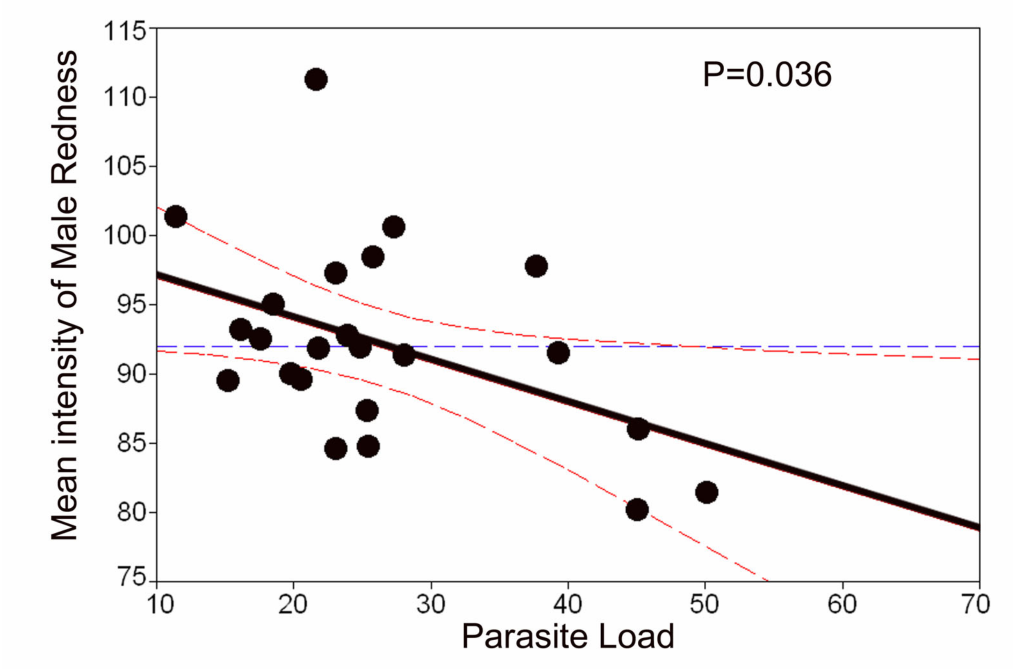


Fig. B.2. Relationship between red male breeding coloration and parasite load. See Chapter 2, Table 2.1.d.

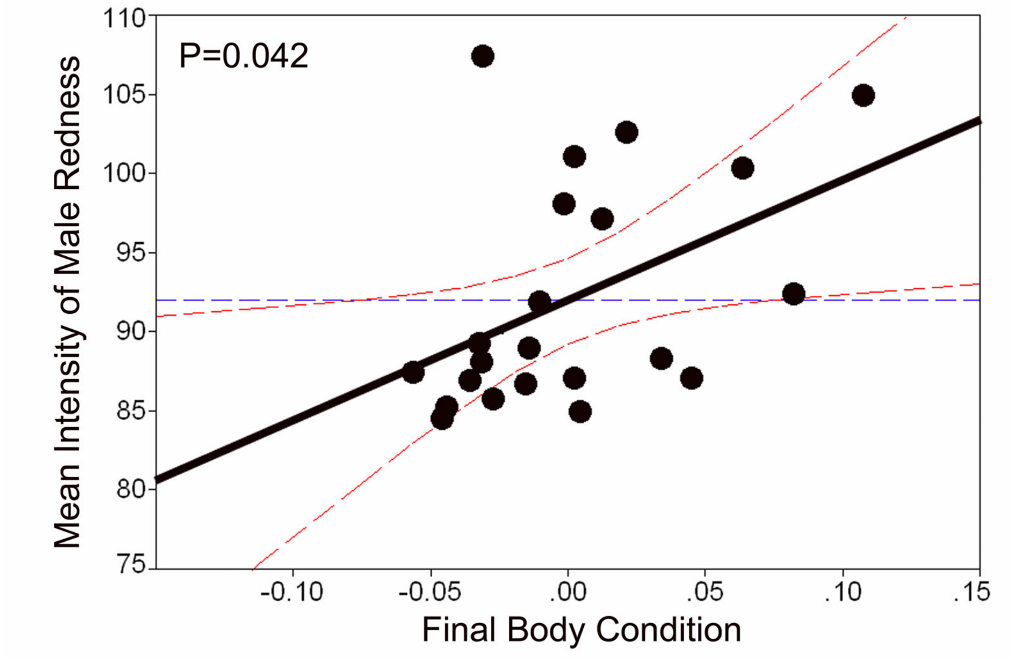


Fig. B.3. Variation of red breeding coloration in male stickleback as a function of the body condition of the fish at the end of the experiment. See Chapter 2, Table 2.1.d.

Table B.1. Multiple primer PCR protocols used for microsatellite typing.

PCR 1		PCR2		PCR3		PCR4		PCR5	
10 x buffer	1.00	10 x buffer	1.00	10 x buffer	1.00	10 x buffer	1.00	10 x buffer	1.00
dNTP's	1.00	dNTP's	1.00	dNTP's	1.00	dNTP's	1.00	dNTP's	1.00
% BSA	1.00	1 % BSA	1.00	MgCl2	0.30	MgCl2	0.30	MgCl2	0.30
MgCl2	0.30	MgCl2	0.30	**STN 2 f**	0.30	**STN 36 f**	0.30	**STN 24 f**	0.30
Stich 5196 f	0.10	**Stich STN18 f**	0.12	**STN 2 r**	0.30	**STN 36 r**	0.30	**STN 24 r**	0.30
Stich 5196 r	0.10	**Stich STN18 r**	0.12	**STN 170 f**	0.30	**STN 114 f**	0.30	**STN 67 f**	0.25
Stich 4170 f	0.08	**Stich STN32 f**	0.08	**STN 170 r**	0.30	**STN 114 r**	0.30	**STN 67 r**	0.25
Stich 4170 r	0.08	**Stich STN32 r**	0.08	**STN 174 f**	0.30	**STN 167 f**	0.45	**STN 185 f**	0.30
Stich 1125 f	0.10	**Stich STN75 f**	0.17	**STN 174 r**	0.30	**STN 167 r**	0.45	**STN 185 r**	0.30
Stich 1125 r	0.10	**Stich STN75 r**	0.17	**Taq (Invitek)**	0.05	**Taq (Invitek)**	0.05	**Taq (Invitek)**	0.05
Stich 1097 f	0.40	**Stich STN 84 f**	0.08	Water	4.85	Water	4.55	Water	4.95
Stich 1097 r	0.40	**Stich STN 84 r**	0.08						
Stich 7033 f	0.35	**Taq (Invitek)**	0.05						
Stich 7033 r	0.35	Water	4.75						
Taq (Invitek)	0.05								
Water	3.59								

All quantities are in µl. The colours represent the label used.

Table B.2. PCR conditions and cycles for each multiple PCR performed.

	PCR 1	PCR2	PCR3	PCR4	PCR5
Original Denaturation	3 min at 94°C	3 min at 94°C	2 min at 94°C	2 min at 94°C	2 min at 94°C
Denaturation	1 min at 94°C	0.45 min at 94°C	0.45 min at 94°C	0.45 min at 94°C	0.45 min at 94°C
Annealing	1 min at 58°C	0.45 min at 56°C	0.45 min at 56°C	0.45 min at 56°C	0.45 min at 56°C
Extension	1 min et 72°C	1 min at 72°C	0.45 min at 72°C	0.45 min at 72°C	0.45 min at 72°C
Final extension	none	none	20 min at 72°C	20 min at 72°C	20 min at 72°C
Number of cycle	27	26	27	27	27

In bold the conditions for each cycle

Table B.3. Table summarizing the prevalence (percentage of infected hosts) and the mean intensity (number of parasite individuals of a given species per infected host) of all recorded parasites in the 53 dissected fish.

	Prevalence (%)	**Mean Intensity**
Protozoa:		
Trichodina sp.	88.46	18.62
Apiosoma sp.	9.62	5.50
Ichthyophthirius multifiliis	11.54	2.33
Monogenea:		
Gyrodactylus sp.	28.85	17.80
Digenea:		
Diplostomum sp. (total)	100.00	15.98
D. pseudospathaceum (lab infection)	100.00	5.06
Cyathocotyle prussica	98.08	4.35
Echinochasmus sp.	98.08	4.83
Apatemon cobitidis	71.15	4.70
Tylodelphis clavata	98.08	6.93
Phyllodistomum folium	25.00	3.75
Cestoda:		
Valipora campylancristrota	84.62	11.93
Proteocephalus filicolis	86.54	6.87
Nematoda:		
Anguillicola crassus	69.23	1.64
Contracaecum sp.	13.46	1.00
Camallanus lacustris	86.54	4.33
Raphidascaris acus	71.15	2.97
Acanthocephala:		
Acanthocephalus clavula	34.62	2.00
Acanthocepalus lucii	78.85	1.00
Crustacea:		
Argulus foliaceus	15.38	1.91
Ergasilus sp.	9.62	1.00
Mollusca:		
Glochidia	23.08	1.00

Appendix C

This part contains supplementary information for Chapter 3, Preventing Dangerous Climate Change: a Collective-Risk Social Dilemma. The paragraph “Equilibrium Points and Rational Decisions” is published as supplementary information alongside the original article. Introduction pages are shown as they appeared in the original experimental game.

Equilibrium Points and Rational Decisions

In keeping with the experimental character of the paper, we do not provide formal definitions and proofs for the following. Rather, this is presented as an illustration of our reasoning regarding rational strategies and stability in the accompanying manuscript.

Here we refer to any choice made by an individual that lowers their personal average take home pay as an irrational choice and a decision that increases their payoff as a rational choice. An inherent assumption is that individuals seek to maximize their payoffs and understand the game well enough to do this. In this climate game players can see the strategies used by other players in the preceding rounds and adjust their strategy accordingly. As an informal definition, if no individual player can gain anything by unilaterally changing their strategy while the remaining players keep their strategies unchanged, the set of strategies is a Nash equilibrium. In the examples provided here, players only learn of the strategy of the other players after it has been played and we show possible responses accordingly rather than using the simultaneous ‘announcement test’ (Holt & Roth, 2004). In addition, we only consider pure strategies for simplicity rather than possible mixed strategies. As an example consider the following matrix of contributions to the public account in the 90% treatment.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€120
2	€2	€2	€2	€2	€2	€2	
3	€2	€2	€2	€2	€2	€2	
4	€2	€2	€2	€2	€2	€2	
5	€2	€2	€2	€2	€2	€2	
6	€2	€2	€2	€2	€2	€2	
7	€2	€2	€2	€2	€2	€2	
8	€2	€2	€2	€2	€2	€2	
9	€2	€2	€2	€2	€2	€2	
10	€2	€2	€2	€2	€2	€2	
Ending	€20	€20	€20	€20	€20	€20	
Expectation	€20	€20	€20	€20	€20	€20	

The 'Ending' row corresponds to each player's personal account value at the end of the ten rounds and 'Expectation' corresponds to the average take home amount. 'Total Contribution' is the game ending balance of the public 'climate saving' account. The expectation is lower than the individual ending account value if the collective target contribution of €120 was not achieved, or, as in this case, equal to the ending account value if this target was accomplished. In this case all players maintained a fair sharer strategy of a €2 contribution per round. If player one unilaterally changed her strategy to that of a free rider she lowers her expected take home money because the target public sum is not met (and she only gets to keep her ending account in 10% of all cases), as in the following example.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€102
2	€0	€2	€2	€2	€2	€2	
3	€0	€2	€2	€2	€2	€2	
4	€0	€2	€2	€2	€2	€2	
5	€0	€2	€2	€2	€2	€2	
6	€0	€2	€2	€2	€2	€2	
7	€0	€2	€2	€2	€2	€2	
8	€0	€2	€2	€2	€2	€2	
9	€0	€2	€2	€2	€2	€2	
10	€0	€2	€2	€2	€2	€2	
Ending	€38	€20	€20	€20	€20	€20	
Expectation	€3.8	€2	€2	€2	€2	€2	

Similarly, if player one adopted an altruist strategy during the game, even at the very end, she will reduce her expected account, but not by nearly as much.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€122
2	€2	€2	€2	€2	€2	€2	
3	€2	€2	€2	€2	€2	€2	
4	€2	€2	€2	€2	€2	€2	
5	€2	€2	€2	€2	€2	€2	
6	€2	€2	€2	€2	€2	€2	
7	€2	€2	€2	€2	€2	€2	
8	€2	€2	€2	€2	€2	€2	
9	€2	€2	€2	€2	€2	€2	
10	€4	€2	€2	€2	€2	€2	
Ending	€18	€20	€20	€20	€20	€20	
Expectation	€18	€20	€20	€20	€20	€20	

Thus, the ‘all fair sharer’ set of strategies is a Nash equilibrium as no single player can unilaterally increase their end game expectation by adopting a different strategy.

Similarly, the ‘all free rider’ set of strategies is a Nash equilibrium. Deviations by single players lower their expectations as player two illustrates in this example.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€0	€0	€0	€0	€0	€0	€12
2	€0	€0	€0	€0	€0	€0	
3	€0	€0	€0	€0	€0	€0	
4	€0	€0	€0	€0	€0	€0	
5	€0	€2	€0	€0	€0	€0	
6	€0	€2	€0	€0	€0	€0	
7	€0	€2	€0	€0	€0	€0	
8	€0	€2	€0	€0	€0	€0	
9	€0	€2	€0	€0	€0	€0	
10	€0	€2	€0	€0	€0	€0	
Ending	€40	€28	€40	€40	€40	€40	
Expectation	€4	€2.8	€4	€4	€4	€4	

The ‘all free rider’ equilibrium is stable, in the sense that once one player has changed their strategy, no shift in strategies by the other players allows them to increase their expectation and, in the above example, player two's best option is to return to the original free rider strategy.

In contrast, the 'all fair sharer' equilibrium is unstable. Once there has been a change in strategy by one player, the remaining players can increase their expectation by changing their strategies. In this example, after player one switched to a free rider, player two can maximize his winnings by also switching to a free rider. Thus, once this equilibrium is deviated from, it is difficult to return to.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€90
2	€2	€2	€2	€2	€2	€2	
3	€0	€2	€2	€2	€2	€2	
4	€0	€0	€2	€2	€2	€2	
5	€0	€0	€2	€2	€2	€2	
6	€0	€0	€2	€2	€2	€2	
7	€0	€0	€2	€2	€2	€2	
8	€0	€0	€2	€2	€2	€2	
9	€0	€0	€2	€2	€2	€2	
10	€0	€0	€2	€2	€2	€2	
Ending	€36	€34	€20	€20	€20	€20	
Expectation	€3.6	€3.4	€2	€2	€2	€2	

In different situations, it is possible for a player to maximize his expectation by compensating for a free rider and adopting an altruistic strategy. In the following example, player two can compensate for player one by becoming altruistic, with an expectation of €6, rather than a free rider with an expectation of €3.4. The difference from the example above is a single altruistic decision by another player: here player four in the second round has made the public sum attainable by player two switching to an altruistic strategy.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€120
2	€2	€2	€2	€4	€2	€2	
3	€0	€2	€2	€2	€2	€2	
4	€0	€4	€2	€2	€2	€2	
5	€0	€4	€2	€2	€2	€2	
6	€0	€4	€2	€2	€2	€2	
7	€0	€4	€2	€2	€2	€2	
8	€0	€4	€2	€2	€2	€2	
9	€0	€4	€2	€2	€2	€2	
10	€0	€4	€2	€2	€2	€2	
Ending	€36	€6	€20	€18	€20	€20	
Expectation	€36	€6	€20	€18	€20	€20	

In the actual data, there are many examples of rational and irrational choices made by the students. Here is an example from the 90% treatment.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€108
2	€0	€0	€2	€2	€0	€2	
3	€2	€2	€0	€2	€2	€0	
4	€2	€4	€0	€2	€2	€2	
5	€0	€0	€2	€2	€2	€2	
6	€2	€0	€0	€2	€4	€4	
7	€2	€2	€4	€2	€0	€0	
8	€2	€2	€2	€2	€4	€2	
9	€4	€2	€2	€2	€0	€4	
10	€4	€0	€4	€0	€2	€2	
Ending	€20	€26	€22	€22	€22	€20	
Expectation	€2	€2.6	€2.2	€2.2	€2.2	€2	

In round two, players one, two and five irrationally switched to free rider strategies, lowering their expectation. Players three and six rationally changed their strategy to that of a free rider in round three. Players one, two and five then switched back to fair sharer strategies in round three even though, based on the other players' previous strategies, a climate saving collective sum was no longer attainable.

In another actual example,

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€0	€2	€4	€0	€114
2	€2	€0	€2	€0	€2	€2	
3	€4	€2	€2	€2	€2	€0	
4	€2	€4	€2	€0	€0	€2	
5	€4	€0	€4	€4	€0	€2	
6	€2	€2	€0	€4	€0	€0	
7	€4	€2	€2	€0	€4	€2	
8	€2	€4	€2	€0	€4	€2	
9	€4	€4	€0	€4	€0	€4	
10	€2	€0	€0	€2	€2	€2	
Ending	€12	€20	€26	€22	€22	€24	
Expectation	€1.2	€2	€2.6	€2.2	€2.2	€2.4	

player three could have switched to an altruist strategy in the ninth round. If the other players had maintained their current strategies this would have resulted in an expectation of €18 rather than €2.2 if player three had maintained the same strategy or €2.6 by adopting a free rider strategy. In general, altruistic strategies increased toward the end of the games, but this is an example of an irrational choice that is consistent with refusing to participate in an unfair outcome. Players four and six would have had higher payoffs if all other strategies had been maintained from the eighth round until the end of the game, as in the illustrative example below.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€0	€2	€4	€0	€122
2	€2	€0	€2	€0	€2	€2	
3	€4	€2	€2	€2	€2	€0	
4	€2	€4	€2	€0	€0	€2	
5	€4	€0	€4	€4	€0	€2	
6	€2	€2	€0	€4	€0	€0	
7	€4	€2	€2	€0	€4	€2	
8	€2	€4	€2	€0	€4	€2	
9	€2	€4	€4	€0	€4	€2	
10	€2	€4	€4	€0	€4	€2	
Ending	€14	€16	€18	€28	€16	€26	
Expectation	€14	€16	€18	€28	€16	€26	

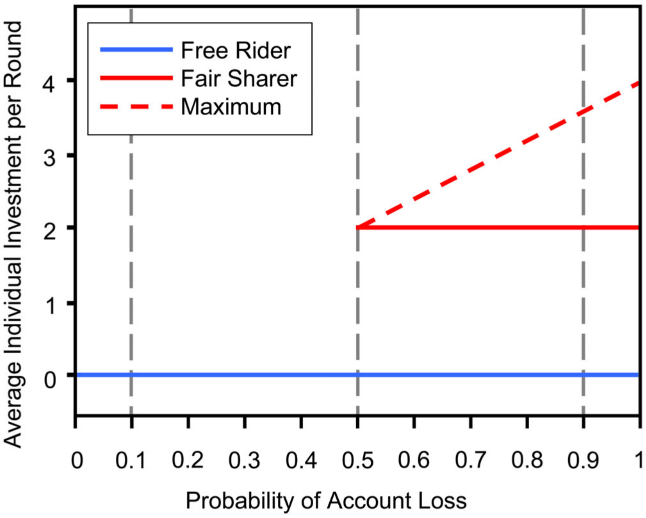
Finally, in the 10% treatment, a higher average payoff can be achieved with a free rider strategy then a fair sharer strategy, even if the game is started with an 'all fair sharer' set of strategies and all the other players maintain a fair sharer strategy as in this example.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€2	€2	€2	€2	€2	€2	€102
2	€0	€2	€2	€2	€2	€2	
3	€0	€2	€2	€2	€2	€2	
4	€0	€2	€2	€2	€2	€2	
5	€0	€2	€2	€2	€2	€2	
6	€0	€2	€2	€2	€2	€2	
7	€0	€2	€2	€2	€2	€2	
8	€0	€2	€2	€2	€2	€2	
9	€0	€2	€2	€2	€2	€2	
10	€0	€2	€2	€2	€2	€2	
Ending	€38	€20	€20	€20	€20	€20	
Expectation	€34.2	€18	€18	€18	€18	€18	

However, in the game the students often contributed even late in the game, lowering their expectations and providing a clearer example of apparently irrational behavior as in this typical example.

Round	Player 1	Player 2	Player 3	Player 4	Player 5	Player 6	Total Contribution
1	€0	€4	€4	€2	€0	€2	€78
2	€2	€4	€2	€2	€0	€0	
3	€0	€4	€0	€4	€2	€2	
4	€0	€4	€0	€2	€0	€0	
5	€0	€2	€0	€2	€0	€2	
6	€2	€2	€2	€4	€2	€0	
7	€0	€2	€4	€4	€0	€0	
8	€0	€4	€2	€0	€0	€2	
9	€2	€0	€0	€0	€0	€0	
10	€0	€0	€0	€0	€0	€0	
Ending	€34	€14	€26	€20	€36	€32	
Expectation	€30.6	€12.6	€23.4	€18	€32.4	€28.8	

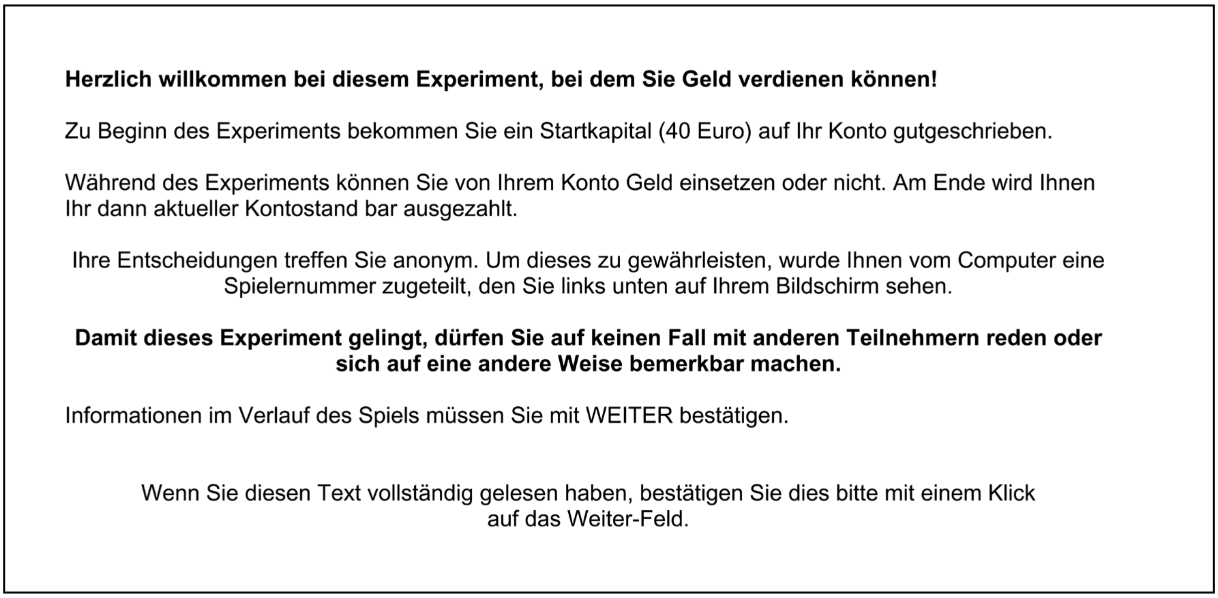
As stated in Chapter 3, “in the 90% treatment, each course of the game that leads to exactly reaching the target sum of €120, irrespective of who contributes how much as long as each player invests less than €36, is a Nash equilibrium.” More generally, there exists a continuum of possible equilibriums with varying probabilities of account loss. The next graph illustrates part of the process involved.



In this figure vertical dashed lines denote the three probabilities of account loss (if the target is not met) used in the experiment. With probabilities below 0.5 there exists only one Nash equilibrium with an average contribution per round of €0. At probabilities of 0.5 and higher a second, albeit unstable, equilibrium appears at an average contribution of €2 per round, which provides a higher take home expectation. The dashed line illustrates the maximum (non-inclusive) possible game contribution, averaged per round, from any single player that still constitutes a rational strategy of maximizing individual pay at the end of the game. As the probability of loss increases, the maximum game contribution linearly increases, providing more flexibility for players to maintain higher expectations despite the inherent instability of the higher equilibrium.

Introduction pages

In this game, all introduction pages were shown before the start.



Herzlich willkommen bei diesem Experiment, bei dem Sie Geld verdienen können!

Zu Beginn des Experiments bekommen Sie ein Startkapital (40 Euro) auf Ihr Konto gutgeschrieben.

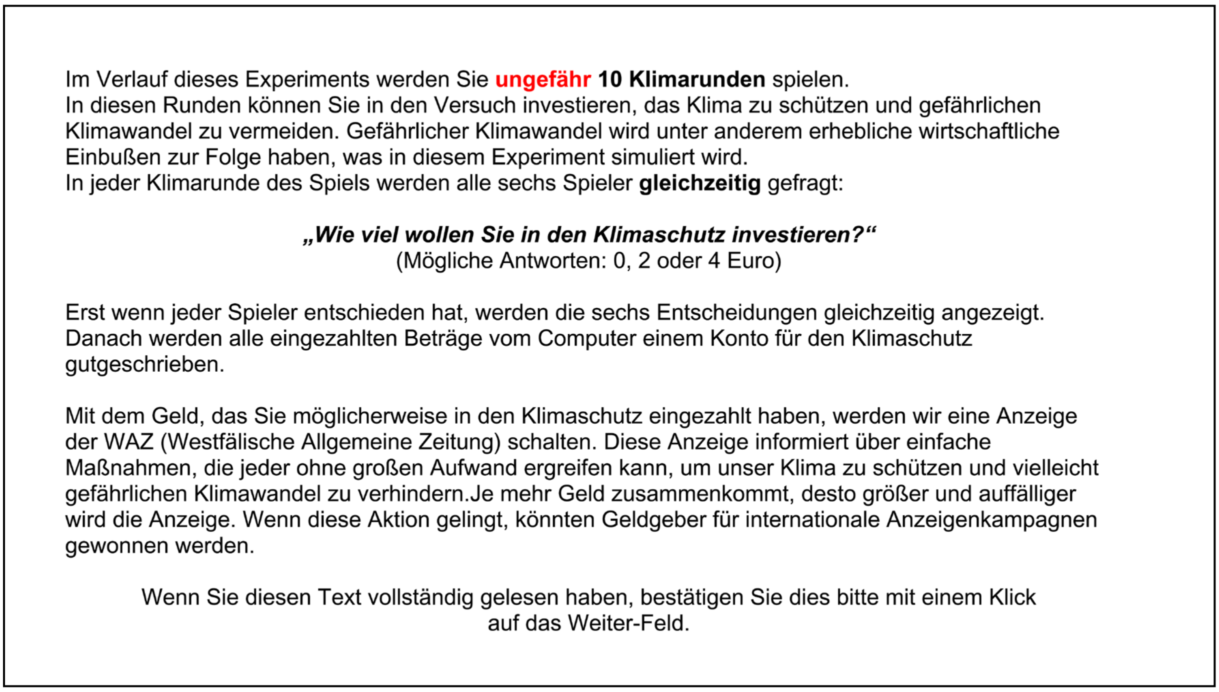
Während des Experiments können Sie von Ihrem Konto Geld einsetzen oder nicht. Am Ende wird Ihnen Ihr dann aktueller Kontostand bar ausgezahlt.

Ihre Entscheidungen treffen Sie anonym. Um dieses zu gewährleisten, wurde Ihnen vom Computer eine Spielernummer zugeteilt, den Sie links unten auf Ihrem Bildschirm sehen.

Damit dieses Experiment gelingt, dürfen Sie auf keinen Fall mit anderen Teilnehmern reden oder sich auf eine andere Weise bemerkbar machen.

Informationen im Verlauf des Spiels müssen Sie mit WEITER bestätigen.

Wenn Sie diesen Text vollständig gelesen haben, bestätigen Sie dies bitte mit einem Klick auf das Weiter-Feld.



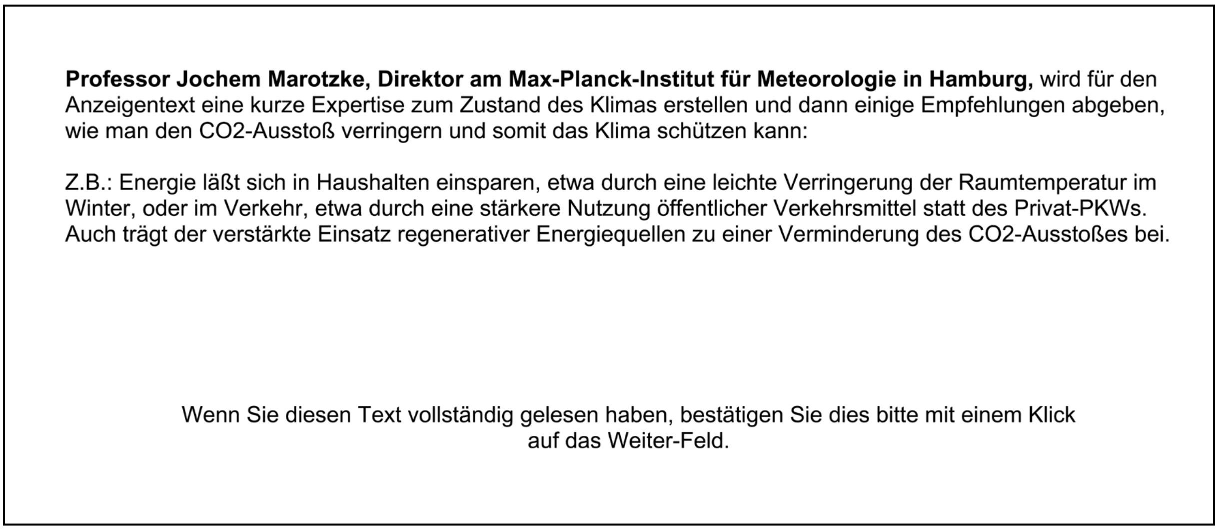
Im Verlauf dieses Experiments werden Sie **ungefähr** **10 Klimarunden** spielen.
In diesen Runden können Sie in den Versuch investieren, das Klima zu schützen und gefährlichen Klimawandel zu vermeiden. Gefährlicher Klimawandel wird unter anderem erhebliche wirtschaftliche Einbußen zur Folge haben, was in diesem Experiment simuliert wird.
In jeder Klimarunde des Spiels werden alle sechs Spieler **gleichzeitig** gefragt:

„Wie viel wollen Sie in den Klimaschutz investieren?“
(Mögliche Antworten: 0, 2 oder 4 Euro)

Erst wenn jeder Spieler entschieden hat, werden die sechs Entscheidungen gleichzeitig angezeigt. Danach werden alle eingezahlten Beträge vom Computer einem Konto für den Klimaschutz gutgeschrieben.

Mit dem Geld, das Sie möglicherweise in den Klimaschutz eingezahlt haben, werden wir eine Anzeige der WAZ (Westfälische Allgemeine Zeitung) schalten. Diese Anzeige informiert über einfache Maßnahmen, die jeder ohne großen Aufwand ergreifen kann, um unser Klima zu schützen und vielleicht gefährlichen Klimawandel zu verhindern.Je mehr Geld zusammenkommt, desto größer und auffälliger wird die Anzeige. Wenn diese Aktion gelingt, könnten Geldgeber für internationale Anzeigenkampagnen gewonnen werden.

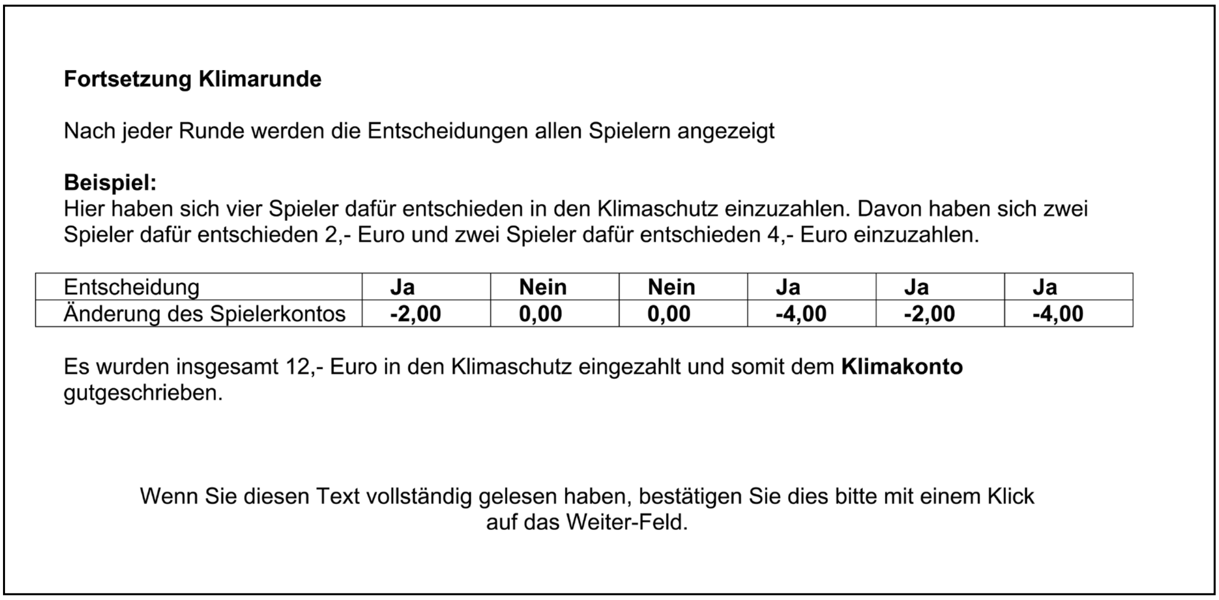
Wenn Sie diesen Text vollständig gelesen haben, bestätigen Sie dies bitte mit einem Klick auf das Weiter-Feld.



Professor Jochem Marotzke, Direktor am Max-Planck-Institut für Meteorologie in Hamburg, wird für den Anzeigentext eine kurze Expertise zum Zustand des Klimas erstellen und dann einige Empfehlungen abgeben, wie man den CO2-Ausstoß verringern und somit das Klima schützen kann:

Z.B.: Energie läßt sich in Haushalten einsparen, etwa durch eine leichte Verringerung der Raumtemperatur im Winter, oder im Verkehr, etwa durch eine stärkere Nutzung öffentlicher Verkehrsmittel statt des Privat-PKWs. Auch trägt der verstärkte Einsatz regenerativer Energiequellen zu einer Verminderung des CO2-Ausstoßes bei.

Wenn Sie diesen Text vollständig gelesen haben, bestätigen Sie dies bitte mit einem Klick auf das Weiter-Feld.



Fortsetzung Klimarunde

Nach jeder Runde werden die Entscheidungen allen Spielern angezeigt

Beispiel:
Hier haben sich vier Spieler dafür entschieden in den Klimaschutz einzuzahlen. Davon haben sich zwei Spieler dafür entschieden 2,- Euro und zwei Spieler dafür entschieden 4,- Euro einzuzahlen.

Entscheidung	**Ja**	**Nein**	**Nein**	**Ja**	**Ja**	**Ja**
Änderung des Spielerkontos	**-2,00**	**0,00**	**0,00**	**-4,00**	**-2,00**	**-4,00**

Es wurden insgesamt 12,- Euro in den Klimaschutz eingezahlt und somit dem **Klimakonto** gutgeschrieben.

Wenn Sie diesen Text vollständig gelesen haben, bestätigen Sie dies bitte mit einem Klick auf das Weiter-Feld.

Note that of the following page ("Das Ende des Spiels") three versions existed according to the treatment: 90% (example below), 50% and 10%. The respective numbers on the page were changed accordingly.

Das Ende des Spiels

Am Ende des Spiels (also nach den ungefähr 10 Runden) vergleicht der Computer das Klimakonto mit einem vorbestimmten Betrag. Dieser Betrag muss erspielt werden, um gefährlichen Klimawandel zu vermeiden. Er wird erreicht, wenn **jeder** Spieler **im Durchschnitt** in **jeder** Runde **2 Euro** in den Klimaschutz einzahlt. In diesem Fall würden pro Runde 12 Euro auf das Klimakonto eingezahlt.

Wurde dieser Betrag für das Klimakonto erspielt, so erhält jeder Spieler den Betrag, der auf seinem Konto verblieben ist. Diese Auszahlung wird unter Ihrer Spielernummer völlig anonym erfolgen.

Wurde der obige Betrag für das Klimakonto **nicht** erspielt, tritt gefährlicher Klimawandel mit einer Wahrscheinlichkeit von **90% (also in 9 von 10 Fällen)** auf, mit erheblichen wirtschaftlichen Einbußen. **Mit dieser Wahrscheinlichkeit verlieren Sie dann das auf Ihrem Konto verbliebene Geld und niemand erhält etwas ausgezahlt.**

(Mit der Wahrscheinlichkeit von 10% (also in 1 von 10 Fällen) behalten Sie Ihr Geld und bekommen den gesamten Betrag nach dem Spiel bar ausgezahlt.)
Das Ergebnis wird mit der entsprechenden Wahrscheinlichkeit vom Computer ausgewürfelt.

Wenn Sie diesen Text vollständig gelesen haben, bestätigen Sie dies bitte mit einem Klick auf das Weiter-Feld.

Jetzt beginnt das Experiment.

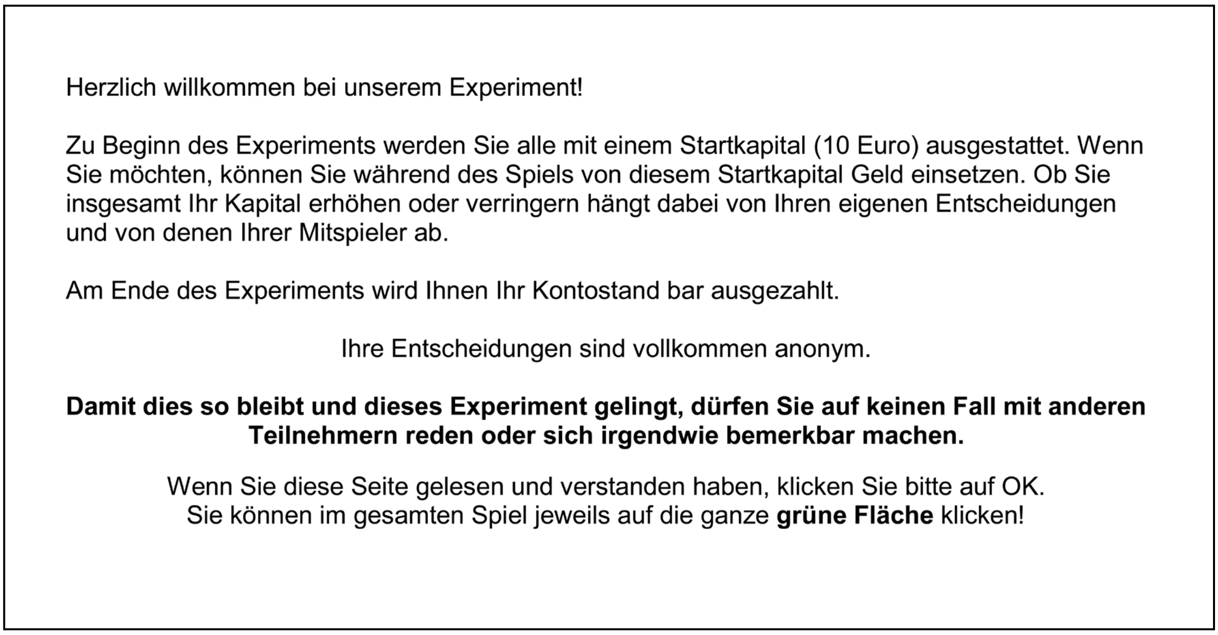
Wenn Sie diesen Text vollständig gelesen haben, bestätigen Sie dies bitte mit einem Klick auf das Weiter-Feld.

Appendix D

This part contains supplementary information for Chapter 4, Gossip as an Alternative for Direct Observation. Introduction pages are shown as they appeared in the original experimental game.

Introduction pages

Pages shown at the beginning of the experimental game (before observer indirect reciprocity rounds, block A; rounds 1 to 6):



Herzlich willkommen bei unserem Experiment!

Zu Beginn des Experiments werden Sie alle mit einem Startkapital (10 Euro) ausgestattet. Wenn Sie möchten, können Sie während des Spiels von diesem Startkapital Geld einsetzen. Ob Sie insgesamt Ihr Kapital erhöhen oder verringern hängt dabei von Ihren eigenen Entscheidungen und von denen Ihrer Mitspieler ab.

Am Ende des Experiments wird Ihnen Ihr Kontostand bar ausgezahlt.

Ihre Entscheidungen sind vollkommen anonym.

Damit dies so bleibt und dieses Experiment gelingt, dürfen Sie auf keinen Fall mit anderen Teilnehmern reden oder sich irgendwie bemerkbar machen.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.
Sie können im gesamten Spiel jeweils auf die ganze **grüne Fläche** klicken!

Im Verlauf des Experiments werden Sie verschiedene Rundentypen antreffen. Ein neuer Rundentyp wird jeweils durch Einführungsseiten (wie diese) vorher erklärt.

Zuerst werden Sie **Paarrunden** spielen.

In jeder Paarrunde wird Ihnen ein Mitspieler zugewürfelt. Auf dem Bildschirm erscheint dann die Frage „Wollen Sie diesem Spieler geben?“.

Nun können Sie sich entscheiden, ob sie JA oder NEIN antworten. Bei JA werden Ihrem Mitspieler 2.00 Euro auf sein Konto gutgeschrieben und Ihnen werden 1.25 Euro vom Konto abgezogen (0.75 Euro kommen von uns dazu). Entscheiden Sie NEIN, so wird weder dem Mitspieler etwas gutgeschrieben, noch Ihnen etwas abgezogen.

Beispiel:

Entscheidung	**JA**	**NEIN**
Spieler (Entscheider)	- 1.25 Euro	+/- 0 Euro
Mitspieler	+ 2.00 Euro	+/- 0 Euro

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Paarrunden (Fortsetzung)

Ab der zweiten Paarrunde wird in diesem Rundentyp wird angezeigt, wie Ihr Mitspieler in den vorangegangenen Paarrunden entschieden hat.

Auch Ihre Entscheidungen werden anderen Spielern (z.B. Ihrem jeweiligen potentiellen Geber) angezeigt.

Während Sie als potentieller Geber eine Paarrunde spielen, spielt auch **ein anderer** Mitspieler mit Ihnen eine Paarrunde, in der Sie Empfänger sind. Da Sie als Empfänger keine Entscheidung zu treffen haben, wird ihnen nur das Ergebnis (= wie viele Euro Sie bekommen haben; 0 oder 2 Euro) der betreffenden Runde angezeigt.

Im Verlauf des gesamten Spiels treffen Sie **NIEMALS** auf einen Mitspieler als Empfänger, dem Sie auch schon mal als Geber begegnet sind oder umgekehrt.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for rounds 7 and 8 (gossip rounds):

Kommentarrunde

Jetzt folgen Kommentarrunden. Dabei sehen Sie entweder eine Auswahl **oder** alle vorangegangen Entscheidungen eines Mitspielers.

Das heisst, entweder sehen Sie **2 vom Computer ausgewürfelte** Entscheidungen (die anderen 4 sehen Sie nicht) Ihres Mitspielers, oder Sie sehen **alle 6** vorangegangenen Entscheidungen. Dann sind Sie aufgefordert über diesen Mitspieler mit Hilfe dieser Information einen Kommentar abzugeben.

In der Wahl des Kommentars sind Sie frei.

Sie dürfen jedoch die Entscheidungen **nicht mit Zahlen** beschreiben (NICHT: "3x Ja, 3x Nein", "50% Nein", "zweimal Ja" oder Ähnliches) und nicht erwähnen, ob Sie viel oder wenig Information sehen. Zudem darf der Kommentar maximal 50 Zeichen lang sein (= Länge des zur Verfügung stehenden Feldes).

Der Kommentar, den Sie nun über diesen Spieler abgeben, wird in späteren Runden anderen Mitspielern als einzige Information über diesen Spieler zu Verfügung stehen. Es kann also vorkommen, dass Ihr Kommentar die **einzige Entscheidungshilfe** für einen Mitspieler in einer Paarrunde sein wird.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for rounds 9 to 12 (special rounds I):

Paarrunden

Es folgen wieder Paarrunden. Dabei ist die Information, die Sie über ihren Mitspieler haben, entweder:

(1) **ALLE** Paarrundenentscheidungen der Runden 1-6,
(2) eine **Auswahl** aus allen Paarrundenentscheidungen (2 vom Computer zufällig ausgewürfelt) der Runden 1-6, oder
(3) ein **Kommentar**, den ein anderer Mitspieler über Ihren Partner geschrieben hat. Dabei sehen Sie nicht, ob der Verfasser des Kommentars alle oder nur einen Teil der Entscheidungen des betreffenden Spielers gesehen hat.

Mit Hilfe dieser Information müssen Sie wie gewohnt entscheiden, ob Sie Ihrem Mitspieler etwas geben oder nicht.

Ihre Entscheidungen werden in späteren Runden anderen Spielern angezeigt (z.B. potentiellen Gebern oder Mitspielern, die einen Kommentar über Sie verfassen müssen).

Sie sind jeweils wieder ein potentieller Empfänger für einen anderen Mitspieler, erfahren Sie diesmal aber erst nach 4 Runden, wie viele Euro Sie erhalten haben.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for rounds 13 to 18 (observer indirect reciprocity rounds, block B):

Paarrunden

In den folgenden Paarrunden sehen Sie wiederum vorangegangene Entscheidungen Ihrer Mitspieler. Die entsprechende Runde, aus der die jeweilige Entscheidung stammt, wird Ihnen ebenfalls angezeigt.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for founds 19 and 20 (gossip rounds):

Kommentarrunden

Es folgen wieder Kommentarrunden, in denen Sie über einen Mitspieler einen (freien) Kommentar abgeben müssen.

Sie dürfen jedoch die Entscheidungen **nicht mit Zahlen** beschreiben (NICHT: "3x Ja, 3x Nein", "50% Nein", "zweimal Ja" oder Ähnliches) und nicht erwähnen, ob Sie viel oder wenig Information sehen. Zudem darf der Kommentar maximal 50 Zeichen lang sein (= Länge des zur Verfügung stehenden Feldes).

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for rounds 21 to 24 (special rounds II):

Paarrunden

In den folgenden Paarrunden sehen Sie eine der folgenden Kombinationen an Informationen:

(1) eine **Auswahl** aus den Paarrundenentscheidungen der Runden 1-6 und zusätzlich einen Kommentar eines weiteren Spielers über diese Auswahl, oder
(2) einen **Kommentar**, den ein anderer Mitspieler über Ihren aktuellen potentiellen Empfänger geschrieben hat, und zusätzlich einen Kommentar über den **Verfasser** dieses Kommentars.

Bitte beachten Sie in den folgenden Runden, dass Sie entscheiden müssen, ob Sie Ihrem **aktuellen potentiellen Empfänger** etwas geben wollen! Für die Verfasser der Kommentare hat Ihre Entscheidung keine Konsequenzen.

Mit Hilfe dieser Information müssen Sie wie gewohnt entscheiden, ob Sie ihrem aktuellen potentiellen Empfänger etwas geben oder nicht. Ihre Entscheidung wird in späteren Runden anderen Spielern angezeigt.

Obwohl auch Sie jeweils ein potentieller Empfänger für einen anderen Mitspieler sind, erfahren Sie wieder erst nach 4 Runden, wie viele Euro Sie erhalten haben.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for rounds 25 to 27 (observer indirect reciprocity rounds, block C):

Paarrunden

In den folgenden Paarrunden sehen Sie wiederum vorangegangene Entscheidungen Ihrer Mitspieler. Die entsprechende Runde aus der die jeweilige Entscheidung stammt, wird Ihnen ebenfalls angezeigt.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for the final gossip ratings at the end of the game:

Bewertungsrunden

Am Ende des Spiels möchten wir Sie bitten, die Kommentare, die Sie während des Spiels angetroffen haben, zu bewerten. Diese Bewertungen sollen bitte ehrlich abgegeben werden und nicht strategisch (werden nicht mehr angezeigt)!

Dazu sehen Sie nun der Reihe nach alle Kommentare, die Sie vorher schon mal gesehen haben. Bitte klicken Sie dann auf eine Zahl von 1 bis 7, die Ihre Bewertung darstellt.

Dabei steht 1 für einen sehr negativen Kommentar und 7 für einen sehr positiven Kommentar. Die Mitte (4 Punkte) repräsentiert einen neutralen Kommentar.

Es ist sehr wichtig, dass dieser Punkt klar ist (**1 = negativ, 4 = neutral, 7 = positiv**)!

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Appendix E

This part contains supplementary information for Chapter 5, Multiple Gossip Statements, Reputation, and Trust. Here, information about the design of preset gossip statements and original introduction pages of the experimental game can be found.

Design of preset gossip statements

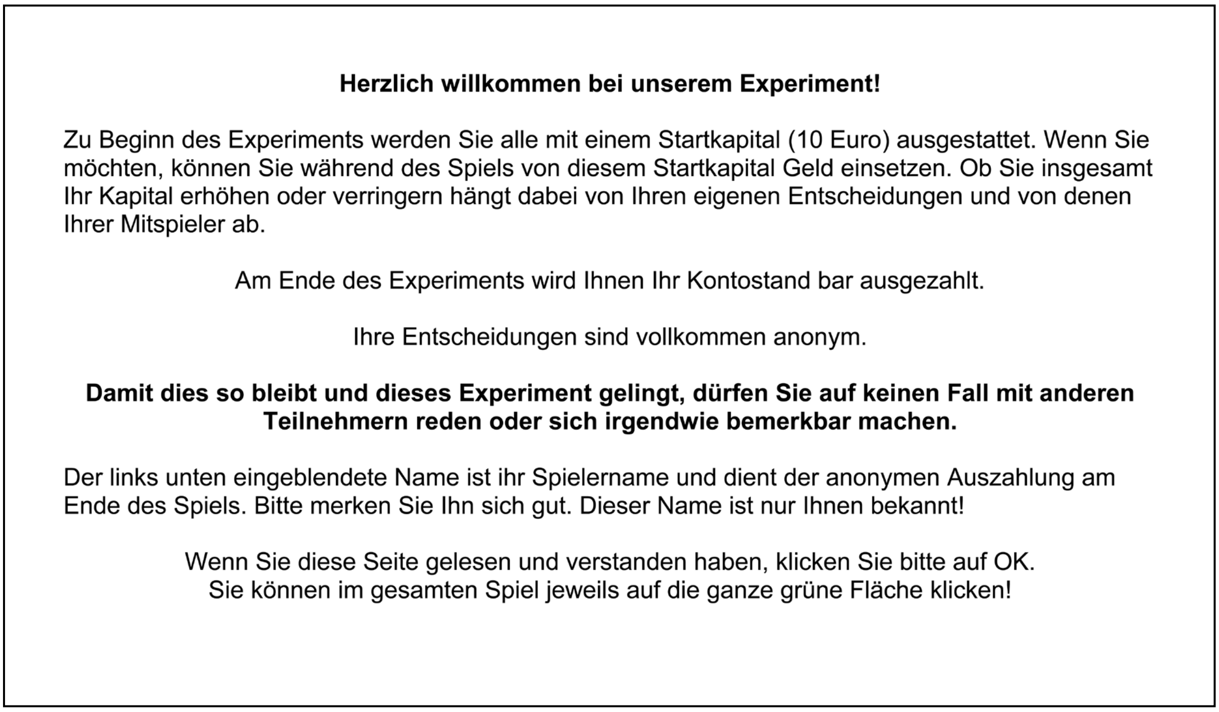
To create a single preset gossip, the programme selected an intensifier (e.g., very, totally, or none at all), a main statement (e.g., egoistic and unreliable as negative examples, or generous and reliable as positive examples), and a tail (e.g., player, participant or none at all). The original German expressions were taken from original student statements of a previous study (Sommerfeld *et al.*, 2007) and were as follows:

Intensifiers: *sehr, aeusserst, total, extrem, ausserordentlich*, or none
Negative statements: *egoistisch, unzuverlaessig, asozial, unsympatisch, geizig, unkooperativ*
Positive statements: *hilfsbereit, vertrauenswuerdig, grosszuegig, zuverlaessig, freundlich, nett*
Tails: *Spieler, Mitspieler*, or none

The particles were combined in a way that the resulting gossip was grammatically and orthographically accurate. Note that umlauts were replaced by the respective combination of vowels to mimic statements typed in by students during the game. Some examples of preset statements are ‘sehr egoistischer Spieler’, ‘unsympatischer Mitspieler’, ‘aeusserst grosszuegig’, and ‘geizig’.

Introduction pages

Pages shown at the beginning of the experimental game (before observer indirect reciprocity rounds, rounds 1 to 6):



Herzlich willkommen bei unserem Experiment!

Zu Beginn des Experiments werden Sie alle mit einem Startkapital (10 Euro) ausgestattet. Wenn Sie möchten, können Sie während des Spiels von diesem Startkapital Geld einsetzen. Ob Sie insgesamt Ihr Kapital erhöhen oder verringern hängt dabei von Ihren eigenen Entscheidungen und von denen Ihrer Mitspieler ab.

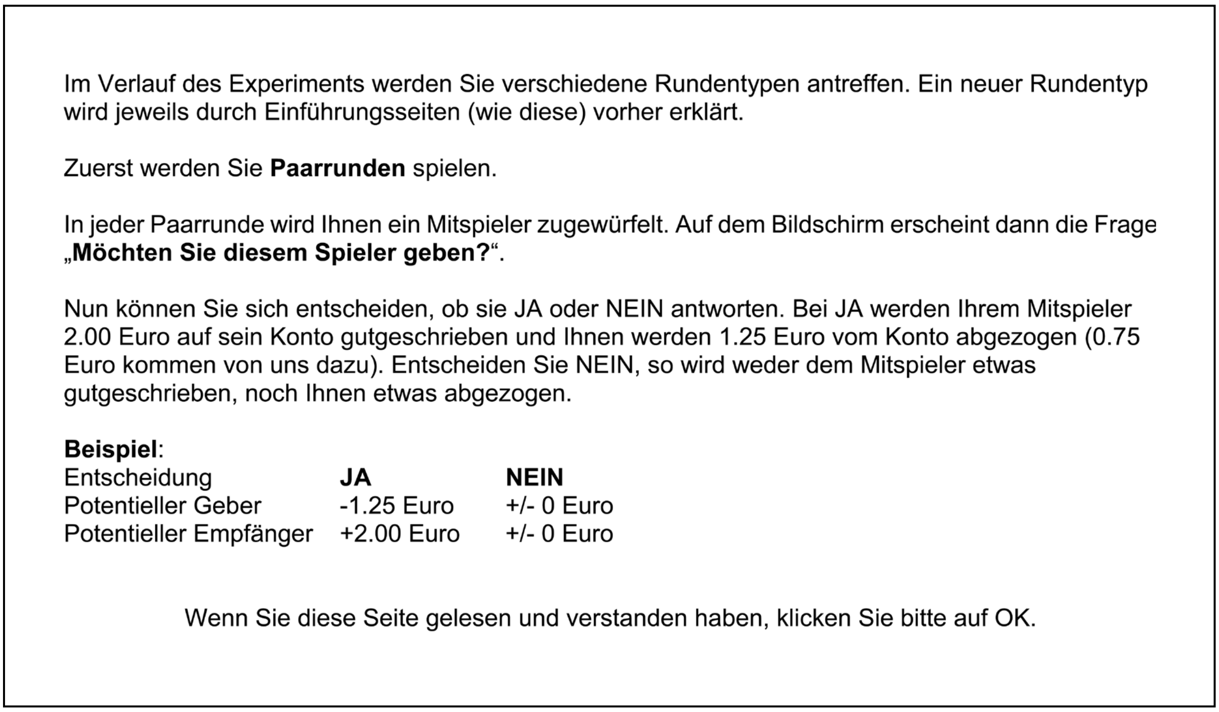
Am Ende des Experiments wird Ihnen Ihr Kontostand bar ausgezahlt.

Ihre Entscheidungen sind vollkommen anonym.

Damit dies so bleibt und dieses Experiment gelingt, dürfen Sie auf keinen Fall mit anderen Teilnehmern reden oder sich irgendwie bemerkbar machen.

Der links unten eingeblendete Name ist ihr Spielername und dient der anonymen Auszahlung am Ende des Spiels. Bitte merken Sie Ihn sich gut. Dieser Name ist nur Ihnen bekannt!

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.
Sie können im gesamten Spiel jeweils auf die ganze grüne Fläche klicken!



Im Verlauf des Experiments werden Sie verschiedene Rundentypen antreffen. Ein neuer Rundentyp wird jeweils durch Einführungsseiten (wie diese) vorher erklärt.

Zuerst werden Sie **Paarrunden** spielen.

In jeder Paarrunde wird Ihnen ein Mitspieler zugewürfelt. Auf dem Bildschirm erscheint dann die Frage „**Möchten Sie diesem Spieler geben?**“.

Nun können Sie sich entscheiden, ob sie JA oder NEIN antworten. Bei JA werden Ihrem Mitspieler 2.00 Euro auf sein Konto gutgeschrieben und Ihnen werden 1.25 Euro vom Konto abgezogen (0.75 Euro kommen von uns dazu). Entscheiden Sie NEIN, so wird weder dem Mitspieler etwas gutgeschrieben, noch Ihnen etwas abgezogen.

Beispiel:

Entscheidung	**JA**	**NEIN**
Potentieller Geber	-1.25 Euro	+/- 0 Euro
Potentieller Empfänger	+2.00 Euro	+/- 0 Euro

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Paarrunden (Fortsetzung)

Ab der zweiten Paarrunde wird in diesem Rundentyp angezeigt, wie Ihr Mitspieler in den vorangegangenen Paarrunden entschieden hat.

Auch Ihre Entscheidungen werden anderen Spielern (z.B. Ihrem jeweiligen potentiellen Geber) angezeigt.

Während Sie als potentieller Geber eine Paarrunde spielen, spielt auch **ein anderer** Mitspieler mit Ihnen eine Paarrunde, in der Sie Empfänger sind. Da Sie als Empfänger keine Entscheidung zu treffen haben, wird ihnen nur das Ergebnis (= wie viele Euro Sie bekommen haben; 0 oder 2 Euro) der betreffenden Runde angezeigt.

Im Verlauf des gesamten Spiels treffen Sie **NIEMALS** auf einen Mitspieler als Empfänger, dem Sie auch schon mal als Geber begegnet sind oder umgekehrt.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Jetzt beginnt das Experiment

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction pages for rounds 7 to 9 (gossip rounds):

Kommentarrunde

Jetzt folgen Kommentarrunden. Dabei sehen Sie jeweils alle vorangegangen Entscheidungen eines Mitspielers. Dann sind Sie aufgefordert über diesen Mitspieler mit Hilfe dieser Information einen Kommentar abzugeben.

In der Wahl des Kommentars sind Sie frei.

Sie dürfen jedoch die Entscheidungen **nicht mit Zahlen** beschreiben (NICHT: "3x Ja, 3x Nein", "50% Nein", "zweimal Ja" oder Ähnliches). Zudem darf der Kommentar maximal 50 Zeichen lang sein (= Länge des zur Verfügung stehenden Feldes).

Der Kommentar, den Sie nun über diesen Spieler abgeben, wird in späteren Runden anderen Mitspielern als einzige Information über diesen Spieler zu Verfügung stehen. Es kann also vorkommen, dass Ihr Kommentar die **einzige Entscheidungshilfe** für einen Mitspieler in einer Paarrunde sein wird.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction pages for rounds 10 to 15 (indirect reciprocity rounds):

Paarrunden

Es folgen wieder Paarrunden. Dabei ist die Information, die Sie über ihren Mitspieler haben, entweder:

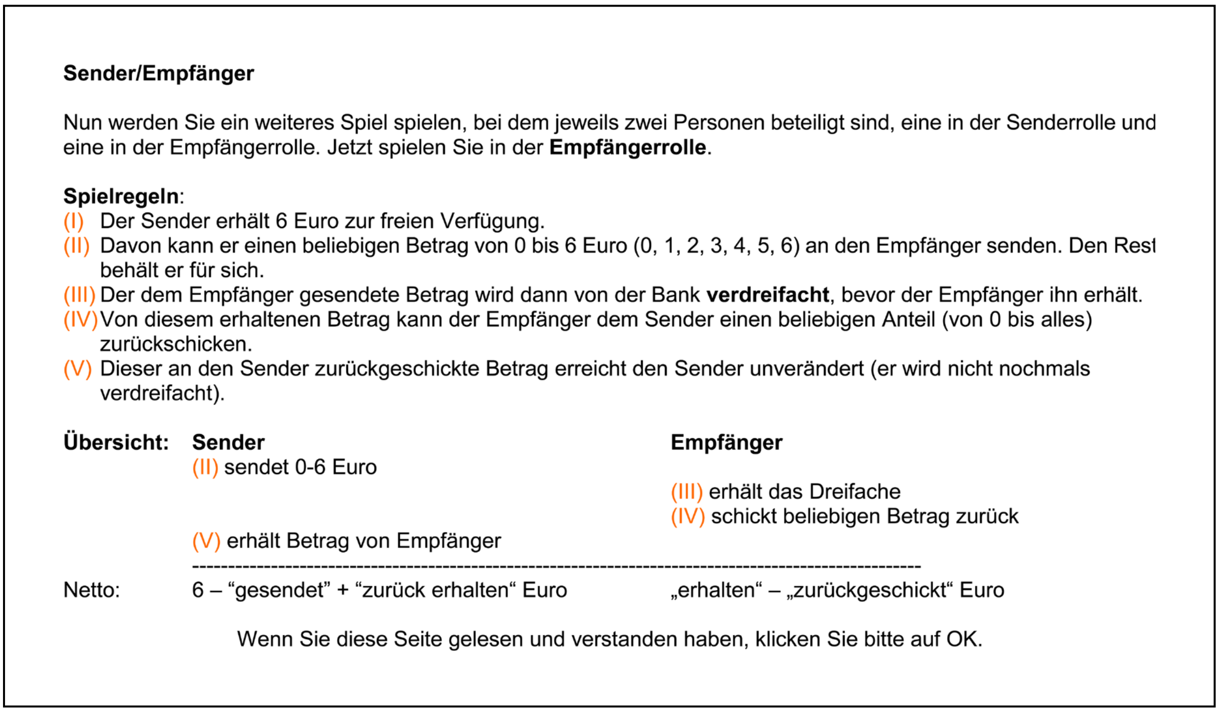
(1) **ALLE** Paarrundenentscheidungen der Runden 1-6,
(2) **ein Kommentar**, den ein anderer Mitspieler über Ihren Partner geschrieben hat.
(3) **mehrere Kommentare**, die andere Mitspieler über Ihren Partner geschrieben haben.

Mit Hilfe dieser Information müssen Sie wie gewohnt entscheiden, ob Sie Ihrem Mitspieler etwas geben oder nicht.

Sie sind jeweils wieder ein potentieller Empfänger für einen anderen Mitspieler, diesmal erfahren Sie aber erst **nach 6 Runden**, wie viele Euro Sie in diesen Runden erhalten haben.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for round 16 (trust game in the role of recipient):



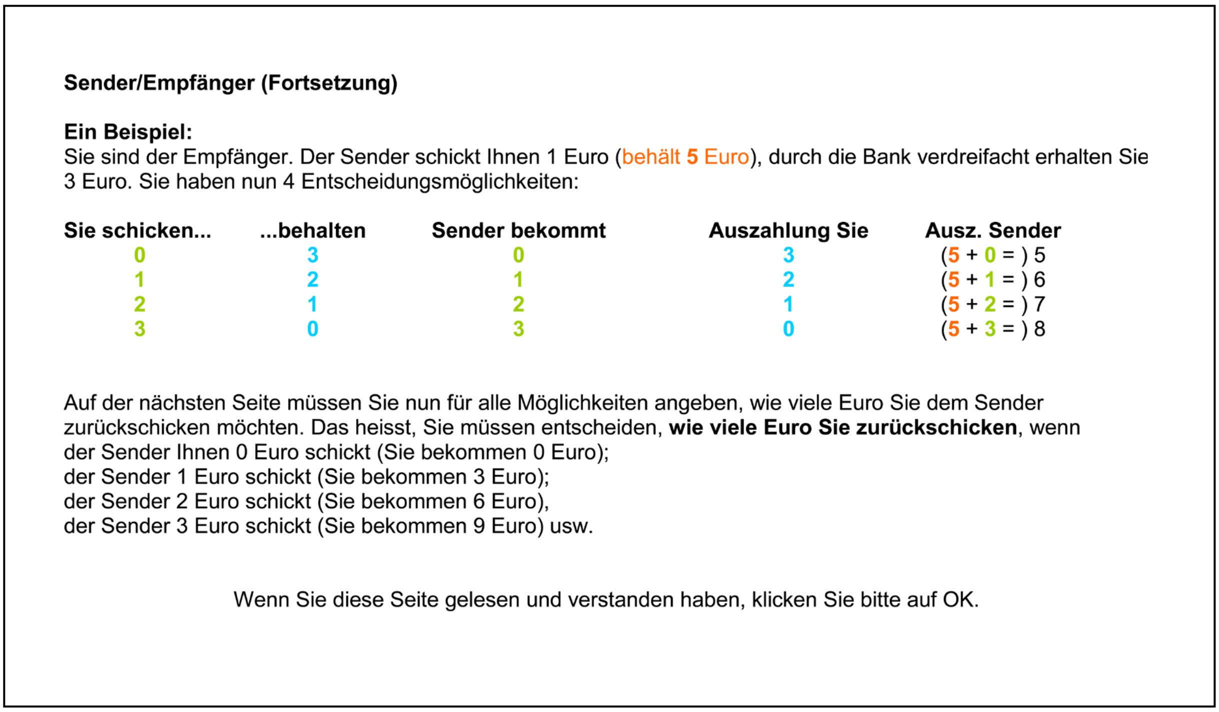
Sender/Empfänger

Nun werden Sie ein weiteres Spiel spielen, bei dem jeweils zwei Personen beteiligt sind, eine in der Senderrolle und eine in der Empfängerrolle. Jetzt spielen Sie in der **Empfängerrolle**.

Spielregeln:
(I) Der Sender erhält 6 Euro zur freien Verfügung.
(II) Davon kann er einen beliebigen Betrag von 0 bis 6 Euro (0, 1, 2, 3, 4, 5, 6) an den Empfänger senden. Den Rest behält er für sich.
(III) Der dem Empfänger gesendete Betrag wird dann von der Bank **verdreifacht**, bevor der Empfänger ihn erhält.
(IV) Von diesem erhaltenen Betrag kann der Empfänger dem Sender einen beliebigen Anteil (von 0 bis alles) zurückschicken.
(V) Dieser an den Sender zurückgeschickte Betrag erreicht den Sender unverändert (er wird nicht nochmals verdreifacht).

Übersicht:	**Sender**	**Empfänger**
	(II) sendet 0-6 Euro	
		(III) erhält das Dreifache
		(IV) schickt beliebigen Betrag zurück
	(V) erhält Betrag von Empfänger	
Netto:	6 – “gesendet” + “zurück erhalten“ Euro	„erhalten“ – „zurückgeschickt“ Euro

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.



Sender/Empfänger (Fortsetzung)

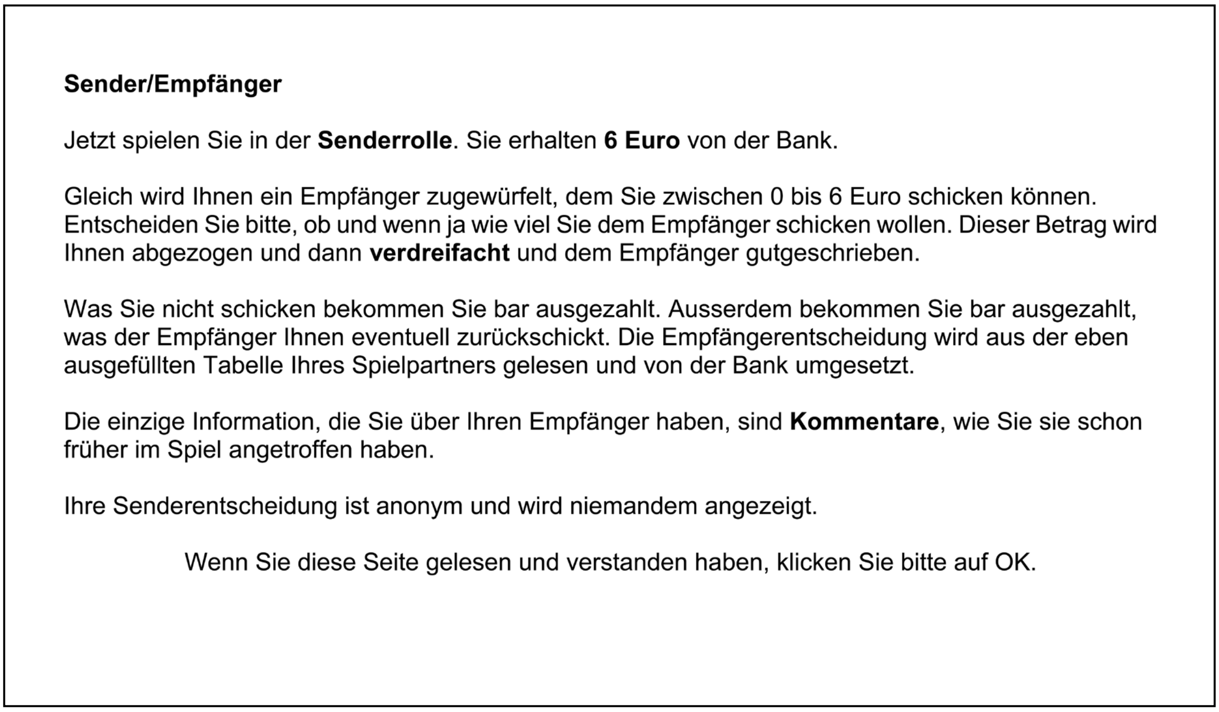
Ein Beispiel:
Sie sind der Empfänger. Der Sender schickt Ihnen 1 Euro (behält **5** Euro), durch die Bank verdreifacht erhalten Sie 3 Euro. Sie haben nun 4 Entscheidungsmöglichkeiten:

Sie schicken...	**...behalten**	**Sender bekommt**	**Auszahlung Sie**	**Ausz. Sender**
0	3	0	3	(5 + 0 =) 5
1	2	1	2	(5 + 1 =) 6
2	1	2	1	(5 + 2 =) 7
3	0	3	0	(5 + 3 =) 8

Auf der nächsten Seite müssen Sie nun für alle Möglichkeiten angeben, wie viele Euro Sie dem Sender zurückschicken möchten. Das heisst, Sie müssen entscheiden, **wie viele Euro Sie zurückschicken**, wenn
der Sender Ihnen 0 Euro schickt (Sie bekommen 0 Euro);
der Sender 1 Euro schickt (Sie bekommen 3 Euro);
der Sender 2 Euro schickt (Sie bekommen 6 Euro),
der Sender 3 Euro schickt (Sie bekommen 9 Euro) usw.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for round 17 (trust game in the role of sender):



Sender/Empfänger

Jetzt spielen Sie in der **Senderrolle**. Sie erhalten **6 Euro** von der Bank.

Gleich wird Ihnen ein Empfänger zugewürfelt, dem Sie zwischen 0 bis 6 Euro schicken können. Entscheiden Sie bitte, ob und wenn ja wie viel Sie dem Empfänger schicken wollen. Dieser Betrag wird Ihnen abgezogen und dann **verdreifacht** und dem Empfänger gutgeschrieben.

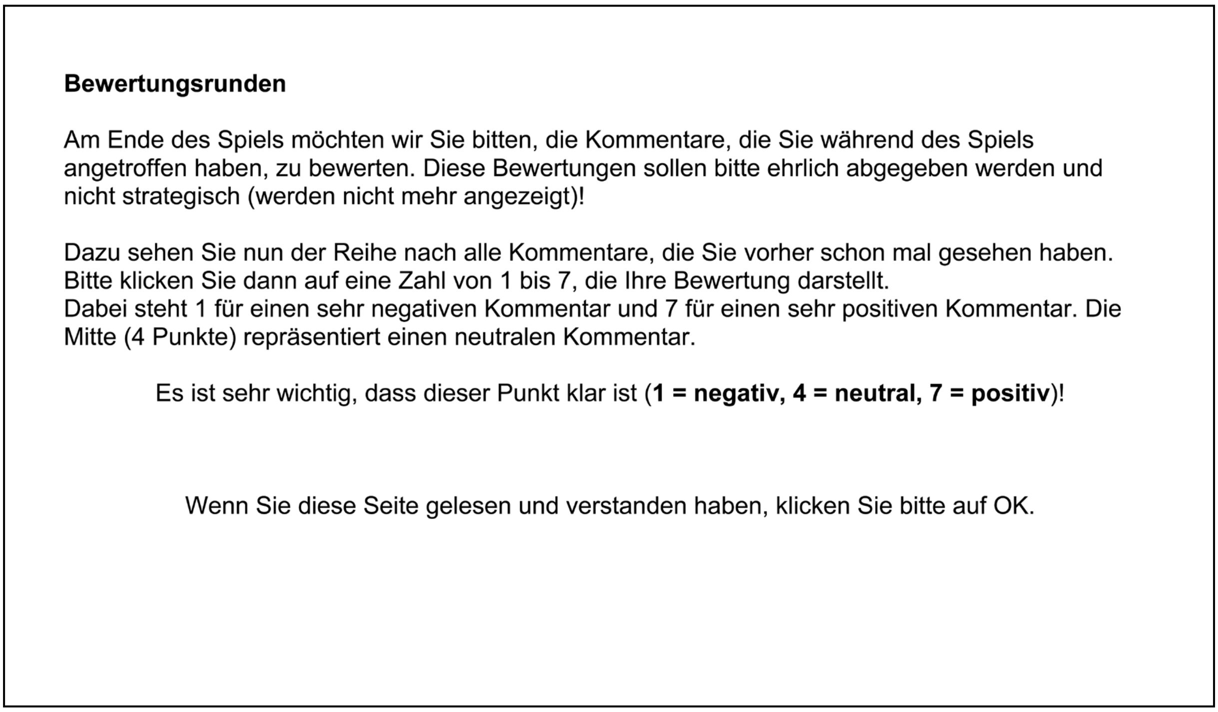
Was Sie nicht schicken bekommen Sie bar ausgezahlt. Ausserdem bekommen Sie bar ausgezahlt, was der Empfänger Ihnen eventuell zurückschickt. Die Empfängerentscheidung wird aus der eben ausgefüllten Tabelle Ihres Spielpartners gelesen und von der Bank umgesetzt.

Die einzige Information, die Sie über Ihren Empfänger haben, sind **Kommentare**, wie Sie sie schon früher im Spiel angetroffen haben.

Ihre Senderentscheidung ist anonym und wird niemandem angezeigt.

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Introduction page for the final gossip ratings at the end of the game:



Bewertungsrunden

Am Ende des Spiels möchten wir Sie bitten, die Kommentare, die Sie während des Spiels angetroffen haben, zu bewerten. Diese Bewertungen sollen bitte ehrlich abgegeben werden und nicht strategisch (werden nicht mehr angezeigt)!

Dazu sehen Sie nun der Reihe nach alle Kommentare, die Sie vorher schon mal gesehen haben.
Bitte klicken Sie dann auf eine Zahl von 1 bis 7, die Ihre Bewertung darstellt.
Dabei steht 1 für einen sehr negativen Kommentar und 7 für einen sehr positiven Kommentar. Die Mitte (4 Punkte) repräsentiert einen neutralen Kommentar.

Es ist sehr wichtig, dass dieser Punkt klar ist (**1 = negativ, 4 = neutral, 7 = positiv**)!

Wenn Sie diese Seite gelesen und verstanden haben, klicken Sie bitte auf OK.

Curriculum vitae

Personal data

Full Name: Ralf Dieter Sommerfeld
Date/place of birth: 13.04.1980, Zurich
Nationality: German and Swiss

Education

1993 – 2000	High school “Kantonsschule Freudenberg”, Zurich
2000 – 2004	Study of Biologie, ETH Zurich Specialisation: Ecology and Evolution
2003 – 2004	Diploma thesis at the ETH Zurich Topic: Feeding Enrichment for Lemurs in the Zurich Zoo
2005 – 2008	PhD thesis at the Max Planck Institute for Evolutionary Biology, Plön / ETH Zurich

Presentations

11th Annual Meeting of PhD Students in Evolutionary Biology, Bordeaux, France, 04.09. – 09.09.05. Lecture: “Interaction between visual and olfactory information in mate choice of three-spined sticklebacks.”

4th Aquavit Symposium, MPI for Limnology, Plön, Germany, 02.03. – 03.03.06. Lecture: “Cheap Punishment: How to Gossip!”

12th Annual Meeting of PhD Students in Evolutionary Biology, St. Andrews, Scotland, 04.09. – 09.09.06. Lecture: “Sending signals – mate choice in the stickleback.”

5th Aquavit Symposium, MPI for Limnology, Plön, Germany, 08.03. – 09.03.07. Lecture: “Human Cooperation and the Use of Gossip”

11th ESEB congress, Uppsala, Sweden, 20.08. – 25.08.07. Poster: “Human Cooperation and Gossip”